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Abstract

The current status and trend of aspen is a topic of debate; some studies have claimed dramatic reductions in aspen stands while others have found no major changes. The actual picture of aspen forests across the West is variable, and the presence of conifers and ungulates in aspen may or may not indicate a progressive loss of aspen. These proceedings summarize the state of knowledge about aspen ecology, the condition and trends in aspen ecosystems in the West, and human dimensions and management options for sustaining aspen.

Keywords: ecosystem management, ecosystem research, sustainable forests, quaking aspen, *Populus tremuloides*

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Compilers' Note

Papers presented from the conference were subjected to peer technical review. The views expressed are those of the presenters.

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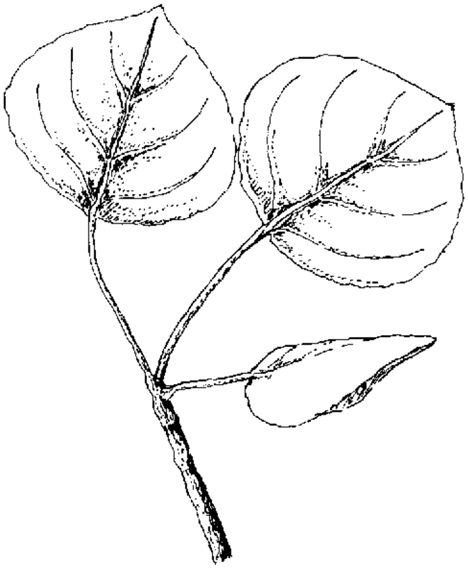

Landscape Dynamics of Aspen and Conifer Forests

Human Dimensions

Animal/Aspen Interactions

Aspen's Ecological Role in the West

Physiology and Production Ecology

Manipulating Aspen Ecosystems

Aspen Forest Products

Foreword:
"We already know all about aspen"

Dan Binkley[1]

As we developed plans for the symposium on sustaining aspen in western landscapes (held in Grand Junction, Colorado, on June 13–15, 2000), we solicited support from state and federal agencies, universities, and the Rocky Mountain Elk Foundation. The widespread support was very encouraging, and only one agency turned down the opportunity to join in supporting this symposium because, it said, "We already know all about aspen." It's true that aspen has been a focal point for research for 100 years in the West, and much of this knowledge was compiled in a wonderful report in 1985 (DeByle and Winokur 1985). But did we really know enough to sustain aspen in western landscapes?

The state of knowledge in 1985 included detailed knowledge of the aspen taxonomy and regeneration, some basic ecology (including site factors), the resource values of aspen forests, and fundamental information on managing aspen forests (DeByle and Winokur 1985). This fundamental knowledge provides much of what we need to know about aspen, but the symposium organizers felt that three critical areas needed further development: (1) the changes in aspen forests across landscapes through time (especially as a result of management decisions), (2) the management options for enhancing aspen forests on landscapes, and (3) the level of collaboration and activity among managers and scientists with interests in aspen.

This volume of proceedings from the conference shows we've learned a great deal about basic ecology of aspen since 1985, including new insights on herbivory, secondary chemistry, functional responses of aspen, elk and wolves, mycorrhizae, and rooting relationships. More importantly, we've learned about the patterns of aspen forests in space and time, including some alarming news about changes in aspen forests over the past few decades. Reports were published that noted dramatic reductions in the area of aspen forests. The combined effects of fire prevention, cattle grazing, and increased ungulate populations had reduced the extent of aspen stands in Utah by more than half in just 50 years (Kay 1997; Bartos and Campbell 1998). The policy of "natural regulation" of elk populations (without the natural levels of predation by humans, wolves, and bears) in Yellowstone and Rocky Mountain National Parks appeared to prevent normal regeneration of aspen (Baker et al. 1997; Ripple et al. 2000). These reports of declines in aspen regeneration appeared to include components of weather patterns (Romme et al. 1995), and spatial variation of aspen regeneration within the Parks (Suzuki et al. 1999).

Many research projects since 1985 have tested management options for sustaining aspen, including fencing to control cattle and ungulate browsing of aspen suckers, and logging and prescribed fire to rejuvenate clones. A major lesson (as noted in these proceedings) has been that successful operations often require multiple approaches; logging a decadent clone may not lead to successful aspen regeneration without controlling browsing levels. Prescribed fires in the absence of browsing controls may lead to the death of ancient aspen clones.

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[1] Colorado State University, Fort Collins, CO.

Aspen is a fascinating species, and changes in aspen forests have great implications for the plants, animals, and people of western landscapes. As our knowledge increased on the status and trends of aspen forests, we still lacked a complete picture across the West. Where were aspen forests increasing, decreasing, or holding steady? Where aspen forests were decreasing, what were the causes? How could land managers prescribe management treatments to enhance aspen stands? We felt that these important questions needed an increase in the level of collaboration or activity to foster and sustain aspen, and this symposium was the first step. These proceedings are the second step, with the information from the meeting documented for use by those who attended, and by those who could not join us in Grand Junction.

The third step will be the development of an Aspen Forest Network. The participants in the symposium were asked to fill out a questionnaire about their interests in developing more collaboration on aspen forests, and 94% of those in attendance said that a new “Aspen Forest Network” would be helpful or very helpful to them. Over the next year or two, we’ll begin to develop a web page for the Aspen Forest Network, which will include basic information about aspen, links to other aspen pages, printable copies of papers on aspen (including this proceedings), and contact information for people interested in aspen. Continue learning more about aspen by visiting the Aspen Forest Network at: http://www.cnr.colostate.edu/outreach/aspen/.

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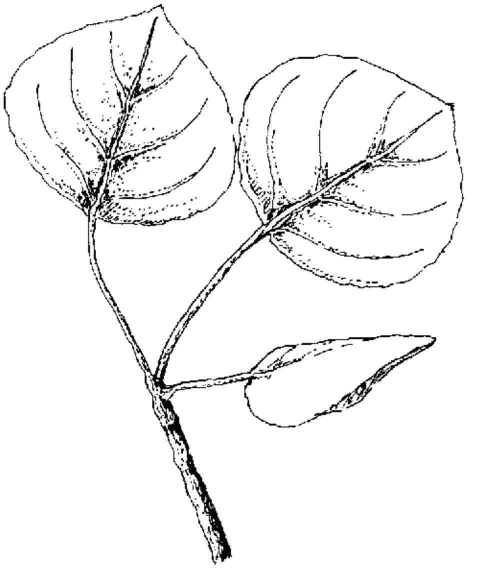

Landscape Dynamics of Aspen and Conifer Forests

Landscape Dynamics of Aspen and Conifer Forests

Dale L. Bartos[1]

Abstract—*Quaking aspen (*Populus tremuloides *Michx.) is widely dispersed across the landscape of North America. Seventy-five percent of the aspen in the western United States occurs in the states of Colorado (50%) and Utah (25%). Reproduction in aspen is primarily by asexual means, e.g., root sprouts that are generally referred to as suckers. An aspen clone consists of numerous stems that are genetically alike that began from a single seed that germinated sometime in the past. Generally, these clones have been perpetuated on site by disturbance that allowed the clones to survive and expand in the area. The importance of aspen in the Interior West is well described and documented in the literature. Besides adding diversity to the landscape, aspen also provides water, forage, wood products, and so on for use by the public. Since European settlement, the natural disturbance regime (usually fire) has been interrupted. This has caused much of the aspen-dominated lands to succeed to conifers. The decline in aspen ranges from 49% in Colorado to 95% in Arizona. Numerous techniques are available to aid the manager in restoring aspen to a level approaching its historical occurrence.*

I have studied quaking aspen (*Populus tremuloides* Michx.) for the past 28 years for Forest Service Research. Early in my career I studied the vegetative responses of aspen systems to various types of disturbances (burning, cutting, spraying, and so on). More recently, I have been involved primarily in technology transfer of knowledge about the functioning and restoration of aspen in the Intermountain West. During this time, there has been a marked increase in public awareness and concern regarding aspen lands, resulting in an urgency, in some areas, for restoring aspen on the landscape.

Introduction

Quaking aspen is the most widely distributed deciduous tree in North America (Little 1971; Sargent 1890). It occurs from the east coast to Alaska in the north and then runs down through the Rocky Mountains (figure 1). In the western United States, aspen occurs on mountainous and high plateaus (Jones 1985); on xeric sites it occurs primarily in riparian zones. Almost 75% of the western aspen occurs in Colorado and Utah.

Aspen Condition Types

Western aspen exist in primarily three different types (Bartos and Campbell 1998a): (1) stable, (2) successional to conifers, and (3) decadent and falling apart.

Stable aspen is considered to be "properly functioning" and replacing itself. In many instances, these clones exist with a "skirt" or "fairy ring" of young regeneration around the edge and numerous sized stems in the interior (figure 2). The stems are of various ages that resulted from pulses of regeneration that

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Figure 1—Map showing the potential distribution of quaking aspen for North America (Little 1971).

occurred at various times in the past. Generally, an individual standing near a stable clone has difficulty seeing into or through it.

Aspen succeeding to conifers are responding to natural forces. Aspen is considered a disturbance species perpetuated on site by fire, disease, or other such occurrences. Some of these forces (primarily fire) have been altered by human intervention, which has given shade-tolerant conifers a marked advantage. We see numerous situations where aspen are being replaced by less desirable vegetation types such as subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (figure 3) or sagebrush (*Artemisia* spp.). In turn, these type conversions are modifying the sites dramatically. In most areas of the West, these modified aspen clones should be given top priority for restoration.

Decadent clones are generally of a single age and are very open; mature trees are not being replaced as they die because successful regeneration is lacking (figure 4). Most of these clones attempt to reproduce, but the new shoots are consumed primarily by wild or domestic ungulates. Clonal vigor is reduced as these regeneration events occur year after year. Fewer and fewer suckers are

Figure 2—Stable (properly functioning) aspen that has a “skirt” or “fairy ring” of regeneration.

Figure 3—Conifer-dominated aspen that accounts for a great deal of the decline of aspen in the western United States.

Figure 4—Decadent aspen that has overmature stems and little or no regeneration. These sites will be replaced by sagebrush or other tall shrubs if treatment is not imposed.

produced and in some areas the old clones are lost from the system. A person standing near a decadent clone can see into or through the clone.

Reproduction

An aspen clone contains numerous genetically identical stems (ramets) that propagated vegetatively from a single seedling that became established at some time in the past. These aspen stems originate from root suckers, some of which still may be interconnected via the root system. Shepperd and Smith (1993) reported that aspen stems establish independent root systems by approximately 25 years of age, with few mature stems still connected by the original root system. These self-regenerating clones have existed for thousands of years according to Barnes (1975), being perpetuated over time by disturbance. These clones usually expanded during this time and, therefore, some occupy large areas. Kemperman and Barnes (1976) report clones as large as 200 acres (81 hectares).

Successful sexual reproduction of western aspen is extremely rare (Mitton and Grant 1996). Jelinski and Cheliak (1992) describe a “window of opportunity” that may allow seedling establishment at intervals of 200–400 years. Therefore, unlike other western tree species, aspen once lost from the landscape generally will not reestablish from seed in the Intermountain West.

Vegetative reproduction by suckers generally requires a disturbance or dieback that alters the hormonal balance within the system (Schier et al. 1985; Bancroft 1989). The flow of two hormones (cytokinin and auxin) within an aspen tree are shown in figure 5 (Bancroft 1989). Basically, when the tree is killed or stressed, the flow of sucker-suppressing auxins from the crown down to the root system is disrupted, which allows cytokinin to stimulate suckering.

In areas where there is extensive ungulate pressure (both domestic and wildlife), however, treatment alone to induce aspen suckering is not enough. Such actions must not be initiated before relief from excessive browsing is obtained (Southwest Region 1994).

Values

Products and benefits derived from the aspen ecosystem are varied and numerous (Bartos and Campbell 1998a,b; DeByle and Winokur 1985). Values attributed to the western aspen system include, but are not limited to, forage for livestock, habitat for wildlife, water for downstream users, esthetics, recreational sites, wood fiber, and landscape diversity. When the aspen system is not functioning properly, many of these values are compromised. Bartos and Campbell (1998b) describe the loss of water, forage, biodiversity, and other benefits when aspen-dominated landscapes are lost.

Generally, when conifers replace aspen there is a potential for a decrease in water yields. Harper et al. (1981) reported a decrease of 5% and Gifford et al. (1984) predicted a decrease of from 3 to 7 inches in water yields when conifers replace aspen. This loss of water means that it is not available to produce undergrowth vegetation, recharge soil profiles, or increase streamflow. In dry climates, such as the Great Basin, this loss of water is substantial and should be of great concern to the public.

Undergrowth vegetation associated with aspen forests is generally considered prime grazing for domestic livestock. When conifers replace aspen there is a marked decline in forage production. Mueggler (1988) reported that aspen

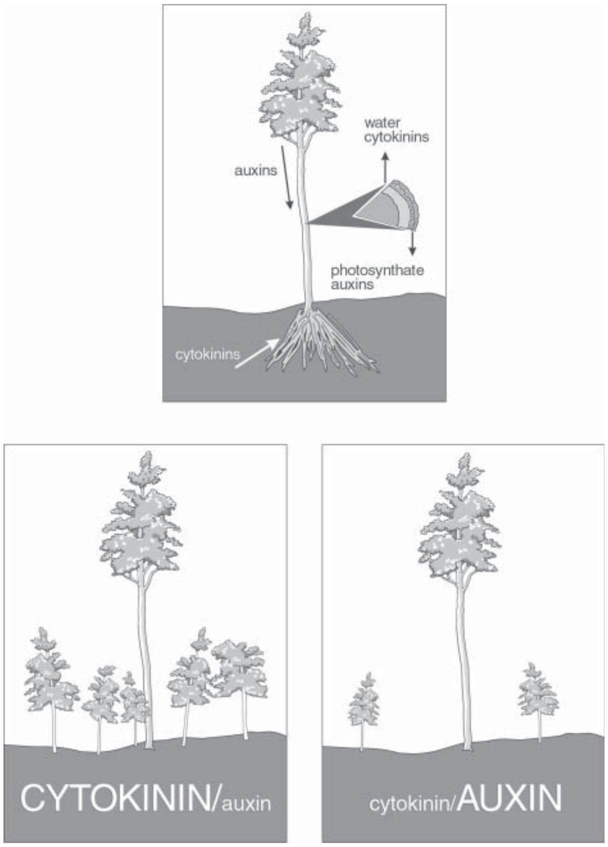

Figure 5—Representation of the flow of hormones (cytokinin/auxin) within an aspen tree and the ratio of hormones' effect on suckering (Bancroft 1989).

communities can produce as much as 3,200 kg/ha (2,900 lb/ac) of air-dry undergrowth material and averaged 1,350 kg/ha (1,200 lb/ac). On the Wasatch Plateau of Utah, undergrowth production can be reduced by 50% when conifers make up as little as 15% of the total tree basal area (Mueggler 1985). In another study, Mueggler (1988) observed that undergrowth production was reduced 67% when conifers made up 15% of the total tree basal area. Once conifer invasion approaches 50% of the total tree basal area in aspen stands, undergrowth production is only a small fraction of what it once was on these formerly excellent grazing lands. In areas where there has been considerable loss of aspen, this dramatic change in forage production should be considered when determining stocking rates.

Aspen-dominated sites are considered to be high in biodiversity—second only to riparian areas on western sites (Kay 1997). When aspen lands change to either conifer or sagebrush dominance, marked changes in both flora and fauna occur. Not only is there a loss of forage production as detailed above, but there is a substantial decrease in plant species richness when there is a loss of aspen. Bartos and Mitchell (2000) synthesized numerous articles from the Rocky Mountain area and found that there were ~29 undergrowth species under aspen compared to only 19 species associated with subalpine fire, lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*). Winternitz (1980) reported that the density and diversity of birds was greater in aspen than conifer stands and McGraw/Bergstrom (1986) observed that mature aspen stands contained more bird species than younger stands or those being invaded by conifers. Bird species diversity also increases with the size of aspen stands (Johns 1993). Other examples of changes in species biodiversity that are not often considered include lichens, bats, and snails (Bartos and Mitchell 2000).

Aspen is portrayed as an excellent indicator of ecological integrity as well as landscape health (Kay 1991a,b; Woodley and Theberge 1992; Woodley 1993; Woodley et al. 1993).

Some consider aspen a keystone species (e.g., "the removal of a keystone species causes a substantial part of the community to change drastically" [Wilson 1992]). Houston (1954) noted that aspen reproduction has long been used as an indicator of range condition. Thus, the importance of aspen on the western landscape cannot be over emphasized.

Decline of Aspen

Repeat photos are one way to evaluate changes on the landscape, especially with the loss of aspen. Locations in historical prints are rephotographed from the same photopoint, thus forming a pair of photos. These photos provide a visual example of the magnitude of the decline of aspen over time. Numerous pairs of photos have been obtained from southern Utah with the originals taken in the late 1800s or early 1900s. Figure 6 shows an example; the change in vegetation is readily apparent.

The Rocky Mountain Research Station's Forest Inventory and Analysis Project (FIA) has collected data on the current and historical acreage of aspen in the Interior West. The historical data are a result of summing all acres that currently contain at least one aspen either living or dead; this assumes that this acreage is, or once was, occupied by aspen. FIA data obtained from National Forest Systems land for the state of Utah shows at least a 60% decrease in aspen domination since the arrival of Europeans (table 1) (Bartos and Campbell 1998a). Similar trends (50–96% decline) have been observed throughout the western United States (table 2) (Bartos and Mitchell 2000).

Similar figures have been reported elsewhere for the West. Using remote sensing and geographic information systems (GIS), Lachowski and others (1996) and Wirth and others (1996) evaluated the loss of aspen in the Gravelly Mountains in southwestern Montana. They found a ~47% decrease in aspen from 1947 to 1992 and attributed most of that change to conifer invasion. In a review article, Brown (1995) found decline values for Oregon and Washington that were very similar to those reported here.

Figure 6—Repeat photographs (1872–1996) from Bee Lake, Fishlake National Forest. Repeat photos and interpretation provided by Dr. Charles Kay, Adjunct Assistant Professor, Department of Political Science, Utah State University, Logan, Utah.

Table 1—Current and historical acres of aspen found in Utah. (Unpublished data provided by the Rocky Mountain Research Station's Forest Inventory and Analysis Project.)

Area	Current aspen	Historical aspen	Decline
	Acres	*Acres*	*Percent*
Ashley National Forest	101,358	322,532	69
Uinta National Forest	174,492	285,351	29
Wasatch-Cache National Forest	128,615	373,837	66
Dixie National Forest	153,053	437,715	65
Fishlake National Forest	141,948	313,724	55
Manti-LaSal National Forest	158,866	338,008	53
Southern Utah	453,867	1,089,447	58
Northern Utah	404,465	981,720	59
Total National Forest in Utah	858,332	2,071,167	59

Table 2—Current and historical acres of aspen in the Interior West. (Unpublished data provided by the Rocky Mountain Research Station's Forest Inventory and Analysis Project.)

Area	Current aspen	Historical aspen	Decline
	Acres	*Acres*	*Percent*
Colorado	1,110,764	2,188,003	49
Utah	1,427,973	2,930,684	51
New Mexico	140,227	1,141,677	88
Wyoming	203,965	436,460	53
Arizona	29,009	720,880	96
Idaho	621,520	1,609,547	61
Montana	211,046	590,674	64
Nevada	118,768	—	
Total	3,863,272	9,617,925	60

Conclusions

The following conclusions can be made regarding the current situation of aspen in the western United States:

1. Aspen is the most widely distributed deciduous tree in North America; it usually needs disturbance to perpetuate itself in the West.
2. Aspen clones consist of numerous stems (ramets) that are genetically alike and these clones have been perpetuated over time, primarily by fire.
3. Numerous products are produced by the aspen type, on which the public has placed high value.
4. Aspen exists in three broad categories: (1) stable and regenerating, (2) converting to conifers, and (3) decadent and deteriorating.
5. Recent data shows that aspen in the western United States has declined 50–96%.
6. Currently, there is considerable interest in restoring aspen to a level that existed prior to European settlement.
7. Numerous techniques (e.g., burning, cutting, spraying, chaining, and ripping) exist for use in restoring aspen. These techniques are covered elsewhere in this proceedings.
8. Before treatments are applied, excessive animal use must be addressed so that aspen regeneration can escape destructive browsing.

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Changes in Landscape Patterns and Associated Forest Succession on the Western Slope of the Rocky Mountains, Colorado

Daniel J. Manier[1] and Richard D. Laven[2]

Abstract—*Using repeat photography, we conducted a qualitative and quantitative analysis of changes in forest cover on the western slope of the Rocky Mountains in Colorado. For the quantitative analysis, both images in a pair were classified using remote sensing and geographic information system (GIS) technologies. Comparisons were made using three landscape metrics: total relative cover, mean relative patch size, and number of patches per major vegetation type. We noted several important changes in the pattern of the landscape and the structure of the forests. The relative area covered by interspersed, nonforested rangelands has decreased significantly, and the total forest cover across these landscapes has increased. Statistical analyses (ANOVA) of other landscape characteristics (patch number and patch size distribution) did not detect changes. However, nonstatistical observation of the trends in these data revealed that in many cases, there has been important, observable change in the configuration of the landscape at many of these locations. Furthermore, our field data show that 96% of the sampled forests have a conifer component in the overstory, understory, or both.*

Introduction

Throughout the Intermountain Region, reproduction of aspen (*Populus tremuloides* Michx.) from seed is rare (DeByle and Winokur 1985; McDonough 1985; Kay 1993). Most successful reproduction occurs via suckering from adventitious buds located on lateral roots. Successful regeneration is associated with early seral communities and gaps in the canopy as a result of the limited ability of aspen to compete in low-light environments (Baker 1925; Barnes 1966; DeByle and Winokur 1985). Aspen reproduction is stimulated by disturbance due to the interruption of hormonal growth inhibitors transported through the stems and roots; the current pattern of fire suppression is suspected as an inhibitor of successful aspen reproduction because it increases the interval between disturbance events (DeByle et al. 1987). Fire is known to stimulate aspen regeneration under a variety of conditions (Bartos et al. 1994; Bartos et al. 1991; Bartos and Mueggler 1981; Brown and DeByle 1987). Further evidence of the effects of fire suppression on aspen ecology is provided by recent surveys of aspen stands in the region, which discovered a predominance of mature to overmature age structure in many aspen forests (Mueggler 1989; Shepperd 1990). If aspen is not reproducing successfully, then we should observe a reduction in the presence of aspen on the landscape over time. This study investigates the relationship between successional development and landscape level changes in forest structure as they relate to aspen ecology.

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We used repeat photography to quantify changes in the Colorado landscape. Previously, multi-temporal series of aerial photographs have been used to quantify changes in vegetation patterns in the western United States and elsewhere (Hart and Laycock 1996; Hester and Sydes 1992; Knapp and Soule 1998; Mast et al. 1998; Snodgrass 1997; Wirth et al. 1996; Zampella and Lathrop 1997). These studies use aerial photographs and/or satellite imagery to assess changes in a specific vegetation type, land-use, or the configuration of landscape elements over time. These studies have successfully demonstrated the temporal and spatial variability associated with ecological systems, but they rarely extend beyond 50 years of change; most are much shorter.

Methods

We selected three measurable landscape parameters to quantitatively represent the configuration of the landscape. Trani and Giles (1999) analyzed 24 landscape metrics for their ability to detect known changes in landscape patterns. Fourteen of these metrics showed the ability to recognize the difference between contiguous and fragmented forested landscapes. However, total area, mean patch area, contiguity, and percent interior forest have nearly linear (therefore easily interpretable) relationships with progressive change toward contiguous or deforested landscape. Many other variables are sensitive to these changes, but curvilinear trends with respect to change make interpretation of these variables difficult using only two sample dates. For a simple and accurate representation of the landscape, we chose total area of cover, mean patch area per type, and number of patches per type.

Our expectations are that there has been a change in the extent and pattern of vegetation cover over the last century. Specifically, we expect that coverage by conifers is increasing. And contrary to popular belief, we expect that coverage by aspen has also increased. As a result, montane areas dominated by shrubs and grasses are decreasing (subsequently referred to as rangelands with recognition that these interspersed communities are only a subset of all communities recognized as rangelands). In addition to changes in the spatial extent of these vegetation types, changes should also be evident within the landscape elements as successional development toward mature community structure continues.

Subsequent to analysis of the landscape patterns, we visited each photographed landscape and sampled the forest for composition and size/age structure. We used the transect data to further assess changes in the landscape structure. Structure (age and size) and species composition of the overstory were compared to the composition of the understory. In this manner, we deduced recent successional patterns in the same forests described by the landscape photograph analysis. Further, we considered the understory composition to be the potential composition of these forests in the future.

Using this landscape level approach and considering patterns of forest development, we hypothesize that:

- Aspen cover has changed significantly since the turn of the century, resulting in more total cover and larger continuous patches of aspen than was found on the landscape near the turn of the last century (circa 1900).
- Conifer cover has increased in the last 90 to 100 years. We do not expect that conifers have replaced aspen on the landscape in this period.

- The cover of open rangelands (interspersed, nonforested shrublands and meadows), within the forest matrix or forested mosaic, has decreased. This is necessary if both aspen and coniferous forest cover have increased.
- Reproductive success of shade-tolerant conifers will outpace the success of aspen reproduction in these closed canopy forests.

The photographed locations in this study are distributed, in two distinct clumps, across a 100-mile portion of the western slope of the Rocky Mountains in Colorado. They are concentrated in the West Elk Mountains of the Gunnison National Forest and the San Juan Mountains of the Uncompahgre National Forest, separated by the Gunnison River Valley, Blue Mesa Reservoir, and the Black Canyon of the Gunnison. These data points are not random; they were determined by the intended subject of the original photographers. In this case, the subjects were geologic features. The authors considered all photographs available in the local collection as potential sample sites, but images picturing nonforested landscapes were removed from consideration. There was not, therefore, intentional bias from the original photographers or the current investigators on the distribution of sample points for the assessment of forest cover. The sample locations resulting from this process are concentrated in the upper montane and subalpine ecoregions.

We collected photographs from the archives of the United States Geologic Survey (USGS) library in Denver, Colorado, to document the previous condition of the landscape. These photographs originate from survey teams documenting Colorado resources from the years 1885 through 1915. We photographed the landscapes in 1995 from the same locations used by the original photographers. Using the paired photographs, we conducted a qualitative and quantitative analysis of changes in forest cover. Qualitative analysis was facilitated by a description of each photograph followed by direct comparison. For the quantitative analysis, both images in the pair were classified using remote sensing and geographic information system technologies. Statistics on polygons, representing continuous patches of major cover types, were collected to determine the change in several landscape variables between the two photographs. Comparisons were made using these metrics (i.e., total relative cover, mean relative patch size, and number of patches per major vegetation type) to represent the landscapes. In order to distinguish obvious differences in landscape history (i.e., disturbance history), we divided the 24 photographed landscapes into two groups. Twelve locations have direct evidence of recent disturbances; 12 intact sites have no evidence of disturbance in the original photograph or the modern photograph. This procedure is subjective, but the photographic evidence is clear in most instances.

Initially, we compared the photograph pairs to qualitatively assess changes in the landscape (see appendix for a sample pair.) To this end, disturbance events (e.g., fire, logging, and mining activities) and the distribution of the dominant cover types (e.g., conifer, aspen, rangeland, bare soil, rock, dead and down timber, forest regeneration) for each photograph were noted. The photographs were compared to identify differences in the pattern and extent of vegetation cover. Qualitative analysis of the photographs was followed by quantitative analysis. The images were scanned at 300 dots per inch resolution and then imported into a Geographic Information System (GIS). Each image was classified using the major vegetation cover (conifer forest, aspen forest, mixed herbaceous and shrub rangeland, and bare ground). Data for total coverage, number of patches, and mean patch size were collected for each major vegetation type. The data representing landscape vegetation were analyzed using a pairwise ANOVA. Total cover and mean patch size were normalized as percentages of the total value within the image. Changes in the number of patches were calculated using a direct comparison (not normalized) between paired photos. Quantitative comparisons were made using these estimates of the landscape metrics. The F-statistic was calculated for each metric to compare the coverage on the old landscape to the modern landscape. Recently disturbed and intact landscapes were analyzed separately.

Subsequent to analysis of the landscape patterns, we traveled to each photographed landscape to analyze the structure of the forests. We used two 500 m^2 transects (2 m x 250 m^2) on each landscape, in most cases, to sample the size and age structure of the forests. Graphs of forest structure were analyzed in association with the landscape history provided by the photograph pairs. The analyses of these data are not presented here, but some of the data are discussed. An example of a size-age distribution showing abundant fir regeneration is provided in figure 1.

Results

The general trend depicted by the photographic histories is an increase in forest cover (coniferous and deciduous) and a decrease in rangeland cover. The qualitative comparison suggests that 92% of the pairs reveal an increase in the total area covered by conifers and aspen, and a decrease in the area covered by rangelands (figure 2). This is supported by the quantitative analysis of these sites where 96% of the classifications show a net increase in forest cover (figure 2). According to the quantitative comparisons, conifer cover increased on 63% of

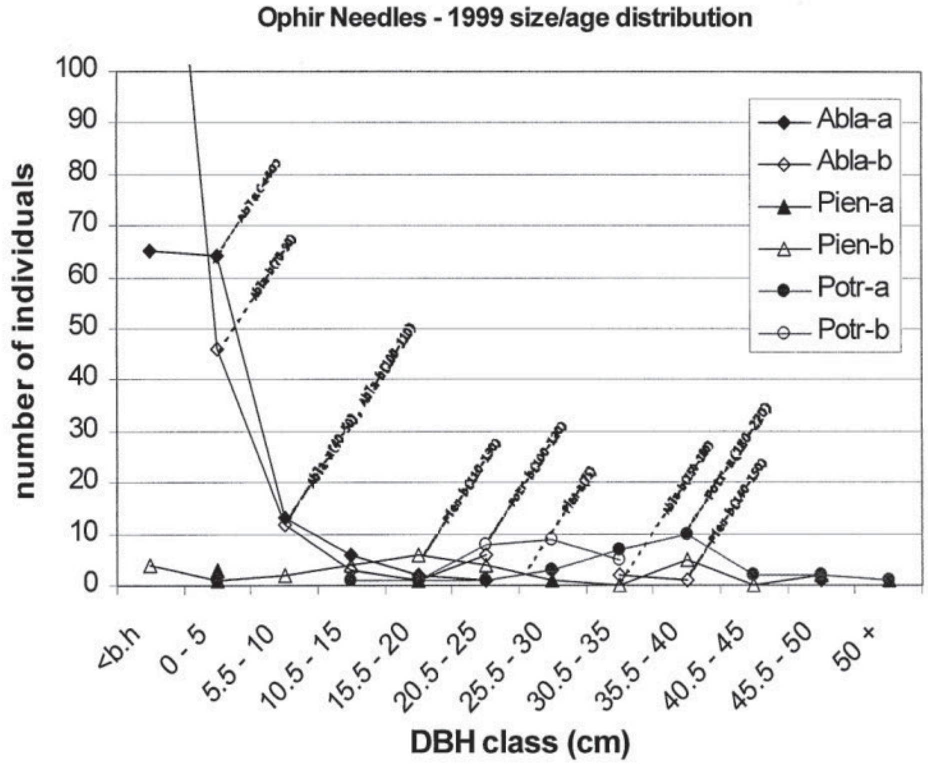

Figure 1—Size-age distribution for Turkey Mesa. Abla = *Abies lasiocarpa*, Pien = *Picea engelmannii*, Potr = *Populus tremuloides*. This example of a size-age distribution used in the analyses was constructed from two transects (designated "a" and "b" on the graph), which stretch across the central portion of the photograph of the mesa in front of the Ophir Needles (Turkey Creek Mesa) (see appendix). The distributions show that although there is an abundance of aspen and conifers in the overstory, the understory composition (recent regeneration and small, older individuals) is dominated by *Abies lasiocarpa*. The maximum age (at breast height) of sampled trees was 220 years. The distributions were created based on the size distributions, and the corresponding ages were added using size-age distributions determined by coring a minimum of 10% of each size class.

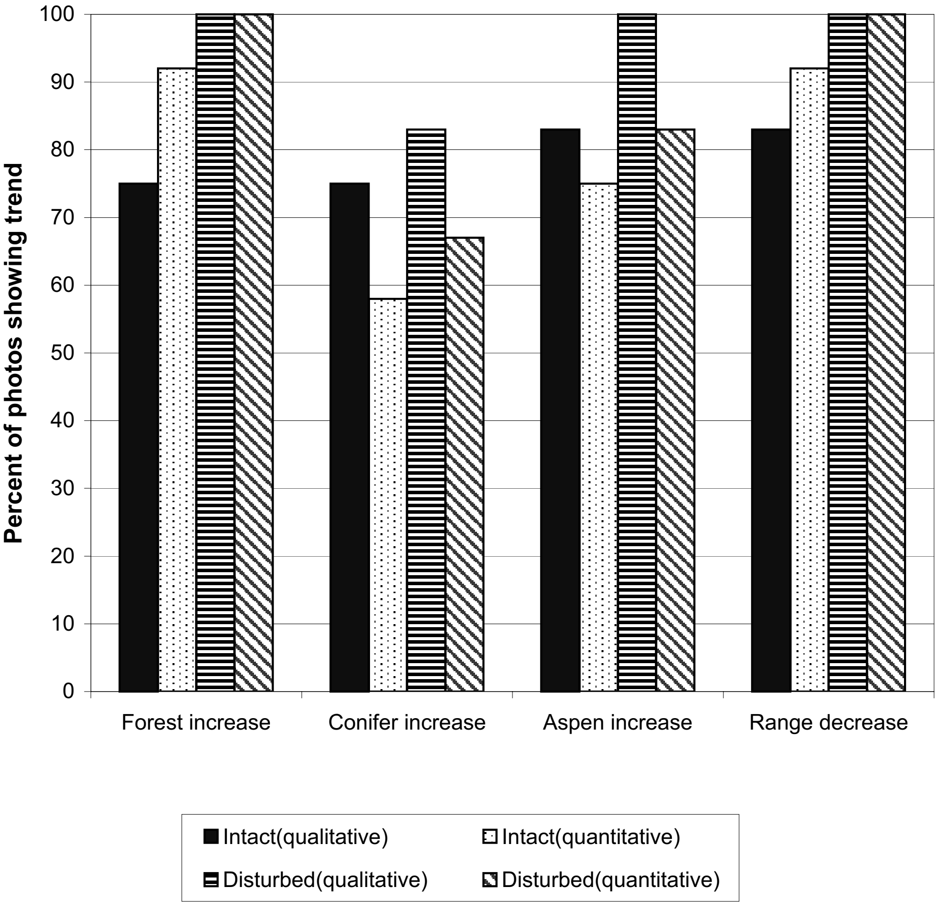

Figure 2—Summary of the changes in total cover, by cover type. Patterns described qualitatively and quantitatively are distinguished; the differences between these values indicate changes apparent to the observer but not detected in the GIS generated data. Note that the change in nonforested rangelands is a decrease, while the changes in forest cover types are increases. This is the cause and effect relationship described in the text.

all sites; aspen cover increased on 79% of all sites; and coverage by rangelands decreased on 96% of all sites (figure 2). The decrease in coverage of open range is significant ($F_{disturbed} = 5.03$, $P_{disturbed} = 0.006$; $F_{intact} = 3.76$, $P_{intact} = 0.003$; df = 11), but there is not a corresponding increase in conifer and aspen coverage. The lack of significance in the statistical analyses of the other cover types is due to the high variability between sites. Simply stated, the relative cover of coniferous and aspen forests and mixed rangeland patches varies more depending on which slope, valley, or watershed you observe than it does over time across these same locations.

Upon sampling the photographed landscapes we discovered that the range of forest ages (based on the age distributions of canopy dominants) was similar for both sets of data. The maximum age for landscapes classified as "intact" was 150–250 years, despite our previous distinction. (Although large, old "remnant" individuals were observed in many of these landscapes, they were rare enough to miss detection in our sampling.) This suggests that these landscapes were disturbed more recently than was apparent in the photography. Further, the patterns in landscape age predicted by photographic interpretation were not as strong as predicted. Our data confirm that many of the sampled forests are entering, or have entered, stages of succession when shade-tolerant conifers have a competitive edge over less-tolerant aspen. These data show that 96% of the sampled forests have a conifer component in the overstory, understory, or both. Twenty-one percent (21%) of the forests have distributions with many young conifers (especially fir); this suggests recent colonization and future competition for aspen. These data suggest that there are two components to landscape level changes in forest cover and composition: (1) expansion of stand borders as trees establish in formerly open meadows, and (2) the expansion of shade-tolerant (later seral) species under the canopy of existing forest dominants.

Discussion

This study is unique because it quantifies changes in landscape pattern over an 80- to 100-year period. The time span is consistent with other repeat photography studies in this region (e.g., Veblen and Lorenz 1991; Houston 1982; Gruell 1983; Progulske 1974) and near to the limit of the photographic history, which extends back to 1866 in some areas (Hart and Laycock 1996). However, these studies have not quantified the change. Although our statistical analysis fails to detect most of the observed differences in the landscape, several significant, and many nonsignificant, quantified changes were observed. Analyses suggest that there is an inverse relationship between relative total forest cover (increasing) and the relative area covered by open rangelands (decreasing). The statistical analysis of other landscape characteristics does not detect changes in patch number or patch size distribution. However, a comparison of individual pairs of images and observation of the trends in the data reveal that in many cases, there has been important, observable change in the configuration of the landscape at many of these locations. (See the images in the appendix for an example of one such area.) The wide range of values in the analyzed variables (variability among sites) is primarily responsible for the reduced statistical significance of the variables. This is reflected in the statistical analysis; further, the wide range in cover type distributions can be easily observed in the images. The details of landscape configuration (i.e., patch size, shape, and distribution) are variable at a more local scale than that used for this analysis and reflect local competition, environmental conditions, and management factors more strongly than a generalized pattern of change. Total cover, an apparently more uniform variable, does demonstrate the significance of the trend of forest increase and rangeland decrease.

Although there is a wide range in the distribution of successful aspen reproduction, there is a strong trend (among all sample locations) for reproductive success of shade-tolerant species. The evidence is the presence of abundant conifer regeneration in half of the forests dominated, or codominated, by aspen (96% of all sampled forests). Thus, it is possible to recognize the expansion of aspen across some landscapes while remaining concerned for the future survival and reproductive success of aspen. The success of shade-tolerant species is often at the expense of the less competitive species (i.e., succession toward later seral stages). These are the same patterns predicted by systemic models of succession in aspen communities (Bartos et al. 1983).

The ability for aspen to reproduce (considered from a landscape perspective) was not strongly influenced by parameters documented in the site histories. This is evidenced by the prominence of aspen regeneration on both disturbed and mature sites. Surprisingly, a higher percentage of aspen stands were found to be reproducing successfully on the intact sites than on recently disturbed sites. Furthermore, even recently disturbed sites show a greater abundance of conifer regeneration than aspen regeneration. These patterns suggest that modern disturbances have had a different effect on forest structure and regeneration than those typical 100 years ago. The patterns are similar to those documented by

Mueggler (1989) and Shepperd (1990) in the Rocky Mountain and Intermountain Regions. This condition must be a concern as we address the long-term persistence of aspen on the landscape. Presumably, as an increasing amount of the landscape develops dense forest cover, the reproductive success of aspen will continue to decrease.

Conclusions

At the present time, and in the landscapes surveyed, there has not been a decrease in the coverage of aspen forest. Instead, our study suggests that there has been an increase in forest cover across the region. We presume that this is primarily the result of fire suppression, but other land uses and land management practices in these areas may also be responsible. The landscape level implication is that early seral communities (those created by recent disturbances resulting in regeneration and recolonization without competition from later seral species, namely conifers) are becoming rare on the landscape. This conclusion is supported by our field data, which suggest that reproduction by shade-tolerant species is prolific under the canopies of mid-seral communities. Regeneration of forests following the major disturbances associated with European settlement of western Colorado is impressive, but it is distinctly different from the patterns created by historical fire regimes. We have entered an era where the control of landscape level disturbances has created a different landscape than that which existed before our management of these forests. Future research and management needs to address the potential paucity of early seral communities. The importance of these communities with respect to their composition (species diversity), their role in wildlife habitat (forage production and nutrition), and their role in forest structure (a range of generations) needs to be elucidated. We need research and management practices, which ensure that the landscape of the future includes multiple generations of forest communities and the species composition and age structure necessary for perpetually healthy forests. Particularly, the distribution of these different communities needs to be addressed from a landscape perspective. Only from this broad perspective can we study, monitor, and manage the distribution of various community types to ensure that our national lands provide the needed structural diversity to ensure healthy systems and the continued availability of wood products, wildlife habitat, and recreational opportunities into the future.

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Appendix follows on next page

Appendix: Ophir Needles and Turkey Mesa, San Miguel County, Colorado

A (top): Original photo by C.W. Cross, 1899, United States Geologic Survey.

B (bottom): Recent photo by D.J. Manier, 1995.

The camera is facing east; the photographed aspect faces west. Elevation ranges between 10,200 feet (3,100 m) and 12,500 feet (3,810 m). The original photo shows a characteristically patchy landscape south of Telluride, Colorado, along Colorado Highway 145. The interspersion of different-sized patches is probably the result of the historical disturbance regime. The contemporary photograph shows extensive forest cover across the mesa. Coverage of aspen has obviously increased through expansion of patches and consolidation of previously isolated clones. Coniferous forest persists interspersed within the aspen matrix. Most open patches (i.e., nonforested, rangeland patches) are gone; some of the large meadows persist in the contemporary image. Forest expansion has reduced the abundance of open patches within the forest. The size of forest patches has increased due to small, isolated patches growing together and occupying former open, grassy patches.

Persistence of Aspen Regeneration Near the National Elk Refuge and Gros Ventre Valley Elk Feedgrounds of Wyoming

David T. Barnett[1] **and Thomas J. Stohlgren**[1,2]

Abstract*—We investigated aspen (*Populus tremuloides*) regeneration in the Gros Ventre River Valley, the National Elk Refuge, and a small part of Grand Teton National Park, Wyoming, to see if elk (*Cervus elaphus*) browsing was as damaging as previously thought. We conducted a landscape-scale survey to assess aspen regeneration across gradients of wintering elk concentrations using 68 randomly selected aspen stands in the 1,090 km^2 study area. Forty-four percent of the stands sampled supported regeneration of saplings (stems greater than 2 m in height but less than 10 cm in diameter). There were no significant differences of regeneration across elk winter range classification (p = 0.25) or distance from feedgrounds (p = 0.96). Our results suggest that some regeneration persists across the landscape at a variety of elk densities.*

Aspen (*Populus tremuloides* Michx.) contributes uniquely to the ecology of the Rocky Mountains. Many studies estimate that aspen occupy 0.5–2% of the landscape (Baker 1925; Krebill 1972), yet it supports floral (Stohlgren et al. 1997), butterfly (Simonson 1998), and bird (DeByle 1985a) species otherwise rare on the landscape. Native ungulates such as elk (*Cervus elaphus*) and moose (*Alces alces*) seek aspen and understory species as a favored food source. Aspen is also an economic asset by providing forage for livestock (DeByle 1985b) and aesthetic and recreational value (Johnson et al. 1985).

A great deal of work has documented aspen decline throughout the Rocky Mountains (Krebill 1972; Loope and Gruell 1973; Schier 1975; Olmsted 1979; Weinstein 1979; Bartos et al. 1991; Baker et al. 1997l; Kay 1997; White et al. 1998). As decadent stems expire, few new stems successfully regenerate to reach tree-size. Elk browsing on juvenile stems (Krebill 1972; Olmsted 1979; Baker et al. 1997), fire suppression that eliminates an important disturbance regime (Gruell and Loope 1974; Kay 1997), or a suite of factors including elk, fire, and climate change (Romme et al. 1995) seem to be responsible for this apparent decline in successful regeneration. The more extreme positions (Krebill 1972; Kay 1997; White et al. 1998) question the long-term persistence of aspen (Olmsted 1979; Baker et al. 1997) in specific landscapes.

Conflicting investigations and a variety of regeneration conditions create uncertainty about aspen decline. Romme et al. (1995) indicated that aspen may not be in immediate danger of extirpation in Yellowstone National Park, Wyoming. In Rocky Mountain National Park, Colorado, Suzuki et al. (1999) expanded the scale and extent of previous studies and recorded vigorous regional aspen replacement except in localized areas that were highlighted in previous studies (Olmsted 1997; Hess 1993; Baker et al. 1997). Both national parks have a history of fire suppression (White et al. 1998), large ungulate herds (Smith and Robbins 1994; Hess 1993), and extensive aspen research. The regions of Yellowstone National Park and Rocky Mountain National Park are ecologically different from each other and from the study site addressed in this paper. But similar trends in aspen population dynamics have been reported across the Rocky Mountain region, so comparison is useful.

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Intense ungulate browsing and a century of fire suppression may jeopardize the condition of aspen in the Southern Greater Yellowstone Ecosystem. Many studies recognize stand deterioration and regeneration suppression (Krebill 1972; Bartos et al. 1991; Gruell and Loope 1974; Weinstein 1979; Romme et al. 1995). The success of fire in stimulating stand-replacing regeneration seems to depend on ungulate browsing pressure (Gruell and Loope 1974; Romme et al. 1995). Fire stimulates a flush of stem regeneration, but often not in quantities that can escape elk browsing pressure (Bartos et al. 1991; Romme et al. 1995). Not even the large Yellowstone fires of 1988 enabled extensive aspen regeneration in highly productive burned areas or in unburned stands with less aspen and less vegetative forage that might make these stands less attractive to elk (Romme et al. 1995). At the scale measured, these aspen were unable to regenerate enough to counteract the effects of elk browsing; few stems survived to tree size (>2 m). Several other studies attribute lack of regeneration to ungulate pressure (Krebill 1972; Weinstein 1979). If elk are significantly browsing new growth, regeneration suppression should be most severe where elk densities are most concentrated.

Given previous findings, we formulated a simple hypothesis. A spatially considerate, highly replicated, landscape-scale survey of aspen regeneration would demonstrate that less regeneration occurs in areas of high elk use.

Study Site

Aspen stands were sampled in and around the Gros Ventre River Valley of the Bridger-Teton National Forest, the National Elk Refuge, and the southeast part of Grand Teton National Park, Wyoming (figure 1). The study site covers an area of 1,090 km^2. Elevations range from 1,890 m on the National Elk Refuge to just under 3,000 m at the upper reaches of aspen in the Gros Ventre River Valley. The average annual precipitation at Moran, WY, is about 57 cm, and the monthly mean temperatures vary from –11 ^{o}C in the winter months to 14.7 ^{o}C in July (Smith and Robbins 1994). The region serves as winter range for elk of the Jackson elk herd. The National Elk Refuge was established in 1912 to protect winter habitat and separate elk from livestock to prevent disease transmission (Smith and Robbins 1994). The National Elk Refuge and the southeastern part of Grand Teton National Park are characterized by rolling hills of grassland, riparian, and mixed conifer vegetation types. The Gros Ventre is more extreme topographically, with a narrow river valley of grassland in the bottomlands and mixed conifer and aspen at higher elevations.

We selected the area because of its long history of aspen investigation (Krebill 1972; Bartos et al. 1991) and because a part of the area functions as important elk winter range for the Jackson elk herd (Smith and Robbins 1994). Several factors make this winter range ideal for testing aspen regeneration theories across a gradient of elk densities. The Wyoming Department of Game and Fish (the agency responsible for management of elk in the Bridger Teton National Forest) and the United States Fish and Wildlife Service at the National Elk Refuge supply elk with supplemental feed during the winter months of the year at specified feedgrounds (Smith and Robbins 1994). Feeding at these locations generates high concentrations of elk during the months elk occupy the winter range. Observations (Smith and Robbins 1994) and aerial survey data indicate elk concentrations decrease as distance from feedground increases. The State of Wyoming Game and Fish winter range classification provides another indicator of elk distribution. They define two types of elk winter range according

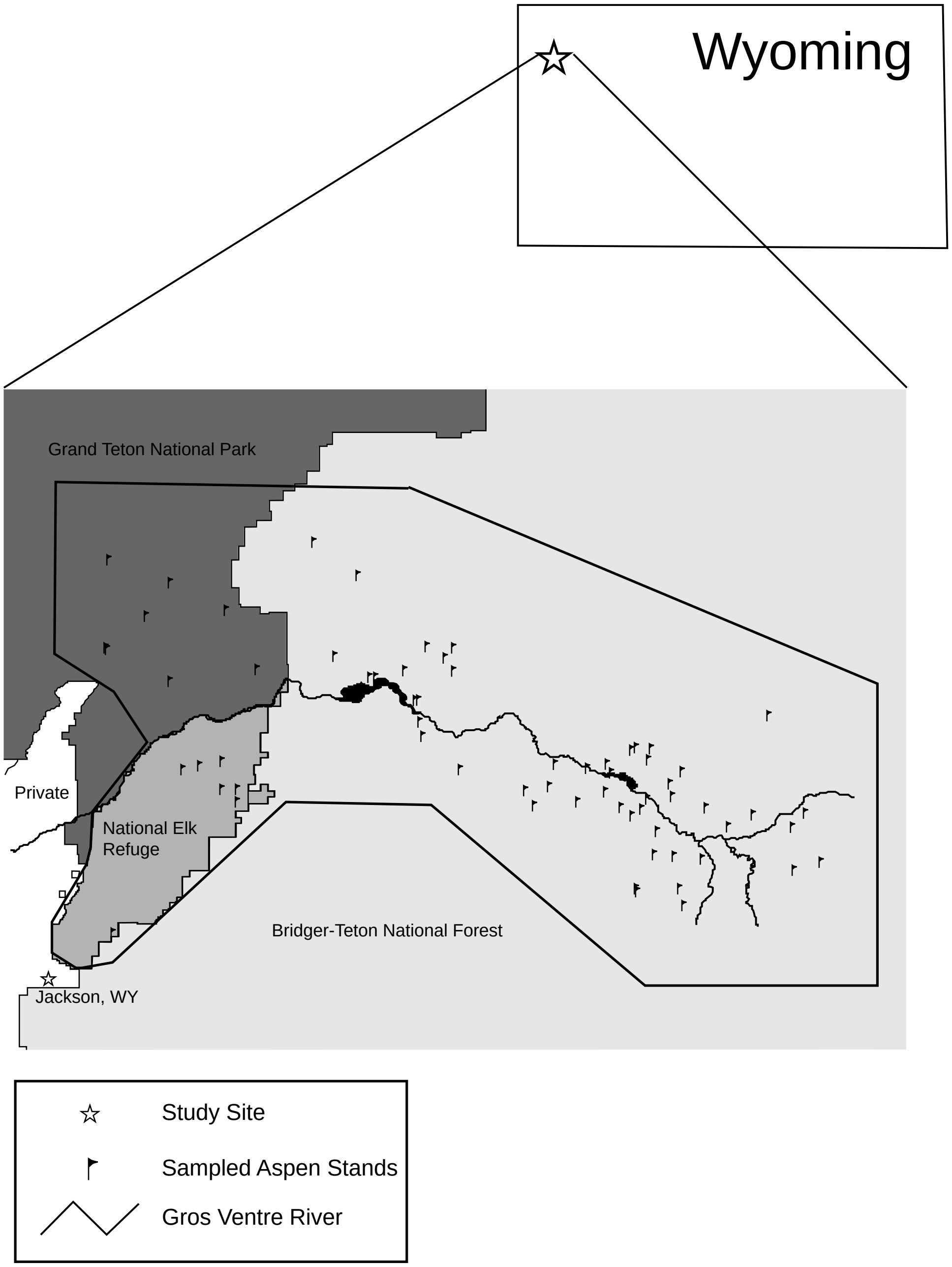

Figure 1—Regional location of study site within the state of Wyoming. The inset displays the study area and location of sampled aspen stands in the Bridger-Teton National Forest, Grand Teton National Park, and the National Elk Refuge.

to elk use: (1) Crucial Winter Range is "range or components of habitat that play a determining factor in a population's ability to meet and sustain population management objectives." (2) Winter Range represents "winter habitat substantially utilized by a population or portion of a population" (Strickland 1985).

Methods

We designed our methods to quickly quantify aspen at landscape scales and measure patchy regeneration within a stand. Stands were selected by randomly generating point locations in the study area. At each location we sampled the closest aspen stand to the north (NNW-NNE). If we did not encounter a stand within 500 m, we returned to the point and tried east, south, and west directions in turn. If no stands were located, we chose another random point to sample. We located and sampled 68 stands in the summer of 1998. At each sample point we recorded the slope in degrees, aspect measured by compass, elevation, stand area, location (Universal Trans Meter coordinate), dominant species in the surrounding canopy, dominant understory species, and evidence of disturbance.

For the purposes of this paper, successful regeneration was defined by saplings, those stems >2 m tall but <10 cm d.b.h. Suckers were stems <2 m in height; the term stem is used in reference to all aspen stems growing in a stand. We based the definition of successful regeneration on studies by Baker et al. (1997) who used stems greater than 2.5 m and 6 cm d.b.h., while Krebill (1972) used 15 cm d.b.h. to isolate pole-like stems indicative of new regeneration.

Once located, a stand was stratified according to patches of saplings (or lack thereof) within the stand, and a 5 x 5 m plot was randomly placed in each stratum (figure 2). Strata were defined as homogeneous patches of regeneration or regions of a stand that had no regeneration. For suckers (<2 m tall), we recorded the number of stems, number of dead stems, and percent of branches browsed. For stems over 2 m in height (>2 m tall), the number of stems, diameter at breast height (d.b.h.), number of dead stems, visual estimates of percent of bark browsed, and percent of branches browsed were recorded. Other stratum characteristics noted included percents of canopy cover, plant cover (combined herbaceous and shrub), rock, litter, soil, woody material, and stratum area (m^2) as measured by tape or calibrated human paces.

Variables measured in all strata within a stand were pooled by a weighted-area average to calculate total regeneration per hectare. The randomly located

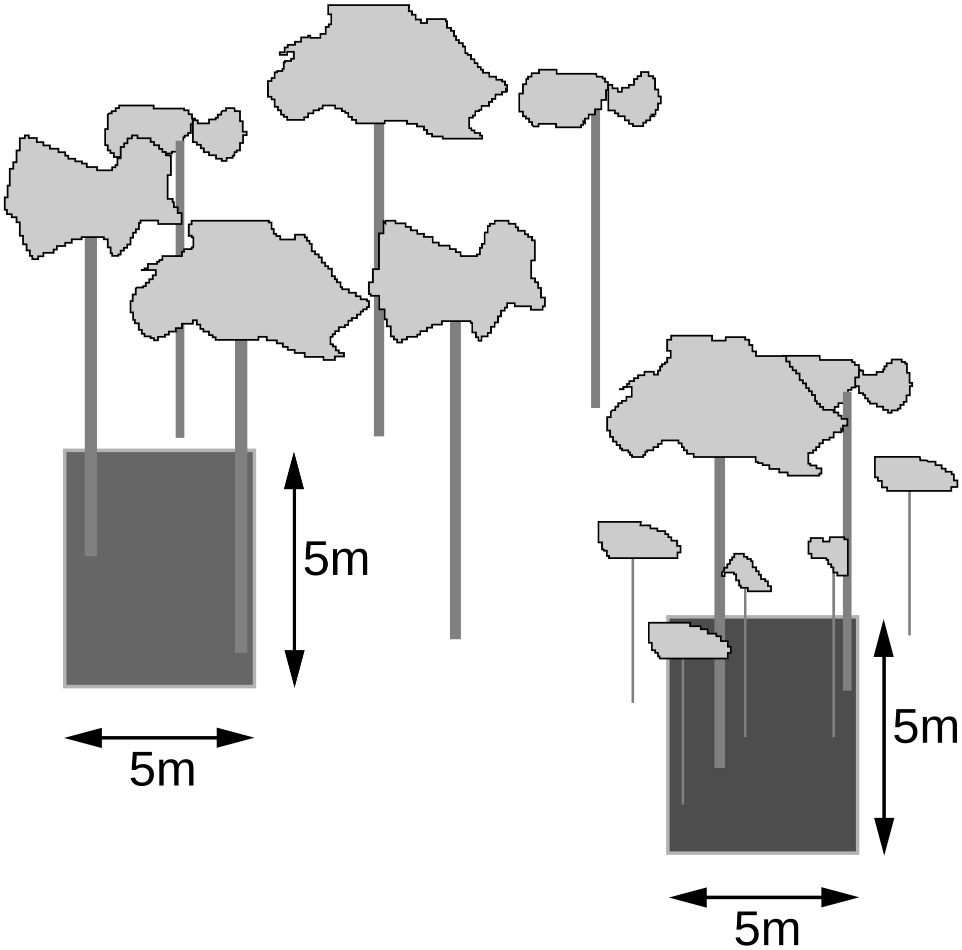

Figure 2—Aspen stands were stratified by patches of regeneration. One 5 x 5 m plot was randomly placed in each stratum to quantify aspen regeneration.

stands were classified in three ways. We used the Wyoming Department of Game and Fish elk winter range classifications of Crucial Winter Range and Winter Range and used a Nonwinter Range classification (stands that fell outside these two ranges) (figure 3). We also used categorical distances from state and federal feedgrounds classed at <1.5 km, 1.5–3 km, and >3 km. These distance classes were chosen to represent potentially different areas of elk use as reflected by field observation from land managers and telemetry data (S. Kilpatrick 1998, personal communication, Wyoming Department of Game and Fish, Jackson, WY). Both classifications were assumed to be indicators of elk density on the winter range.

Statistical Analyses

A one-way analysis of variance (ANOVA) of the sapling per hectare values was used to determine differences between mean sapling stem density for both the winter range classifications and the categorical distances from feedgrounds. A log transformation of the number of saplings was performed to meet ANOVA assumptions of normality. One-way ANOVAs with the same classes were used to evaluate differences in density of suckers (<2 m tall; density of suckers was square-root transformed for distance and classification ANOVAs to meet ANOVA assumptions of normality), percent browse on suckers (<2 m), percent browse on branches of saplings (square-root transformation for distance and classification), percent stem browse on saplings, and percent bark browse on stems <10 cm. When the ANOVA indicated significant differences between means, individual comparisons were made by controlling mean experiment wise error rate with the REGWQ method (SAS Institute 1996). ANOVA statistical manipulations were carried out in SAS (SAS Institute 1996).

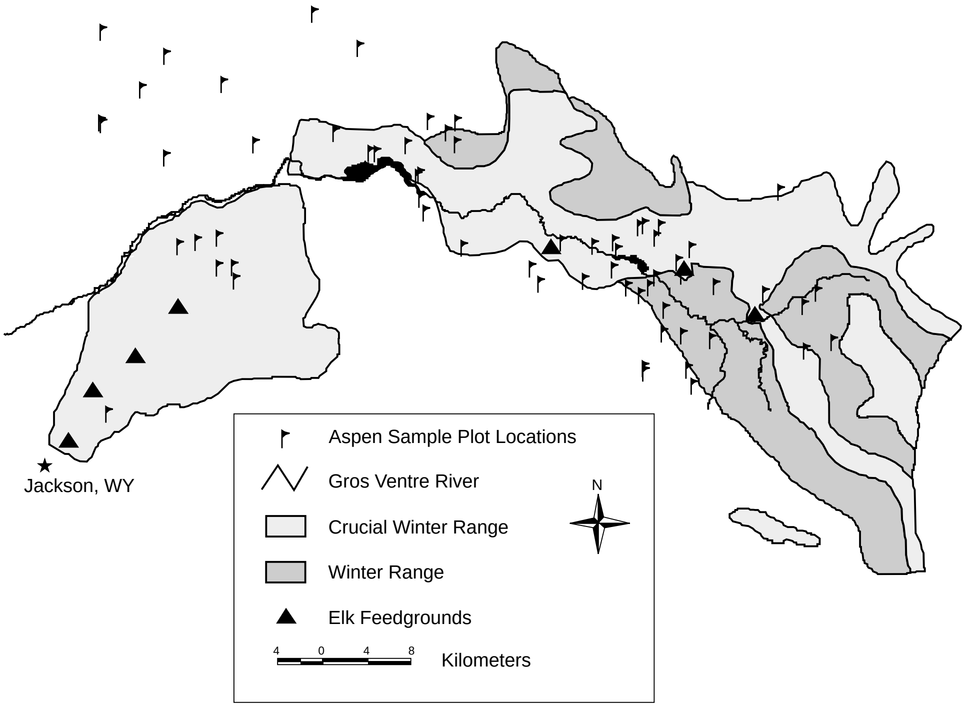

Figure 3—Location of aspen regeneration sample plots and State of Wyoming Game and Fish Elk Winter Range classifications in the study area.

Results

We sampled 68 aspen stands in and around the Gros Ventre River Valley and southeastern part of Grand Teton National Park. Thirty of the 68 stands sampled, 44%, demonstrated some evidence of successful aspen regeneration (saplings) in the stand. Sapling values ranged from zero to 2,900 stems per ha (table 1).

Elk Winter Range Classification

There was no significant difference ($p = 0.25$) between the number of saplings in the three winter range classifications (table 2). However, the amount of bark browsing on saplings was higher (2% ± 0.7) in the Crucial Winter Range as compared to the Nonwinter Range and Winter Range (0.2% ± 0.1). The Winter Range had significantly more suckers than the Crucial Winter Range and Nonwinter Range ($p = 0.01$; table 2).

Distance From Elk Winter Feedground

There were no significant differences in the number of saplings or any of the other variables analyzed at increasing distance classes from elk winter feedgrounds (table 3). The percent browse on suckers (<2 m tall) was nearly significant

Table 1—Summary statistics for aspen stands sampled by winter range class and distance to feeding grounds in the southern Greater Yellowstone Ecosystem.

Stand characteristic	Crucial winter range	Winter range	Non-winter range	<1.5 km from feeding grounds	1.5–3 km from feeding grounds	>3 km from feeding grounds
Number of stands sampled	26	15	27	8	18	42
Percent stands w/saplings (regeneration stems/ha)	50	53	33	37	44	43
Minimum stand saplings (regeneration stems/ha)	0	0	0	0	0	0
Maximum stand saplings (regeneration stems/ha)	2,900	1,400	1,200	900	2,900	1,700

Table 2—Comparison of aspen stands in Wyoming Department of Game and Fish elk winter range classifications in the southern Greater Yellowstone Ecosystem. Mean and standard errors (SE in parentheses) are presented. Significantly different means in a row have different subscripts.

Stand characteristic	Crucial winter range	Winter range	Nonwinter range
Saplings (regeneration stems/ha)	370 (137)	227 (105)	188 (72)
Percent bark browse on saplings (regeneration stems)	2.0a (0.7)	1.0 (0.6)	0.2b (0.1)
Percent stem browse on saplings (regeneration stems)	22 (7)	21 (9)	7 (2)
Percent bark browse on mature stems	42 (8)	20 (6)	40 (7)
Suckers (stems <2 m tall/ha)	1433a (330)	2975b (583)	1127a (533)
Percent browse on suckers (stems <2 m tall)	47 (7)	61 (5)	39 (6)

Table 3—Comparison of aspen stands in <1.5 km, 1.5-3 km, and >3 km from elk feeding grounds in the southern Greater Yellowstone Ecosystem. Mean and standard errors (SE in parentheses) are presented.

Stand characteristic	<1.5 km from feeding ground	1.5-3 km from feeding ground	>3 km from feeding ground
Saplings (regeneration stems/ha)	243 (140)	332 (183)	222 (70)
Percent bark browse on saplings (regeneration stems)	1.0 (1.0)	2.0 (1.0)	1.0 (0.3)
Percent stem browse on saplings (regeneration stems)	21 (12)	17 (7)	15 (4)
Percent bark browse on mature stems	39 (15)	47 (8)	31 (5)
Suckers (stems <2 m tall/ha)	1552 (805)	2138 (535)	1463 (379)
Percent browse on suckers (stems <2 m tall)	51 (12)	60 (7)	40 (4)

($p = 0.07$), indicating that browsing 1.5–3 km from the feedgrounds might be greater than the areas closer or farther away.

Discussion

We expected to find no aspen regeneration in this high elk density study area. That 56% of the aspen stands sampled on the landscape showed no sign of aspen regeneration might indicate that aspen is doing poorly under present conditions. Current regeneration rates may not be sufficient to replace all aspen stands on the landscape. However, in 44% of the stands, we did find some regeneration scattered throughout the landscape (table 1).

The Pattern

The absence of significant differences in aspen regeneration at various elk densities (tables 1 and 2) refutes our primary hypothesis that we would find less successful regeneration at higher elk densities. Given the number of stands without sapling regeneration, these results suggest a certain evenness or spatial ubiquity of elk browsing on the landscape at the scale we sampled. There is neither indication of less regeneration in the heart of the elk winter range, nor more in areas presumed to be less frequented by elk.

There were more suckers (stems <2 m tall) in the Winter Range than Crucial Winter Range and Nonwinter Range. This result may be irrelevant as the majority of these stems were browsed, but some were just new stems. The difference may suggest that elk tend to feed more on supplemental feed in the Crucial Winter Range and browse more aspen in the Winter Range. We did see an indication that the bark of sapling (>2 m, <10 cm d.b.h.) stems may be browsed more heavily in the Crucial Winter Range. However, this result may be inconsequential given the low browsing percentages as compared to mature stems, and that these stems often grow in dense cohorts that can make elk bark browsing difficult (Gruell and Loope 1974). Furthermore, this trend was not reflected in the number of these sapling stems, which ultimately contributes to maintenance of mature aspen canopy cover. The resulting pattern is one of no saplings in just over one-half of the aspen stands with some saplings in under one-half of the aspen stands scattered throughout the landscape.

Why the Pattern Is Different

Our results of widely scattered aspen saplings do not concur with the findings of many other investigations in the area. Given the variability of heterogeneous landscapes, extrapolation to unsampled areas must be presented tentatively. Additionally, any study that disagrees with such an abundance of literature from the same region should proceed with caution and critical logic. We offer three possible hypotheses that may explain why many studies predict a near complete demise of aspen while our data suggest its persistence. The hypotheses are presented in the order of least to most likely:

Hypothesis 1: The sample size may inadequately represent the entire landscape

This study had a small sample size relative to the larger, unsampled-heterogeneous landscape, and some might suggest that a larger sample size is needed to adequately represent the extensive landscape and adequately confirm the suggestion that aspen will persist on the landscape. While theoretically possible, a retro-analysis of our data through the use of Monte Carlo simulations suggests that about 30 randomly selected plots would have yielded approximately the same results as our 68 plots (figure 4). The upward trend of the simulation suggests that a larger sample size would likely detect even more regeneration. The initial findings also agree with casual field observations, where sporadic aspen regeneration was often seen while hiking to and from the random plot locations.

Hypothesis 2: Successful regeneration has increased since the earlier studies in the 1960s and 1970s

Many studies that predicted the demise of aspen through regeneration suppression were conducted 30 or 40 years ago (Beetle 1968; Krebill 1972), and the regeneration situation in the region covered by this study may have changed. General climate warming (VEMAP 1995) or favorable microclimates may have stimulated more successful aspen regeneration. However, climate effects are difficult to evaluate at landscape scales due to the lack of spatially extensive, long-term data on microsite variation and interactions with temporal and spatial variation of local browsing pressure. A series of large, long-term, randomly located plots and perhaps wide belt transects that span large environmental gradients (e.g., Stohlgren et al. 1999b) are needed to fully evaluate this

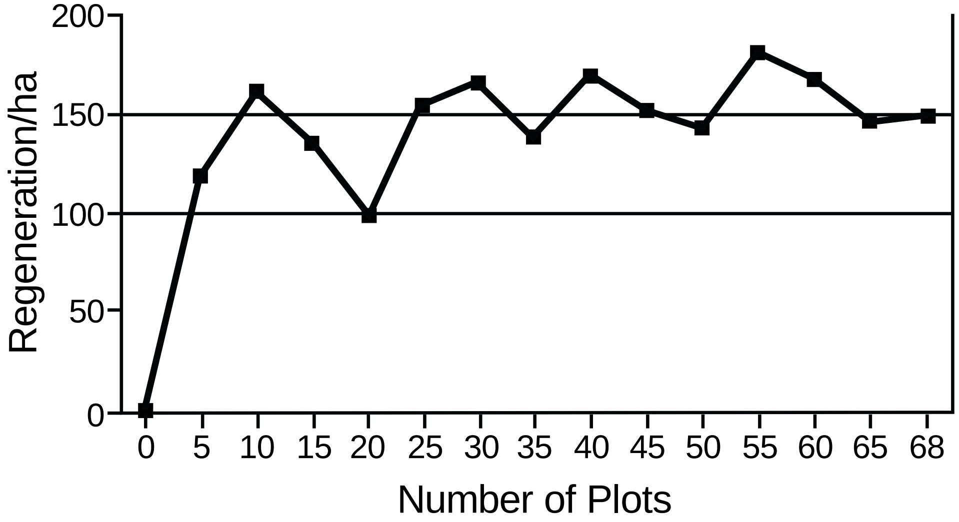

Figure 4—Monte-Carlo simulations predict that approximately 30 aspen stands may have been sufficient to capture significant aspen regeneration. See Methods section for details.

hypothesis. It should be noted that revisiting the few, subjectively selected stands measured in the original studies can't be used reliably as the foundation for an unbiased time series, nor can they isolate the interaction of climate and browsing pressure at plot to landscape-scales.

Hypothesis 3: Patches of successful regeneration were simply missed in previous studies

The previous investigations may have missed aspen regeneration due to small plot sizes and subjective plot location. This hypothesis has been tested indirectly in Rocky Mountain National Park, Colorado, where Suzuki et al. (1999) and Stohlgren et al. (1999a) showed that spatially restricting study sites can greatly underestimate aspen regeneration in the broader landscape. As in the present study, sampling objective, randomly selected plot locations yields far more aspen regeneration than previously realized.

We see this third hypothesis as the most likely answer to the question of aspen regeneration on this landscape. Landscapes are inherently variable in space (Stohlgren et al. 1999b). Subjective sampling, and/or small sample sizes common in many studies (Beetle 1968; Krebill 1972; Gruell and Loope 1974; Weinstein 1979), could have missed patchy but successful aspen regeneration, and therefore support the common conclusion of a threatened aspen population.

The results of our relatively large number of randomly located stands across the landscape might suggest that aspen persists in a patchy mosaic. It is important to note that regeneration of some stems does not guarantee stand replacement. Our weighted average regeneration densities for a stand do not satisfy stocking requirements (Gruell and Loope 1974) aimed to maintain aspen dominance across the whole stand. The regeneration stem densities that we report highlight the fact that much of the regeneration encountered was patchy even within a stand.

Persistence might be defined as the continued presence of a species in a specific area for a specific time (Donalson and Nisbet 1999; Fagan 1999). Most species are rare, few are dominant, and the strategy for rare species is to survive, reproduce, and persist in the presence of dominant species and many environmental stresses. The presence of patchy stem regeneration may be evidence of temporary persistence. Long-term stand persistence and extirpation remain fertile areas of research (Margot Kaye, Colorado State University, unpublished data). Scientists, resource managers, or society may have reasons to protect individual stands or restore aspen to 4% forest cover or 4,000 regenerating stems per hectare, but these human-imposed quotas for local areas may be unrelated to aspen persistence at larger spatial scales or over long time periods.

Historical photographs and tree-ring data (Gruell and Loope 1974; Baker et al. 1997; Romme et al. 1995) indicate a flux of regeneration occurred in the region during the years of 1850–1900. Given the age of many of the even-aged stands, this burst of regeneration resulted in the aspen cover we see today. With aspen decline, it is a likely possibility that these aerial cover percentages may not be sustained. The pockets of aspen persistence observed in this study may represent important sources or refuges of aspen and other obligate species in periods between conditions suitable to abundant regeneration. Disturbance to an apical meristem reduces auxin levels in the roots and permits suckering or development of new stems (Schier et al. 1985). Disturbances such as fire, clearcutting, or avalanches frequently encourage flushes of regeneration that could represent an opportunity for aspen to increase aerial cover if conditions were suitable (Romme 1995). Additionally, even under significant browsing pressure, root systems may be maintained indefinitely through the presence of small-shrub aspen or young shoots (Despain 1990). The 200-year life cycle of an aspen stem (Krebill 1972) and much longer life cycles of large clones make investigations of historical fluctuations and trends difficult. Since only one incidence of episodic regeneration has been documented, the applicability of this notion over longer time frames still needs to be tested.

Conclusion

Our work indicates that aspen is regenerating in patches throughout the winter range in the Gros Ventre River Valley, the National Elk Refuge, and the southeastern portion of Grand Teton National Park. Consideration of aspen on large yet detailed scales is essential as aspen regenerate and may persist on these scales. Many previous assessments of the condition and trend of aspen are not wrong, but their lack of appreciation for temporal and particularly spatial variability may prevent them from telling the whole story. Most studies, even those that do recognize patches of regeneration (Gruell and Loope 1974; Baker et al. 1997), tend to focus on the grave implications of aspen deterioration. We see the spatially intricate patches of successful regeneration as potential for future aspen success and continued persistence in elk winter range landscapes.

Acknowledgments

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Landscape-Scale Dynamics of Aspen in Rocky Mountain National Park, Colorado

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***Abstract**—Past studies of quaking aspen in Rocky Mountain National Park suggested that the aspen population is declining due to intensive browsing by elk (Cervus elaphus). These studies were conducted in the elk winter range, an area of intensive elk impact. The elk summer range experiences less intense grazing pressure. We tested the hypothesis that impacts of elk would be greater in the elk winter range than the summer range with landscape-scale data from the Park. The detrimental effects of elk on aspen are highly localized and, at larger spatial scales, elk browsing does not seem to be influencing the aspen population.*

Quaking aspen forests can be considered both a rare and important habitat type in the central Rocky Mountains. In the region of Rocky Mountain National Park, Colorado, aspen forest covers less than 10% of the forested landscape. However, considerable floral and faunal diversity is associated with the forest type (DeByle 1985; Turchi et al. 1995). Aspen has been called a “hotspot” of diversity (Stohlgren et al. 1999), and it is valued for its aesthetic beauty. Within the Park, many studies have concluded that aspen forests are in decline due to excessive browsing by elk (*Cervus elaphus*) (Baker 1997; Olmsted 1979; Packard 1942). These studies have focused on portions of the elk winter range within the Park, which itself is only a fraction of the landscape (figure 1).

The elk winter range represents the area in the Park that is most likely to be highly impacted by elk (DeByle 1985). Large numbers of animals (approximately 2,000 individuals in 1999) rely on these low-elevation areas for winter forage. The browsing of stems and shoots of aspen trees by elk both removes new growth and creates wounds for pathogen introduction (Hinds 1985; Krebill 1972). The summer range, in contrast, is a much larger, high-elevation area where elk densities are lower and forage availability is much higher due to the summer growing season and the loss of snowpack. Due to differential use of the winter and summer ranges within the Park, one would expect the impacts of elk to be much greater in the winter range than the summer range.

The spatially dependent foraging patterns of elk indicate that the effects of elk browsing should be site dependent, and therefore studies of the effects of elk on aspen will likely be influenced by their spatial scales. Previous studies of aspen that focused on the elk winter range in the Park considered small spatial scales. To gain a broader understanding of the status of aspen in the Park, landscape-scale studies are necessary to measure the status of aspen throughout the Park, where elk forage intensity ranges from low to high.

This paper summarizes the results of two landscape-scale studies of aspen conducted within Rocky Mountain National Park. A goal of both studies was to determine the effects of elk on aspen. The first study measured regeneration in aspen stands in the elk summer and winter ranges in the Park and the surrounding Roosevelt National Forest (Suzuki et al. 1999). We only used the data collected from the Park by Suzuki et al. (1999). The second study surveyed

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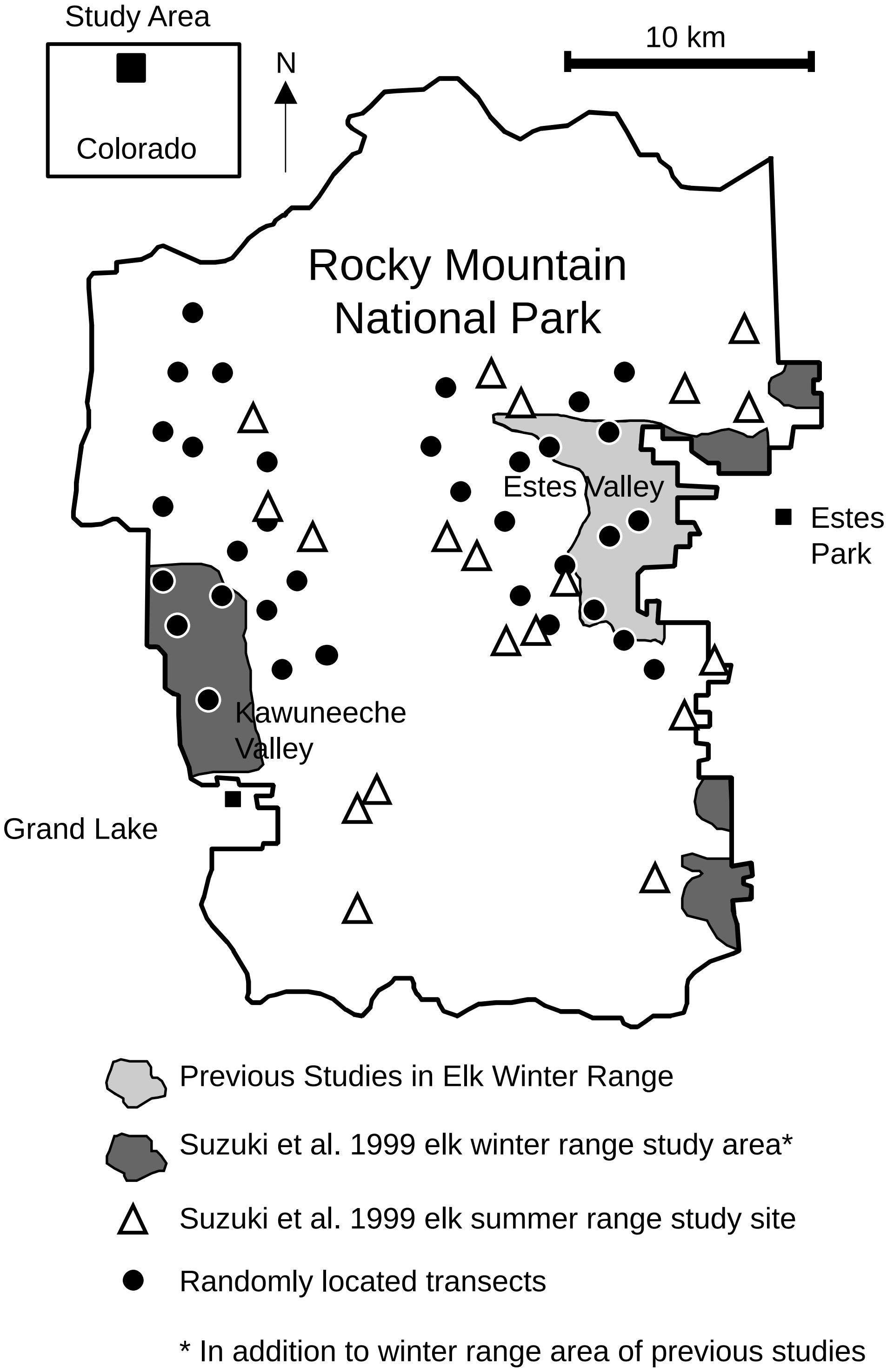

Figure 1—Location of study sites within Rocky Mountain National Park. Light gray areas represent the study areas in Estes Valley for Packard (1942), Olmsted (1979), and Baker et al. (1997). Suzuki et al. (1999) collected data from the Estes Valley area, as well as from other sites in the elk winter range (dark gray) and elk summer range (open triangles). Randomly located belt transects were surveyed throughout the park to describe the aspen population (black circles).

aspen in randomly selected areas throughout the Park and described aspen patch characteristics and degree of elk browsing. Based on the results of previous studies (Baker 1997; Olmsted 1979; Packard 1942), we hypothesize that the effects of elk browsing will be higher in aspen stands within the elk winter range than in stands in the summer range. The effects of elk browsing on aspen were measured by the amount of aspen regeneration, degree of browsed bark, and other forest metrics that represent stand condition (e.g., aspen basal area, density, and cover).

As mentioned above, aspen covers a small portion of the landscape but it is an important habitat type. An accurate description of the amount of aspen on the landscape requires high-resolution data. Many of the estimates of aspen cover in the region of the Park have been based on remotely sensed data such as LANDSAT imagery and aerial photographs and have found a cover of approximately 2%. We used the data from the ground survey to calculate the percent cover of aspen throughout the Park and to compare the resolution of remotely sensed data to field data.

Methods

Rocky Mountain National Park is located in the Front Range of north-central Colorado and straddles the Continental Divide. The Park covers an area of approximately 107,536 ha and elevations ranging from 2,300 m to 4,300 m. Aspen covers less than 10% of the forested area of the park and is found at all forested elevations.

Suzuki et al. (1999) gives a detailed description of the methods used to determine the extent and timing of regeneration throughout the Park. We divided the Park landscape into three zones relative to the intensity and season of elk use: (1) highest use—elk winter range in Estes Valley, between 2,400 and 2,800 m elevation (using data from Baker et al. 1997 and additional data from this project); (2) moderate use—elk winter range inside the Park, but outside Estes Valley; and (3) lowest use—elk summer range inside the Park, above 2,800 m elevation (figure 1). In each zone, all aspen stands were mapped and then a sub-sample of stands was chosen at random for measurement. We focused only on aspen stands that did not have major conifer encroachment and that had dominant individual trees that were >50 years old.

In the elk winter range of Estes Valley, Baker et al. (1997) identified 72 stands of aspen (stand defined as >10 trees), and they selected 17 stands for measurement. We mapped an additional four stands and sampled two. In the elk winter range outside Estes Valley, we mapped 34 stands and sampled 16. In the elk summer range, we mapped 387 stands and sampled 23 stands.

We followed the measurement procedures used by Baker et al. (1997) to allow comparisons between the studies. In each sampled stand, 10 x 10 m plots were subjectively located to represent a typical portion of the stand. In each plot, we tallied (by 20-mm diameter classes) the number of live aspen trees >2.5 m tall (above the reach of elk browsing, a value used by Baker et al. [1997]) and >20 mm diameter at 1.4 m d.b.h. (diameter at breast height). Ten or more increment cores were taken in each plot to determine stem ages, covering the entire range of diameter classes. Tree ages were determined to within five years of accuracy. We used the relationship between diameter and age within each plot to estimate the age of the uncored trees.

In the second study, an unbiased description of the aspen population, we conducted a ground survey. Thirty-six points were randomly located throughout the forested area of the central portion of Rocky Mountain National Park. From each point we surveyed two perpendicular belt transects, each 1,000 m long and 50 m wide. We recorded the position and size of each patch encountered within the belt transects and collected descriptive data within sample plots.

Within each aspen patch encountered in the belt transects, we subjectively located 5 m x 5 m plots to represent a typical portion of the patch. Within each plot, the following information was recorded for stems >1.5 m in height: number of stems, d.b.h. (taken at 1.4 m), height, and a visual estimate of percent bark browsed. We counted the number of stems <1.5 m in height, what we will refer to as "aspen regeneration." We calculated averaged percent of bark browsed for all stems within the plots, patch basal area (m^2/ha), and density (stems/ha). We separated data from patches based on their locations within elk summer or winter ranges, and we compared means using analysis of variance with a significant *p*-value of less than 0.05.

Results

We used data from 58 aspen stands and 36 randomly located transects throughout Rocky Mountain National Park to determine the impacts of elk on aspen (figure 1). Aspen regeneration was low in Estes Valley, with 20% of the aspen stands developing a regeneration cohort in the past 25 years (figure 2). Regeneration was higher in other areas of elk winter range in the Park (45% of stands) and in the elk summer range (high elevation) of the Park (70% of stands) (figure 2).

We ground-surveyed a total of 238 hectares throughout the Park. In that area, we encountered 112 aspen patches that covered 6.4% of the landscape—more than three times as much cover as the 2% estimated from remotely sensed data. Of the 112 aspen patches, 49 were within the elk winter range of the Park and 63 within the summer range. Mean percent bark browsed in the elk winter range (mean = 67%, SE = 4.9) was higher (p = 0.005) than mean percent bark browsed in stands within the summer range (mean = 49%, SE = 4.1) (figure 3a). Mean regeneration for elk winter range and mean regeneration for elk summer range were not significantly different (winter range mean = 21,906 stems/ha, SE = 4,175; summer range mean = 19,095 stems/ha, SE = 4,411) (figure 3b), but it is interesting to note that the mean number of regenerating stems per hectare in the elk winter range was higher. Mean basal area and density for aspen patches in the elk winter and summer ranges were not significantly different (winter range mean basal area = 23.75 m^2/ha, SE = 4.25; summer range mean basal area = 26.16 m^2/ha, SE = 3.62; and winter range

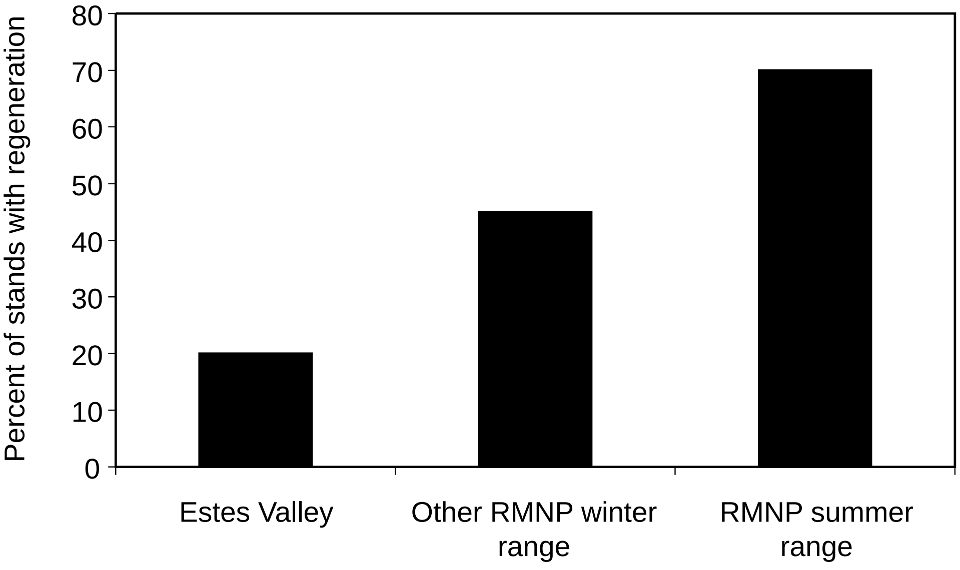

Figure 2—Percent of stands with regeneration in the past 25 years from Suzuki et al. (1999). Nineteen stands were sampled in Estes Valley, the region of highest elk foraging. Sixteen stands in other regions of the elk winter range in the Park than Estes Valley were sampled. The area of lowest elk browsing was the elk summer range in the Park, where 23 stands were sampled.

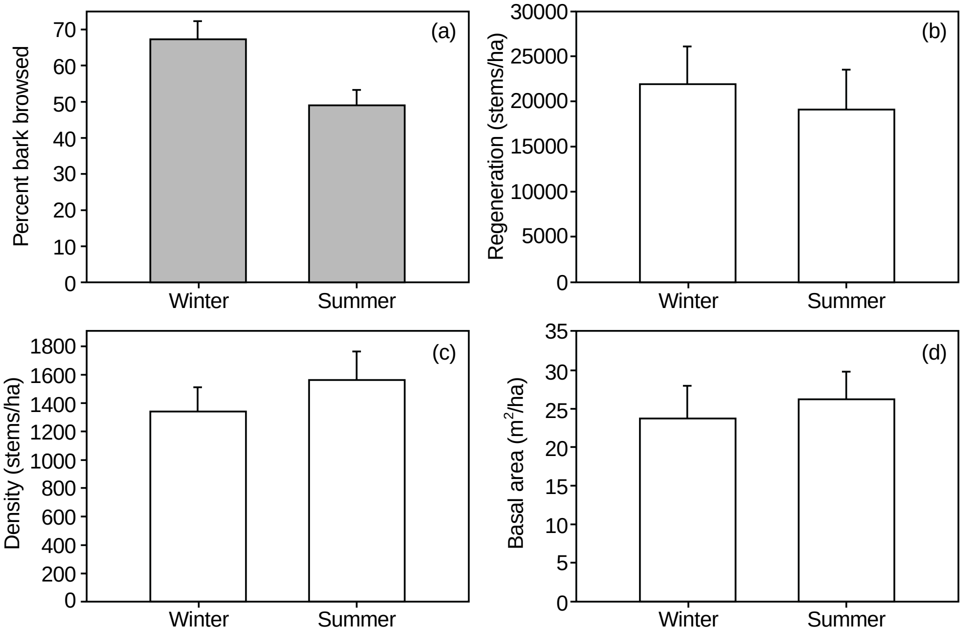

Figure 3—Comparison of aspen characteristics in the summer and winter range, based on data from the randomly located ground survey. Based on ANOVA analysis, only percent bark browsed (a) was significantly different. Regeneration (b), density (c), and basal area (d) were not significantly different between the elk summer and winter ranges.

mean density = 1,339 stems/ha, SE = 169; summer range mean density = 1,558 stems/ha, SE = 199) (figure 3c and 3d). Percent aspen cover in the elk winter range was 6.8% and 5.7% in the elk summer range.

Aspen patch size ranged from over 1 hectare in size to less than 1 m^2, with 44% of the patches being less than 200 m^2 (figure 4). Patches larger than 1 hectare were too large to measure accurately on the ground. Over a quarter of the aspen patches had 100% aspen in the canopy, while approximately 40% of the aspen patches had greater than 50% conifers in the canopy (i.e., more conifer in the canopy than aspen) (figure 5).

Discussion

For five decades, researchers have predicted the demise of aspen in Rocky Mountain National Park (Berry et al. 1997; Olmsted 1979; Packard 1942; White et al. 1998). Packard (1942), based on his study of aspen in the elk winter range, predicted that within a few years of his study all the aspen would have died and would not be replaced by new stems. This dire forecast has not come true, as we documented with the percent cover of aspen found in the elk winter range and throughout the Park. Subsequent studies of aspen in the Park also attributed aspen decline to elk browsing (Baker et al. 1997; Olmsted 1979). Our results showed that in local areas of high elk browse, aspen regeneration is depressed. However, when we looked at a broader scale and at areas where elk browsing was less intense, we found that aspen has been regenerating in at least 50% of the stands in the past 25 years. The Park began its policy of natural regulation for the elk population in 1968 and since then the elk population has increased to approximately 2,000 individuals. During the past 25 years, elk impacts should have been at their highest. The highly localized impacts of elk on aspen regeneration in the past 25 years allows for small-scale preservation efforts such as elk exclosures to protect particular aspen clones or patches.

Patterns of aspen regeneration showed high variability within zones and locations. Although aspen regeneration in most of Estes Valley was low (as

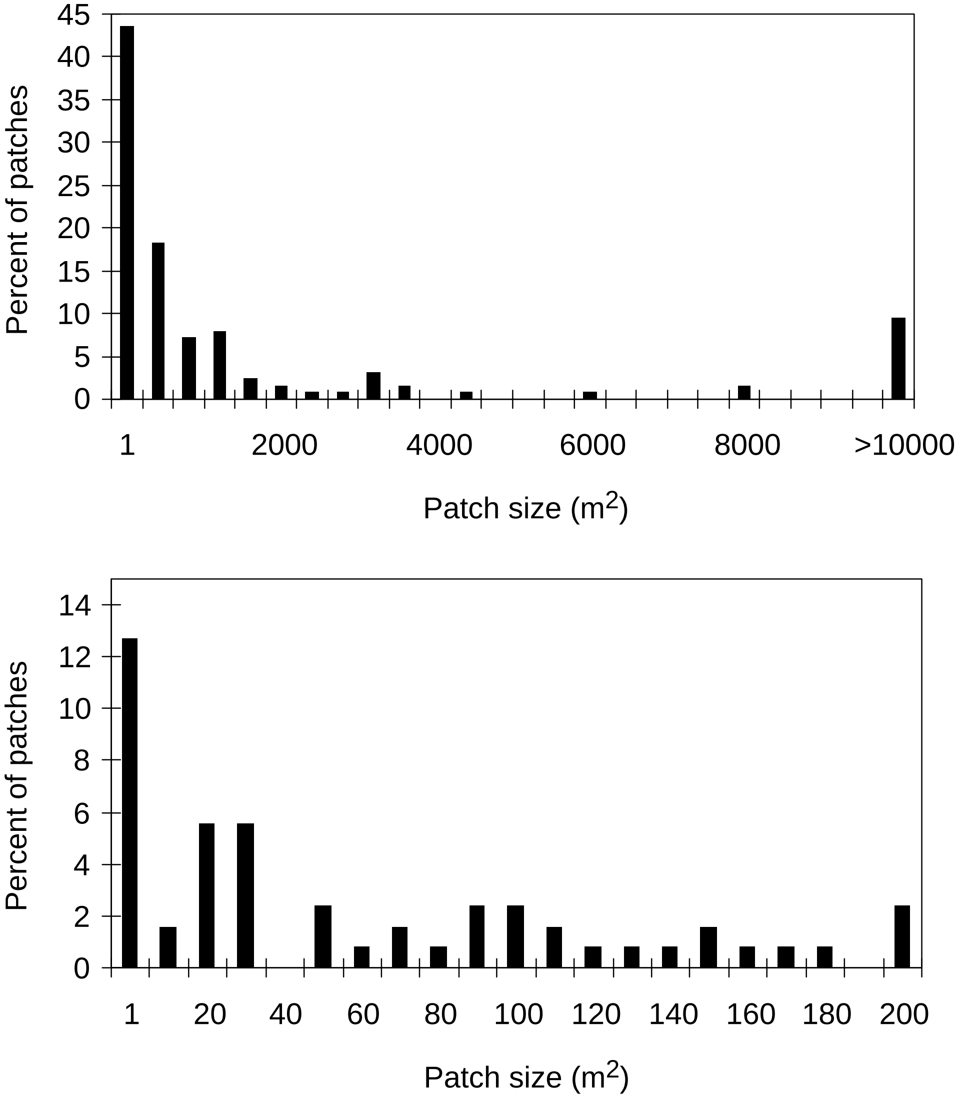

Figure 4—Distribution of patch size 1-10,000 m^2 (a, top graph) and 1-200 m^2 (b, bottom graph). Approximately 13% of all patches were smaller than 10 m^2 (b), which was the smallest patch detected by aerial photographs. Ten percent of all patches were >10,000 m^2 (a). Ground measurements of large patches were inaccurate, so remotely sensed data may be more suited to describe such patches.

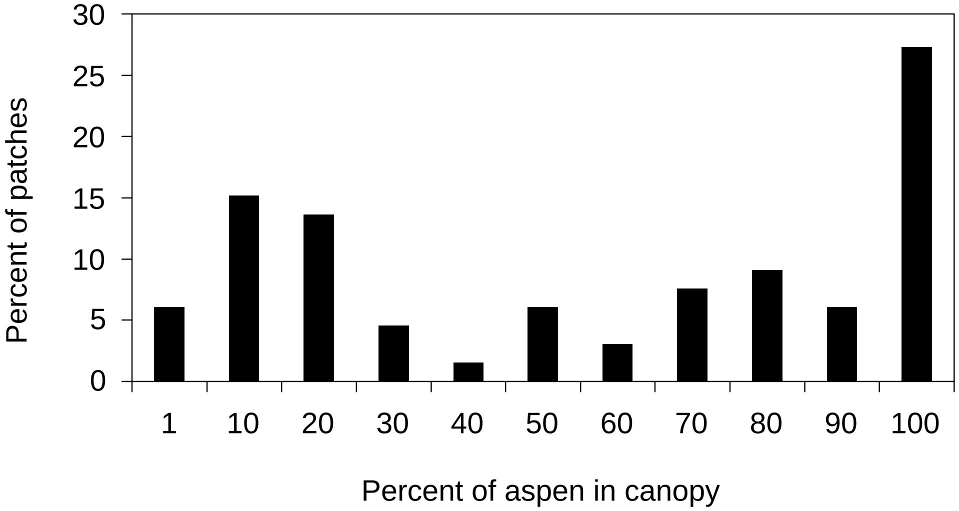

Figure 5—Percent of aspen in the canopy of aspen patches encountered in the belt transects. Twenty-eight percent of the patches had 100% aspen within the canopy, but 40% of the patches had less than 50% aspen in the canopy. The remaining species in the canopy are conifers.

reported by Baker et al. [1997]), we found two regenerating stands of aspen in Estes Valley. On the west side of the Park, stands sampled in the elk winter range (Kawuneeche Valley) showed no cohort establishment since 1926. Aspen regeneration was strong in many areas of the elk winter range, except for Estes Valley and Kawuneeche Valley. Elk density is extremely high in Estes Valley, where >90% of elk in the Park spend the winter (Larkins 1997). The winter elk population is much lower in Kawuneeche Valley, but summer use is very heavy (Larkins 1997).

The unbiased ground survey allowed us to compare the condition of aspen in the elk winter and summer ranges. The only significant difference we found between aspen in the two ranges was the percent of bark browsed. Wounds created by elk browsing on aspen bark and cambium allow for the introduction of pathogens into the stem. Consequently, bark browsing may affect the long-term condition of aspen patches by increasing aspen mortality due to disease. However, current measurements of aspen stands in the winter range show that neither stand density nor basal area have been affected by elk browsing. Interestingly, bark browse is the most visible characteristic we measured in aspen patches. The higher amount of bark browsed in the elk winter range could lead to unfounded alarm over the status of aspen in this area.

Other aspen patch characteristics such as regeneration, density, and basal area were not statistically different between the two ranges. Our values of regeneration from the ground survey may over-represent the amount of successful regeneration that occurs in the Park. Stems that are under 2 m in height are susceptible to elk browsing and self thinning (Brown and DeByle 1987), so many of the short stems may not successfully grow into the canopy. However, the high densities of stems shorter than 2 m indicate that aspen has the potential to recruit new stems into the canopy. White et al. (1998) suggested that declining aspen stands would have low density (<500 stems/ha). We found that aspen in the elk winter range, where we expected aspen decline due to intense elk browsing, had average densities of 1,339 stems/ha. This average density in the elk winter range falls within the range of known values for aspen in the Rocky Mountains (Kemperman and Barnes 1976), as do our values of basal area (Brown and DeByle 1987; Chen et al. 1998; Peet 1988).

Data from the ground survey showed that there is more aspen in the central portion of the Park than previously expected. Aspen covers 6.8% of the landscape, which is approximately three times more aspen than detected by remotely sensed data. Over a third of the aspen patches encountered in the ground survey had more conifer stems in the canopy than aspen. These patches may be difficult to detect with remotely sensed data. The smallest patch identified with aerial photographs (1:15,800) was 10 m^2. Over 10% of the patches that we encountered were smaller than 10 m^2. These patches may not contribute much to the total percent cover of aspen in the Park and they are not likely “hotspots” of diversity, but they represent the source of aspen available on the landscape. Aspen is a clonal species that quickly colonizes canopy openings (Parker and Parker 1983). In the case of a forest disturbance such as fire, windstorms, or insect outbreaks, these small aspen patches may quickly invade the disturbed area and create larger aspen stands.

Conclusions

Based on the presence of aspen regeneration in the elk winter range and lack of significant differences in aspen characteristics between the elk winter and summer ranges, we did not find enough evidence to support our hypothesis that that the effects of elk browsing were greater in the elk winter range than the summer range. Therefore, we reject our hypothesis. Suzuki et al.'s (1999) study showed that elk browsing has affected aspen regeneration in local areas such as Estes Valley. At larger spatial scales, there is no evidence that elk browsing has prevented aspen regeneration in the elk winter and summer ranges in Rocky Mountain National Park during the past 25 years. The unbiased ground survey provided evidence that elk browsing in the winter range has not brought about a change in stand characteristics when compared to the summer range where elk use is less intense.

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Sustaining Aspen Productivity in the Lake States

Douglas M. Stone[1]

Abstract—*Sustaining forest productivity requires maintaining soil productivity. Management activities that decrease soil porosity and remove organic matter can reduce productivity. We determined effects of three levels of organic matter removal (OMR) and soil compaction on aspen regeneration and growth following winter harvest of aspen-dominated stands in northern Minnesota, western Upper Michigan, and northern lower Michigan. The OMR treatments were merchantable bole harvest (MBH), total tree harvest (TTH), and total woody vegetation harvest plus forest floor removal (FFR). Compaction treatments were applied to increase surface soil bulk density by either 0, 15, or 30%. Sucker density increased with level of OMR on all three sites. On the sand site, mean diameter, height, and biomass were greatest with MBH and decreased with increasing OMR, indicating a potential decline in productivity with repeated total tree harvesting on sand soils. Soil compaction tended to increase mean sucker diameter and height on the sand, and decrease them on the fine-textured soils. Compaction greatly reduced sucker density and growth on the most productive silt-loam site, partially due to late spring treatment. These results apply to planning of operational harvest of aspen-dominated stands on similar soils throughout the northern Great Lakes region.*

Sustaining forest productivity over multiple rotations requires both maintaining soil productivity and prompt establishment of adequate regeneration. Forest management activities that decrease soil porosity and remove organic matter have been associated with declines in site productivity (Agren 1986; Greacen and Sands 1980; Grier et al. 1989; Standish et al. 1988). As part of an international network of cooperative studies on long-term soil productivity (LTSP) (Powers et al. 1990; Tiarks et al. 1993), we are evaluating effects of soil compaction and organic matter removal (OMR) in the aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.) forest type across the northern Lake States region and in northeastern British Columbia (Kabzems 1996; Stone and Elioff 1998; Stone et al. 1999). The research is designed to determine how changes in soil porosity and organic matter content affect soil processes controlling forest productivity and sustainability; and secondly, to compare responses among major forest types and soil groups across the United States and Canada.

The objective of the Lake States studies is to monitor changes in soil properties following forest harvesting and application of the soil compaction and OMR treatments, and to measure responses by the forest regeneration and herbaceous vegetation. Fifth-year results from four treatments in a pilot study were reported earlier (Stone and Elioff 1998). This paper reports results on aspen development after five growing seasons on sites in northern Minnesota, western Upper Michigan, and northeastern lower Michigan.

Ecology and Management

In the Great Lakes region, aspen is an intolerant, rapidly growing, short-lived species that regenerates primarily by root suckers following removal of the

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parent stand (Perala and Russell 1983). Suckers exhibit more rapid early height growth than seedlings or sprouts of associated species, so they normally form the dominant overstory during the early and midstages of stand development. On medium and fine-textured soils, pure aspen stands are rare; most include a component of more tolerant, longer lived species typical of these sites in the absence of disturbance. Until the 1960s, aspen was considered a "weed" species and little was harvested (Graham et al. 1963), resulting in an unbalanced age class distribution. Over much of the region, a relatively small portion of the type is less than 30 years old, and a much larger proportion is older than 60 years. On most commercial forest land, aspen is managed for wood products or for a combination of fiber and wildlife habitat. Where wood production is a primary objective, the stands typically are harvested by a complete clearcut of all species and the aspen is regenerated from root suckers. Presumably, the procedure can be repeated and the aspen maintained indefinitely (Perala and Russell 1983), provided the root systems are not damaged by severe site disturbance during logging (Stone and Elioff 2000).

Methods

Stand and Site Conditions

Four sites were selected to represent a range of soil conditions and aspen productivity on national forests across the northern Lake States region (table 1). The overstory of each stand was dominated by mature aspen but included a codominant component, or a subcanopy of more tolerant conifer and northern hardwood species. The most productive site is on the Chippewa National Forest (NF) in north-central Minnesota. The study is located on the Guthrie till plain; the surface soils are silt loam, formed from a loess cap 30 to 40 cm deep, over clay loam till. Site index (age 50) for aspen is about 23 m (75 ft); the associated species were predominantly red maple (*Acer rubrum* L.), basswood (*Tilia americana* L.), sugar maple (*A. saccharum* Marsh.), northern red oak (*Quercus rubra* L.), and eastern white pine (*Pinus strobus* L.). The pilot study reported earlier is on the Marcell Experimental Forest (part of the Chippewa NF) and represents our medium site (Stone and Elioff 1998). The surface soils are loamy sand over clay loam till; site index is about 21 m (70 ft). Our medium- to low-quality site is on an outwash plain on the Huron NF in northeastern lower

Table 1—General characteristics of the aspen long-term soil productivity (LTSP) sites in the Lake States.

Installation date	National Forest	Relative productivity	General soil description	Approximate site index[a]	
				m	*ft*
1991	Marcell	Medium	Loamy sand/clay loam till at 110 cm; well drained	21	70
1992	Ottawa	Low	Deep, calcareous clay; moderately well drained	17-18	55-60
1993	Chippewa	High	Silt loam cap/clay loam till at 30 to 40 cm; well drained	23	75
1994	Huron	Medium to low	Deep, acid sands; excessively drained	19	62

[a] Aspen, age 50.

Michigan; the soils are deep, acid sands with a site index of about 19 m (62 ft). Both trembling and bigtooth aspen occur on this site, and the predominant associated species were red maple, red oak, white pine, and black cherry (*Prunus serotina* Ehrh.). The least productive site is on the Ottawa NF in western Upper Michigan. The study is on a glacial lake plain and the soils are moderately well-drained, calcareous, lacustrine clay; site index for aspen is 17 to 18 m (55 to 60 ft). White spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and red maple (*Acer rubrum* L.) made up about 35% of the pre-harvest basal area.

Design and Treatment

Three levels of harvest intensity and OMR and three levels of soil compaction were applied to 50 x 50 m (0.25 ha, 0.62 acre) plots in a complete 3 x 3 factorial design with three replications. The levels of OMR were: (1) merchantable bole harvest (MBH) to a 10 cm (4 inches) top diameter; (2) total aboveground tree harvest (TTH); and (3) total woody vegetation harvest plus forest floor removal (FFR). The FFR treatment was included to represent those areas in skid trails and landings where most or all of the forest floor materials are removed during harvest. It also could provide an indication of productivity trends following repeated rotations of total tree harvesting. The compaction treatments were designed to provide: (1) no additional compaction above that due to harvesting; (2) light, to increase bulk density of the surface 10 to 20 cm of soil by 15%; and (3) "heavy," to increase bulk density of the surface soil by 30%. Four noncut control plots were installed in the adjacent stands, for a total of 10 treatment combinations on each site. Prior to harvest of each stand, the plots were established to minimize variation in soil properties and all trees ≥10 cm (4 inches) d.b.h. were measured and their location mapped.

Ottawa

The stand was harvested between 13 January and 3 February, 1992. During logging, snow depths averaged 76 to 91 cm (30 to 36 inches); the soils were not frozen. All merchantable stems were cut using a Caterpillar model C-227 feller-buncher with 61 cm (24 inches) tracks and placed in bunches between the plots. The bunches were immediately skidded to a landing with John Deere 648D, John Deere 740A, and Timberjack 450B grapple skidders. All skidder traffic was restricted to the areas between plots. The FFR treatment consisted of manually removing all coarse woody material and then removing the forest floor materials. The treatment was applied between 21 April and 21 May by inmate crews using fire rakes; the materials were piled outside of a 5- to 10-m-wide buffer zone surrounding each treatment plot. The compaction treatments were applied between 6 and 21 May by traversing the plots with a 20.9 Mg (23 ton) Hough model H-100 front-end loader with 63.5 cm (25 inches) tires, advancing one tire width each pass. Two passes at right angles provided the light treatment, and two passes with the bucket empty and two passes with the bucket filled with soil provided the heavy compaction.

Chippewa

The stands were harvested during January and February 1993. During November and December 1992, snowfall was somewhat greater than normal and mean monthly temperatures were slightly above average. Thus, soil frost was discontinuous initially, and ranged from 5 to 10 cm (2 to 4 inches) when logging was completed. Snow depth increased from about 30 cm (12 inches) initially to 46 cm (18 inches) during the logging operation. On the noncompacted plots, the trees were felled with chainsaws and winched off the plots with a cable skidder located outside the plot boundaries. On all other plots, the stems were cut with a Case-Drott model 40 feller-buncher and placed outside the plot boundaries; skidders did not enter any of the plots. The FFR treatment consisted of manually removing all coarse woody material and windrowing the forest floor materials, using a power-driven sidewalk sweeper with a revolving wire brush head 46 cm (18 inches) in diameter and 90 cm (36 inches) wide; the materials were piled outside of the 5- to 10-m-wide buffer zone surrounding the treatment plots. The light compaction treatment consisted of a double pass, at right angles, across the plots with a model D-7 Caterpillar tractor, advancing one track width (61 cm) each pass. The heavy compaction treatment included the light treatment followed by a double pass with a Michigan model 75C front-end loader with 52 x 63.5 cm (20.5 x 25 inches) tires, advancing one tire width each pass.

Huron

The stands were harvested in late January 1994; the winter was colder than normal, with several days below –30 °C (–20 °F). During harvest, the surface 20 to 25 cm (8 to 10 inches) of soil was frozen and covered by 35 to 40 cm (14 to 16 inches) of snow. All merchantable stems were cut with a tracked Bobcat shear on the noncompacted plots, and with a Hydro-Ax feller/buncher on the rest of the units, and skidded using a Caterpillar 518 and a Timberjack 380B grapple skidder. Tops from the MBH plus compaction treatments were piled adjacent to the plots and replaced after the compaction treatments were completed. In mid-April, the coarse woody debris and forest floor materials were removed using the same methods as on the Chippewa, and piled outside the 5- to 10-m-wide buffer zone around each treatment plot. In late April, when the soil was at field capacity, the compaction treatments were applied using a 9.5 Mg (10.5 ton) Hough model 60 front-end loader with 44.4 x 63.5 cm (17.5 x 25 inches) tires, advancing one tire width each pass. The light compaction treatment was accomplished with a single pass of the loader with a tire pressure of 172 kPa (25 psi). The “heavy” compaction treatment included the light treatment plus a second pass of the loader, at right angles, with the bucket filled with sand and tire pressures of 276 kPa (40 psi). This provided a total machine weight of about 12.7 Mg (14 tons).

Measurements and Analyses

On each site, all measurements and sampling were made within the interior 40 x 40-m area of each treatment plot. In late July to early August, the fifth-year aboveground herbaceous vegetation was collected from four 1.0-m^2 subplots per plot, dried at 75 °C, and weighed. In September or October, after five growing seasons, the basal diameter of all woody stems (>15 cm height) was measured and recorded by 2-mm diameter classes on eight 5.0-m^2 subplots per plot. Mean height of aspen suckers in each diameter class was recorded to the nearest 5-cm class. Aboveground biomass was estimated using allometric equations developed by Perala and Alban (1994). The form of the equations is:

Component weight = Constant*D15 ^ b*Age ^ c*Soil (and other treatment multipliers),
where weight = g, D15 = mm, and Age = years.

For each site, all subplot data were composited, and treatment effects were evaluated by analysis of variance of the plot-level means. First, the overall effects of compaction level, OMR, and compaction-OMR interactions were evaluated. Few of the interactions were significant, so the effects of OMR were evaluated across compaction levels, and effects of compaction were evaluated across levels of OMR. Comparisons among means were made with the Least Significant Difference procedure at the 95% confidence level (Analytical Software 1998).

Results and Discussion

Organic Matter Removal

Stand Density

Winter harvesting by MBH produced abundant aspen regeneration on all three sites. After five growing seasons, sucker density ranged from 10,000 (10 k) to 22 k ha^{-1} (figure 1). With uniform distribution, the 10 k stems ha^{-1} on the Chippewa is equal to a 5-yr-old sucker on every m^2 of the site. The TTH and FFR treatments further increased sucker density, frequently at the expense of the associated commercial species. The differences were marginally significant ($p = 0.102$) on the clay soils on the Ottawa, highly significant on the silt loam on the Chippewa, and nonsignificant on the sand soils on the Huron. Graham et al. (1963) considered first-year sucker density of 15 k ha^{-1} as minimal stocking and 30 k ha^{-1} as optimal. The FFR treatment resulted in a first-year sucker density of >260 k ha^{-1} on the loamy sand site in northern Minnesota (Alban et al. 1994), and about 220 k ha^{-1} in British Columbia (Kabzems 1996), most likely due to increased soil temperatures and removal of competing vegetation (Kabzems 2000b). By the fourth year, sucker density had declined to about 55,000 ha^{-1} in British Columbia (Kabzems 2000a), and by the fifth year, to about 40 k ha^{-1} in Minnesota (Stone and Elioff 1998).

Diameter

Mean basal diameter (at 15 cm) tended to be greater with TTH on the fine-textured soils, although the difference between MBH and TTH was not significant on the Ottawa clay (figure 2). The aspen on the Huron sands responded differently than those on the other sites. Both trembling and bigtooth occur on this site, but the differences in diameter and height were not significant, so they were analyzed together. Mean diameter was significantly greater with

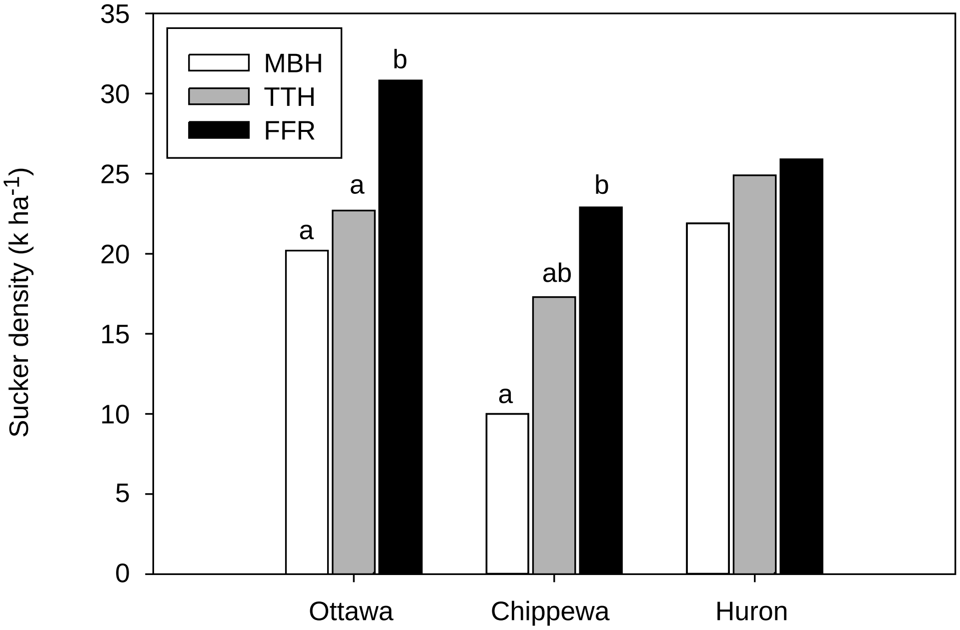

Figure 1—Mean sucker density by harvest intensity and level of organic matter removal; MBH, merchantable bole harvest; TTH, total tree harvest; FFR, total woody vegetation and forest floor removal. (Within sites, bars with the same letter, or without letters, do not differ significantly at the p = 0.05 level.)

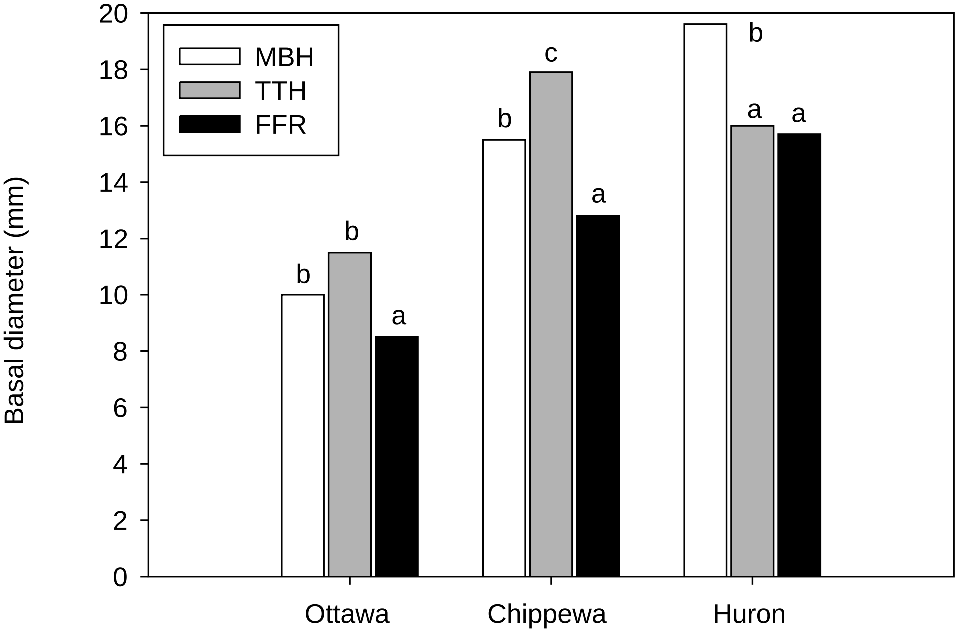

Figure 2—Mean basal diameter (15 cm) by harvest intensity and level of organic matter removal.

the MBH treatment and tended to decline with increasing level of OMR, as indicated by the fourth-year data (Stone et al. 1999). The smallest mean diameters occurred with the FFR treatment on all sites, indicating a potential problem of sustaining productivity with repeated total tree harvesting, particularly on sand soils.

Height

On the fine-textured soils, mean sucker height on the TTH plots was significantly greater than the MBH plots (figure 3). As with diameter, mean sucker height on the sand site was significantly greater in the MBH treatment and tended to decline with increasing level of OMR. This raises the question of whether the additional biomass removed by total tree harvesting is worth the cost in soil resources—nutrients, organic matter, and water-holding capacity (Stone et al. 1999). On both the Chippewa and Huron sites, the lowest mean height was in the FFR treatment, partially due to high sucker densities and the resulting intraclonal competition. Stone et al. (these proceedings) found that retaining 18 to 38 dominant aspen ha^{-1} (7 to 15 $acre^{-1}$) reduced first-year sucker density by >40% and increased basal diameter and height growth by about 30%.

Biomass

Dry weight production per unit area integrates sucker density, diameter, and height in a single value. On the fine-textured soils, aspen dry weight was nonsignificantly greater with TTH (figure 4). On these sites, the TTH treatment produced intermediate sucker densities with greater mean diameter, height, and dry weight, while total woody vegetation plus FFR produced greater numbers of suckers, but with lower mean diameter, height, and dry weight. On the sand site, MBH produced the lowest number of suckers with significantly greater mean diameter and height and dry weight. The differences among sites were much greater than the treatment effects within sites. For example, mean fifth-year aspen dry weight on the sand was more than three times that of the clay, and that on the silt loam was about four times as great.

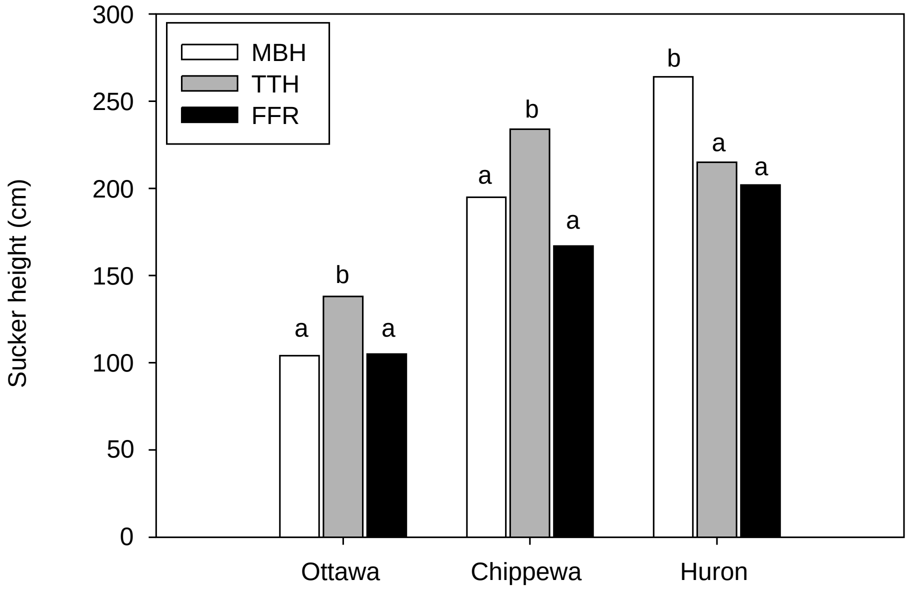

Figure 3—Mean sucker height by harvest intensity and level of organic matter removal.

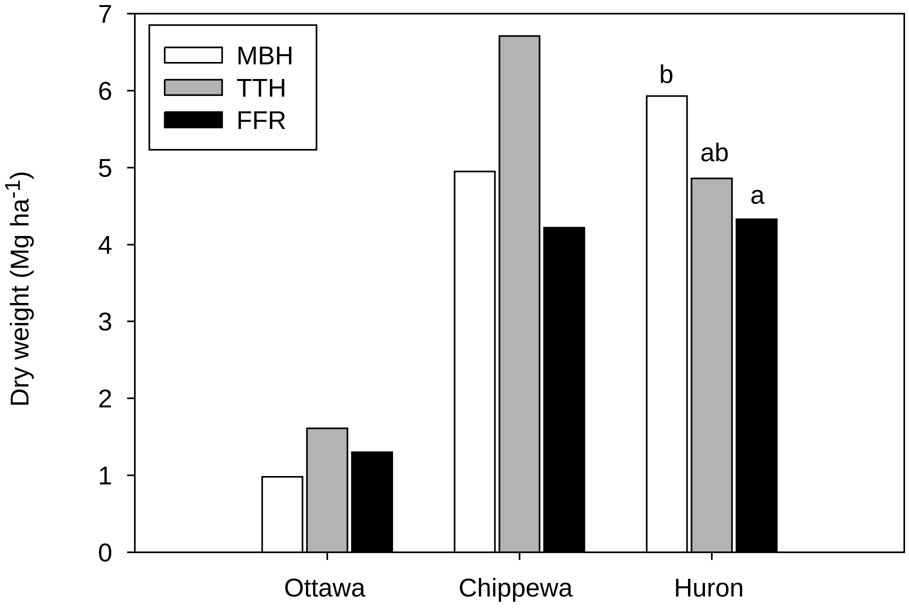

Figure 4—Mean aspen biomass by harvest intensity and level of organic matter removal.

Soil Compaction

The objective of the compaction treatments was to increase bulk density of the surface soil by either 15 or 30% without damaging the root systems by rutting. This was accomplished successfully on the Marcell, Ottawa, and Huron sites. However, spring and early summer rainfall were higher than normal in 1993 and delayed study installation on the Chippewa. The frequent rainfall, and the desire to avoid rutting, caused numerous delays in application of the treatments. Thus, the suckers had begun to emerge by the time the soil had drained sufficiently to complete the compaction treatments, and many were broken by the machine traffic.

Stand Density

As with the FFR treatment, soil compaction also increased mean sucker density on the clay and sand sites, and after five growing seasons the differences are still significant on the clay (figure 5). The compaction treatments also tended to increase first-year sucker density in the British Columbia study, but by the fourth year there were no differences by level of compaction (Kabzems 2000a). Presumably, these increases are due to root injury during compaction. Disturbance of aspen root systems and increased soil temperatures are known to stimulate sucker production (Schier et al. 1985; Peterson and Peterson 1992). Soil compaction significantly decreased sucker density on the Chippewa installation, primarily because of the late spring treatment. On this site, effects of the compaction treatments on reducing sucker density were dramatic, and not unlike many operational logging jobs in the northern Great Lakes region (Bates et al. 1990, 1993).

Diameter

Soil compaction tended to decrease mean diameter of suckers on the fine-textured soils, but the differences were significant only on the Chippewa (figure 6). The decreased growth on these sites most likely is due to a combination of direct and indirect effects (Greenway 1999). Sucker growth could be reduced directly by reduced soil aeration, and indirectly by the increased sucker density. In contrast, the compaction treatments tended to increase mean basal diameter on the Huron sands, despite the substantially greater stand density (figure 5). Low to moderate levels of compaction will convert a portion of the macropore space to micropores, thereby increasing the water-holding capacity of the soil, thus decreasing water stress in the regeneration (Powers and Fiddler 1997; Powers 1999). We emphasize that these experimental levels of compaction are well below those encountered on major skid trails and landings found on conventionally harvested sites (Stone et al. 1999). On those areas, we have measured substantial reductions in both sucker density and growth. Moreover, the effects are likely to persist for decades (Grigal 2000).

Height

As with diameter, the compaction treatments tended to decrease mean height of suckers on the fine textured soils, but the differences were significant

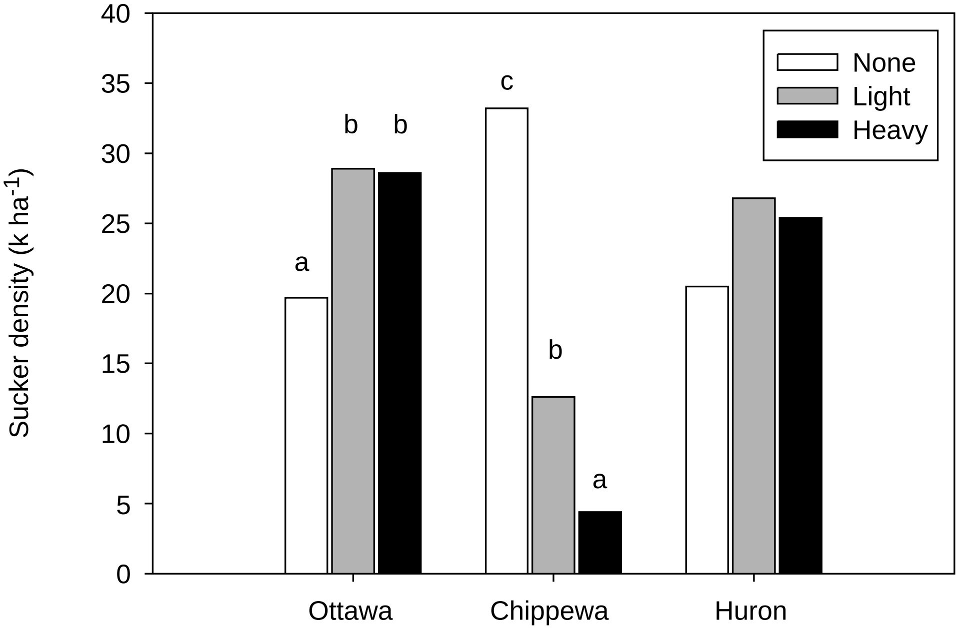

Figure 5—Mean sucker density by level of soil compaction.

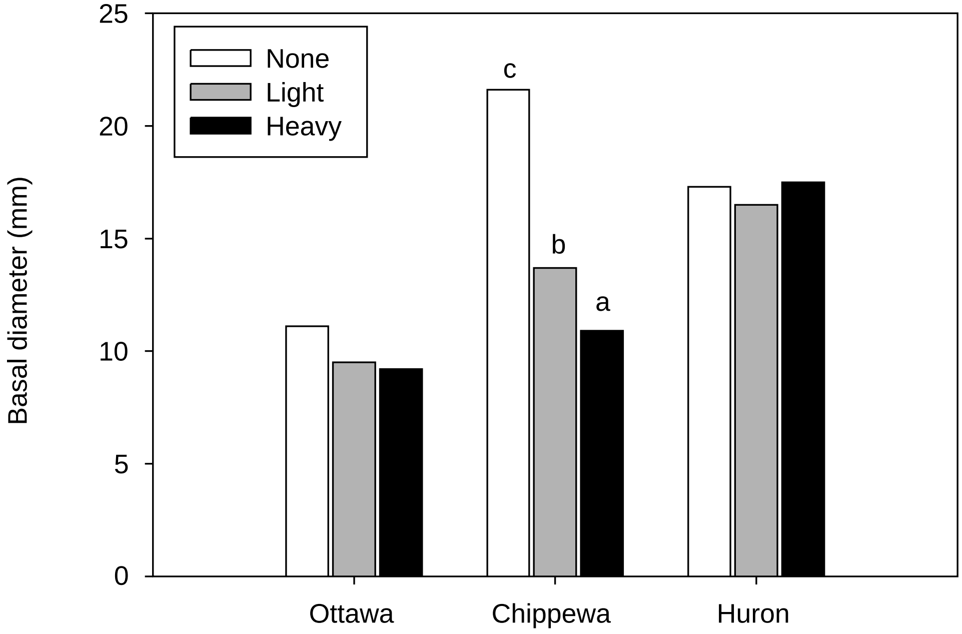

Figure 6—Mean basal diameter by level of soil compaction.

only on the Chippewa (figure 7). Likewise, the decrease can be attributed to the combination of reduced soil aeration and increased sucker density. On the Huron sands, increased water-holding capacity of the soil and decreased water stress in the suckers would account for the small but consistent increases in sucker height with level of compaction.

Biomass

The compaction treatments produced little difference in dry weight of aspen on the clay soil, but dramatic differences on the silt loam, primarily due to the

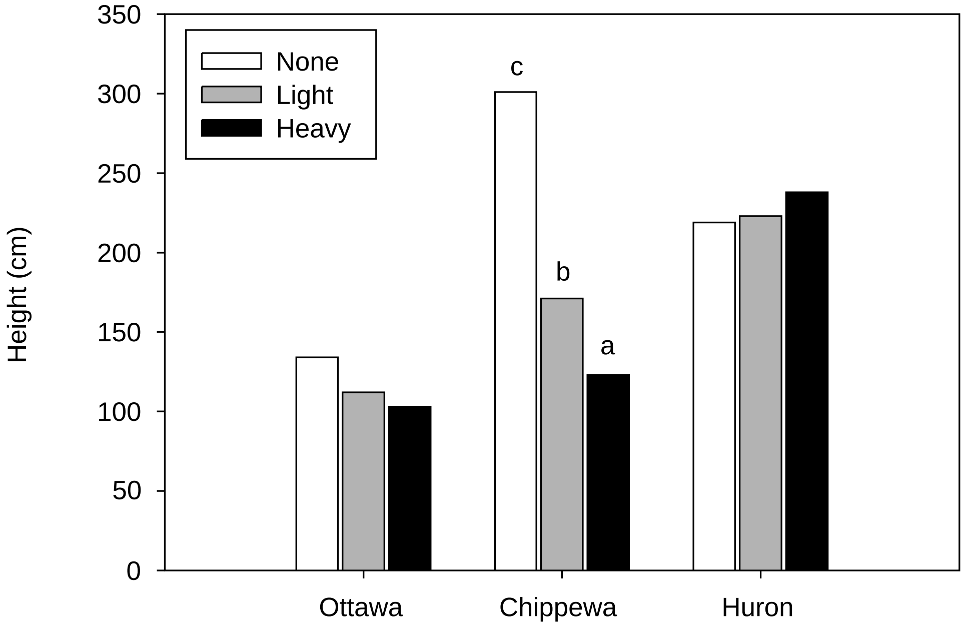

Figure 7—Mean sucker height by level of soil compaction.

delayed application of the treatments (figure 8). On these clay sites, rutting has been more detrimental to aspen regeneration and growth than has compaction (Stone and Elioff 2000). On the sand site, compaction resulted in slight, but nonsignificant increases in aspen biomass. Again, the differences among sites were far greater than those of the compaction treatments. Comparison of the noncompacted plots, for example, illustrates a 10-fold difference in potential aspen productivity between the least productive clay soil and the most productive silt loam. Likewise, despite the relatively small (<5 ft) difference in aspen site index, fifth-year aspen biomass on the sand was nearly four times that on the clay site.

Summary and Management Implications

Organic Matter Removal

Harvest intensity and OMR significantly affected one or more of the regeneration parameters on each site, and the responses differed greatly by site. These fifth-year data illustrate much larger differences in productivity between sites than might be expected from site index data. Increasing levels of OMR increased sucker density on all sites. On the fine-textured soils, fifth-year sucker diameter and height were greater in the TTH treatment. On the sand soil, both the TTH and FFR treatments significantly reduced mean diameter and height. In fact, the FFR treatment generally showed the smallest diameter and height on all three sites. Treatment differences in fifth-year aspen biomass were not significant on the fine-textured soils, but declined significantly with increasing level of organic matter removal on the sand. This raises the question of whether the additional biomass gained by total tree harvesting is worth the cost in soil resources—nutrients, organic matter, and water-holding capacity. The question also needs to be addressed in other forest types that occur on sand soils, such as jack pine (*Pinus banksiana* Lamb.) in the upper Great Lakes region.

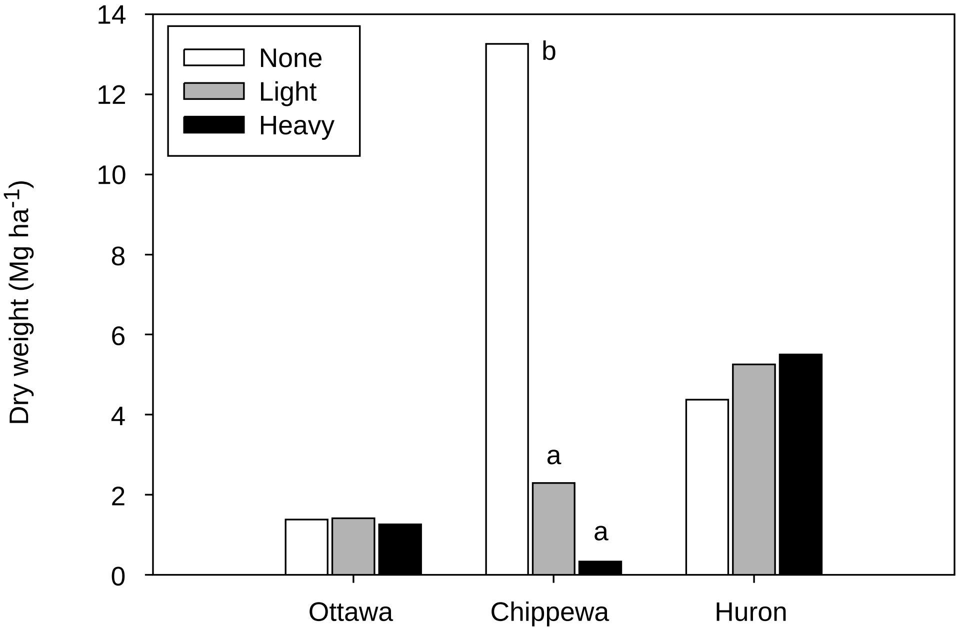

Figure 8—Mean aspen biomass by level of soil compaction.

Soil Compaction

Responses to soil compaction also differed greatly among sites. Compaction prior to sucker emergence tended to increase sucker density, but after they had emerged, machine traffic drastically reduced sucker density, diameter and height growth, and biomass production; the differences were highly significant after five years. Compaction on the clay site produced small, but nonsignificant reductions in sucker diameter and height. On these kinds of soils, rutting has shown greater impacts on aspen regeneration and growth than has compaction. In contrast, the levels of compaction applied on the sand site produced small, but nonsignificant increases in sucker diameter, height, and biomass. However, the more severe compaction that routinely occurs on major skid trails and landings severely reduces both sucker density and growth. Moreover, the effects are likely to persist for decades. Thorough pre-harvest planning is required to designate these areas—and to minimize the area affected—in order to sustain the future productivity of these sites.

Acknowledgments

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Predation Risk and Elk-Aspen Foraging Patterns

Clifford A. White[1] **and Michael C. Feller**[2]

Abstract*—Elk-aspen foraging patterns may be influenced by cover type, distance from roads or trails, the type of user on road or trail (park visitor, human hunter, or predator), and two general states of aspen condition (open-grown or thicket). Pellet group and browse utilization transects in the Canadian Rockies showed that elk were attracted to roads used by park visitors and avoided by wolves, and that elk possibly avoided aspen and conifer patches near backcountry trails used by wolves. In high predation risk landscapes, aspen stands were dense, lightly browsed, and rarely entered by elk. As risk decreased, elk density and aspen browsing increased proportionally faster on edges of aspen stands compared to the interior of aspen stands. In low risk landscapes, edge and interior plots were intensively used, and stands had a low density of heavily browsed stems. Regeneration of aspen stands likely requires low densities of risk-sensitive elk.*

Introduction

Trembling aspen (*Populus tremuloides*) is an indicator species for low elevation, montane ecoregions in Rocky Mountain national parks (Achuff et al. 1996; White et al. 1998a). Aspen stands are typically long-lived clones, regenerated by frequent fires (Mitton and Grant 1996; Kay 1997a). In the Rocky Mountains, aspen communities are second only to riparian zones for species richness (DeByle 1985a; Finch and Ruggiero 1993). Aspen stands historically had a range of age and size classes (Gruell 1979; Houston 1982). However, since the late 1800s to 1930s (depending on the location), new aspen stems have rarely grown to heights >1 m on elk (*Cervus elaphus*) winter ranges in several national parks and wildlife refuges (Packard 1942; Cowan 1947; White et al. 1998a) including Yellowstone National Park (Houston 1982; Kay 1990; Romme et al. 1995), near Jackson Hole, Wyoming (Gruell 1980; Boyce 1989), in Rocky Mountain National Park, Colorado (Olmsted 1979; Baker et al. 1997), Banff and Jasper National Parks in Alberta (Kay et al. 1999), and Yoho and Kootenay National Parks in British Columbia (Kay 1997b).

The factors responsible for aspen decline (figure 1) remain controversial (Kay 1997a; Huff and Varley 1999) but there are three broad theories for long-term aspen condition (Keigley 1997; Singer et al. 1998):

1. Heavily browsed aspen stands persisted under intense herbivory by abundant, food-regulated elk (Romme et al. 1995; Boyce 1998). This is termed ecological carrying capacity (Caughley 1976, 1979). The current decline of aspen is simply a return to long-term conditions as elk populations recover from overhunting by humans during the late 1800s. Episodic events such as a combination of cool-moist climate and fire could result in pulses of aspen stems periodically reaching tree size (Romme et al. 1995).

2. Aspen was historically vigorous, lightly browsed, and coexisted with moderate to high densities of elk, but has recently degenerated due to the combination of herbivory, fire suppression, and possibly climate change (Gruell 1979, 1980; Houston 1982).

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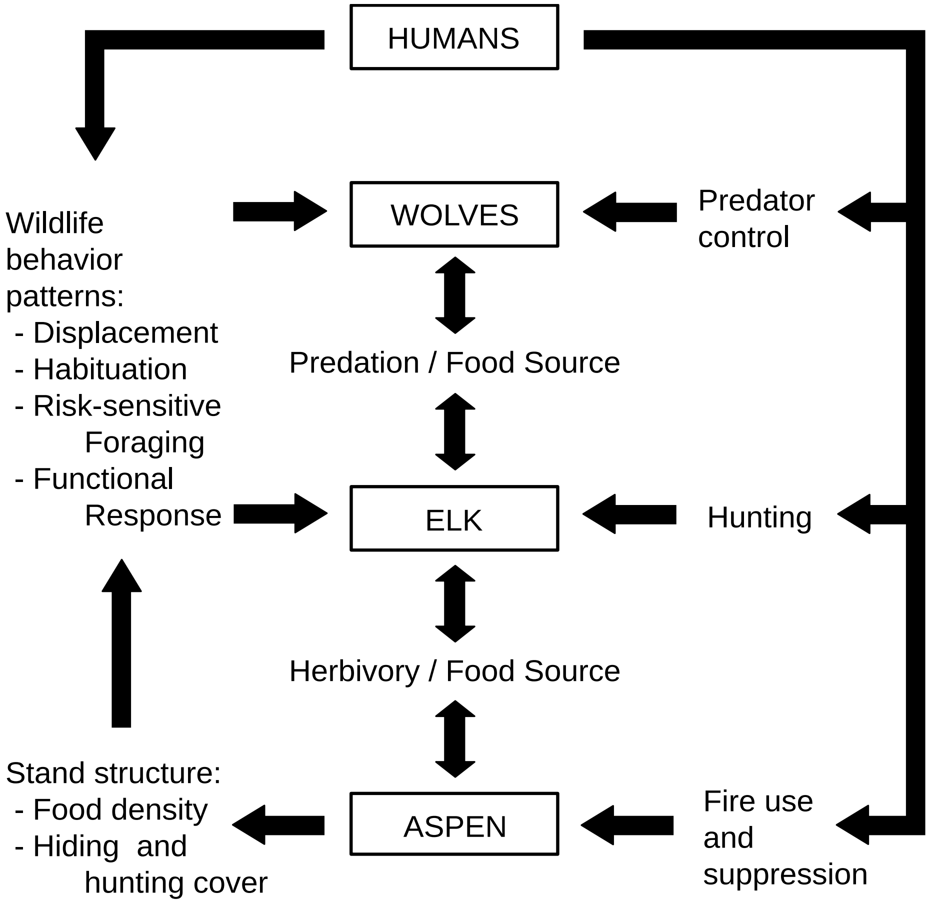

Figure 1—A trophic-level model for interactions between humans, wolves, elk, and aspen.

3. Aspen persisted under conditions of low elk density and herbivory (Packard 1942; Cowan 1947; Olmsted 1979), maintained by intense predation on elk from humans, wolves, and other carnivores (Kay 1990, 1998; White et al. 1998a,b).

Analysis of aspen abundance, fire effects, and historical and current elk distribution patterns in Rocky Mountain national parks (Kay 1990; White et al. 1998a; Ripple and Larsen 2000) provided support for hypothesis 3; recent (since about 1900) reductions of predation rates on elk have resulted in increased elk herbivory on aspen. If this hypothesis is valid, predators could influence the elk-aspen herbivory interaction in two ways: first, the lethal effect of killing elk thus reducing elk density and herbivory; and second, the nonlethal effects where predation risk alters elk behavior in ways that reduce herbivory on aspen (figure 1). Direct effects on aspen due to general elk density and browsing levels are significant (Olmsted 1979; Kay 1990; White et al. 1998a). However, nonlethal consequences of predation risk are also important influences on animal foraging behaviors (Lima and Dill 1990; Lima 1998; Kie 1999). After reviewing historical conditions in Yellowstone National Park, Ripple and Larsen (2000) hypothesized that elk behavioral responses to wolves could have influenced aspen herbivory levels in riparian areas of Yellowstone National Park.

In this study we explored two possible effects of predation risk on elk foraging patterns on aspen during winter (October through March): (1) effects of travel routes used by predators (humans and wolves) on elk habitat use; and (2) effects of aspen stand structure (thicket versus open-grown) and predation or hunting risk on elk foraging behavior. We test the general hypothesis that these nonlethal effects are important determinants of aspen condition.

Theory and Predictions

Plants and large mammalian herbivores have two-way interactions (Noy-Meir 1975; Caughley 1976; Schmitz and Sinclair 1997). Plants provide food, shelter, and cover for herbivores and their predators. Herbivores alter plants or their habitats directly by feeding and trampling on plant parts, and indirectly by nutrient additions through defecation and urination (Hobbs 1996; Augustine and McNaughton 1998).

Predation Theory

Elk browsing rates on aspen appear to increase with decreasing stem density (Debyle 1985a,b; Kay and Wagner 1996; C. White, unpublished data). In predation theory, this is described as a Type 2 functional predation response (Holling 1959; Taylor 1984). Type 2 functional responses are common in simple one predator-one prey herbivory systems (Lundberg and Dannell 1990). However, in the multi-prey, elk-aspen situation, where numerous alternative plant forage species are readily available, the Type 2 response indicates that aspen is highly preferred by elk. High priority prey will be used even at low densities, and may have few refuges from predation (Pech et al. 1995; Sinclair et al. 1997; Augustine and McNaughton 1998). The high value of aspen as ungulate forage has been noted in other studies (e.g., Nelson and Leege 1982; Hobbs et al. 1982; Dannell et al. 1991). DeByle (1985b) described increased browsing rates when aspen stem densities are low. In Yellowstone National Park, Kay and Wagner (1996) found that ongoing high herbivory had reduced most aspen clones to low numbers of heavily browsed stems, and for approximately one-third of aspen stands shown in early photographs, both the stems and roots appeared to have completely died out.

Olmsted (1979) estimated that the twig browsing threshold between viable and declining aspen stands occurred when approximately 30% of current annual growth was browsed. Theoretically, the Type 2 functional response will cause this threshold to be a curved isoline for a range of aspen and elk densities (figure 2). At high aspen stem densities, per elk twig consumption declines, and

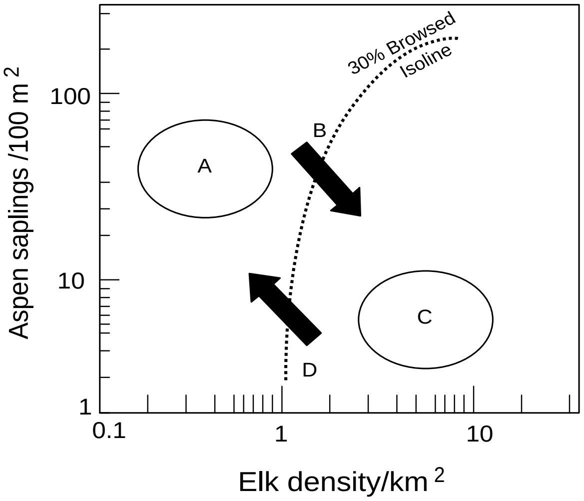

Figure 2—A state and transition model of aspen sapling density as a function of elk density. Stands near A have abundant aspen saplings, and stands near C have few saplings. Transitions between states occur near the 30% browsed isoline and are shown by arrows at B and D.

aspen can sustain a higher density of elk. The curvilinear response could result in elk-aspen herbivory being approximated by a state-and-transition type model (e.g., Noy-Meir 1975; Walker et al. 1981; Westoby et al. 1989). Aspen would have two general alternative states (Gruell 1980; Kay 1990; White et al. 1998a): dense sapling (stems 2 to 6 m height) thickets (around A in figure 2), and few saplings (around C). The transitions (at B and D) between states could be rapid but have different pathways and mechanisms depending on the direction of change. At high aspen sapling density (A), elk density could be moderate (e.g., 1 to 3 elk/km^2; White 1998a) with aspen sapling survival because the per capita elk foraging rate is lower in denser sapling stands. The transition toward few, heavily browsed aspen saplings probably occurs around B at 3 to 5 elk/km^2, or 1 to 2 elk pellet groups/100 m^2 (White et al. 1998a; C. White, personal observation). At low aspen sapling densities (C), per elk foraging rates on suckers and saplings would be high (DeByle 1985a,b). Elk densities might have to be <1 elk/km^2 (<1 pellet group/100 m^2) for stands to cross the transition at D toward more abundant aspen saplings (White et al. 1998a).

In traditional predation theory (Holling 1959), a Type 2 response is attributed to the limitations imposed by handling time, which for herbivores is a complex set of interactions between the competing activities of searching, biting, cropping, and chewing (Spalinger and Hobbs 1992). However, an alternative explanation is reduced herbivore foraging rates when higher vegetation density increases predation risk (Fritz 1992; Hare 1992).

Risk-Sensitive Foraging

Three-level trophic communities (predators-herbivores-plants) are influenced by multi-way interactions (Price et al. 1980; Hunter and Price 1992; Fryxell and Lundberg 1997; Krebs et al. 1999) that may change herbivore abundance or behavior and hence regulate community structure (Hairston et al. 1960). Predation-sensitive foraging models are based on tradeoffs between the benefits of energy intake and the costs of a shortened reproductive life due to predation (Sih 1987; Lima and Dill 1990; Lima 1998). Successful herbivores should utilize their environments in ways that balance safety with feeding. In situations where predation risk is low, animals should forage in high-resource habitats where energy intake is maximized. If predation risk is high in these habitats, however, safer locations with less forage availability may be used. In situations where low-resource habitats are risky, animals should concentrate in better habitats until resources are greatly depleted (Fryxell and Lundberg 1997). Where three-level trophic systems have coevolved, development of plant structures that increase the risk of predation on herbivores, thus providing "enemy-free space" with low herbivory, could increase plant fitness (Price et al. 1980; Jeffries and Lawton 1984; Fritz 1992).

Elk and Predator Behavior Patterns

Previous research provides several areas of knowledge for potential elk-aspen foraging patterns under predation risk. First, studies of elk habitat use in the Rocky Mountains report a general cover type preference of grassland > aspen > conifer (Collins and Urness 1979; Houston 1982; Holroyd and Van Tighem 1983). Numerous studies rank aspen as a highly favored elk forage species (Nelson and Leege 1982). Aspen twigs, leaves, and bark have relatively high concentrations of important nutrients (Jelinski and Fisher 1991), and at northern latitudes they are a valuable food source for elk, particularly during winter (Hunt 1979; Rounds 1979). Second, wolves (*Canis lupus*) and humans, two of elk's dominant predators (Cowan 1947; Huggard 1993a; Kay 1994), have consistent travel corridors in the Rocky Mountains. Both species usually follow valley bottom trails or lightly used roads, and in winter they may utilize ice-covered streams (Carbyn 1974; Huggard 1993a; Paquet et al. 1996; Kunkel 1997). Wolves prefer trails with snow depths <20 cm (Huggard 1993b) and often follow routes packed or plowed by humans (Paquet et al. 1996). Third, in areas with low herbivory, recently disturbed aspen stands and the edges of older stands often have dense patches (<1 m spacing) of young stems (DeByle 1985a; Shepperd and Fairweather 1994). These thickets could provide cover for stalking carnivores such as cougar (*Felis concolor;* Kunkel et al. 1999) and impede elk escape if predator attack does occur (e.g., Lima 1992). Finally, an important elk defense against predation may be group foraging in open areas where stalking predators such as cougars are more detectable (Kunkel et al. 1999) and elk have running room to escape (Geist 1982). Also, in the Rocky Mountains, snow depths are often lower in wind-swept open areas, which increase elk's ability to forage (Skovlin 1982; Lyon and Ward 1982) and escape predation (Huggard 1993b).

These previous observations suggest that patterns of elk and predator foraging could occur in spatially nested scales (Senft et al. 1987; Bailey et al. 1996), which for this study we characterize as landscapes, corridors, and patches (figure 3). At a macro-scale (>10 km^2), human land-use structures elk habitats into high-predation risk and low-predation risk landscapes. High risk landscapes could have wolves and human hunters. A low risk landscape could be a busy national park where elk are unhunted and predators are few such as the Bow Valley in Banff National Park, Alberta, or Rocky Mountain National Park in Colorado (White et al. 1998a). The landscape level defines general elk population densities and behavior patterns. At the meso-scale corridor level (1 to 10 km^2), trails, roads, and streams provide corridors for human and predator travel. Depending on the rates of human hunting and predator control, elk and predators may either be attracted to or avoid corridors near these travel routes (Lyon 1979; Dekker et al. 1995; Ripple and Larsen 2000). At the micro-scale (0.01 to 1 km^2) patch level, macro- and meso-scale phenomena determine

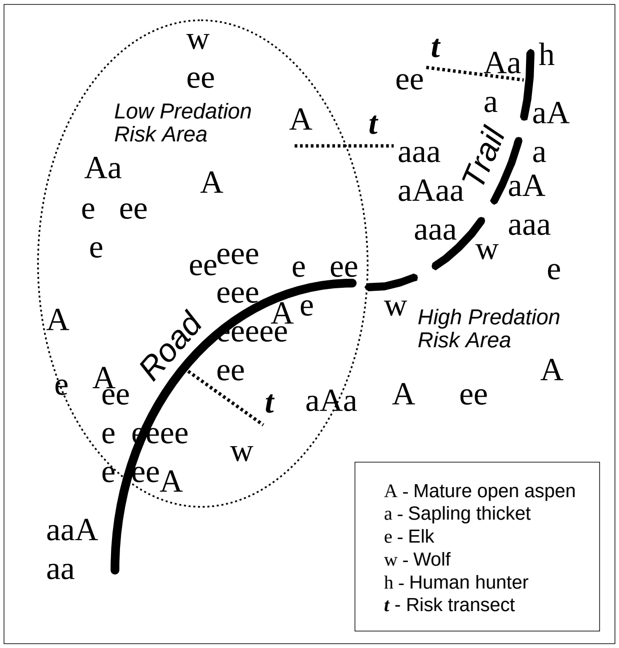

Figure 3—A spatial model of elk-aspen distribution patterns at 3 scales: macro-scale (high and low predation risk landscapes), meso-scale corridors (distance from road or trails), and micro-scale (aspen stand habitat patches). The stylized locations of the predation risk transects used in this study are shown with dotted lines.

differential elk foraging strategies within patches. For this study, these patch types include grass, aspen and conifer cover types, or dense aspen thickets versus open stands.

Predictions on Effects of Human and Predator Travel Routes

Given predator travel patterns, we predicted that in high predation landscapes (figure 3), elk will trade off food availability for safety, and forage relatively less in corridors next to trails used by wolves and humans than at distances farther from trails (table 1). For example, in studies of human-hunted elk, significant reduction in elk use (>60%) was found up to at least 500 meters from roads in Montana (Lyon 1979), and within 200 meters from roads in Colorado (Rost and Bailey 1979). In contrast, in low predation risk landscapes, elk are often unhunted and human-habituated (White et al. 1998a). They should be attracted to corridors next to busy roads avoided by wolves (Dekker et al. 1995; Paquet et al. 1996). The differential effect of trails or roads on elk use should be evident as an interaction (table 1) between the effects of landscape type (high or low risk) and distance from road or trail (close, moderate, or far).

At the patch level, nested within corridors, we expected a response of elk use to interactions between region, distance from road or trail, and cover type (table 1). As risk increases, elk selectivity for grassland cover, which is most preferred by elk and could offer the safest foraging areas, should increase while low resource-value conifer habitats should most rapidly be abandoned (Houtman and Dill 1998; Fryxell and Lundberg 1998). Aspen habitats, with intermediate value, should have intermediate trends.

Predictions on Effects of Aspen Stand Structure

At the micro-scale level, elk use of aspen patches in comparison to the surrounding matrix of grassland can be viewed as an integrator of local habitat preference, competition, and predation risk (Brown 1988). In landscapes with high predation risk, low elk density, and abundant forage in grasslands (A in figure 2), we predicted that dense aspen sapling thickets, which could provide cover for predators, would rarely be entered by risk-sensitive elk (table 2). Under low browsing pressure, thickets persist because regeneration of aspen remains continuous at the edge of clones, thereby inhibiting herbivore use. If predation risk decreases and elk density increases (toward the 30% twigs browsed isoline between B and D), elk use should increase most rapidly in grasslands next to aspen. If thickets continue to discourage elk use, this will create a maximum difference in elk use between grasslands and aspen. As elk densities increase

Table 1—Predictions for elk corridor and patch use for high predation and low risk predation landscapes at three distances from trails used by predators.

Distance from main valley bottom trail or highway	Landscape risk	
	High predation risk with trail used by wolves	Low predation risk with busy highway avoided by wolves
Close (<100 m)	Lowest Grass >>> Aspen >>> Conifer	Highest Grass > Aspen > Conifer
Moderate (100 to 500 m)	Moderate Grass >> Aspen >> Conifer	Moderate Grass >> Aspen >> Conifer
Far (500 to 1,000 m)	Highest Grass > Aspen > Conifer	Lowest Grass >>> Aspen >>> Conifer

Table 2—Predictions for elk patch use and browsing rates for grasslands on the edge of aspen stands, and the interior of stands for three predation risk levels.

Predation risk	Relative elk habitat use and browsing rates	Remarks
High	Edge > Interior	Heavily hunted area, or area near trail used by wolves, elk use low in both edge and interior patches
Moderate	Edge >> Interior	Elk use increases first at edge of aspen stands
Low	Edge = Interior	Aspen thickets removed, elk use all areas

farther in low risk landscapes (toward C), the risk-sensitive foraging tradeoff should result in strong pressure for elk to utilize areas within aspen thickets. Higher elk browsing of thickets will in turn, over time, reduce thicket density. Where thickets are removed, elk should have similar use levels in aspen and grassland cover types.

Table 3—Study areas and data collected in each area.

Study area	Road and trail pellet count transects on risk gradients	Paired edge: interior aspen stand transects on risk gradients	Model thickets
Jasper National Park-Willow Creek	5 transects—running from 500 to 800 m from trail to edge of trail, plus >15 km of wolf scat counts on trails	1 transect—running from 600 m away from trail to the trail in Mud Creek meadow	
Ya Ha Tinda Ranch		1 transect—running across ranch boundary from east at Eagle Creek	
Banff National Park-Bow Valley	5 transects—running from 500 to 1,000 m from Trans Canada Highway to edge of highway fence, plus >15 km of wolf scat counts on trails	1 transect—running across east park boundary near Harvey Heights, Alberta	5—located from 0.3 to 5 km from Banff townsite at Recreation Grounds, Hoodoos, Golf Course and Indian Grounds and Duthill
Bow Valley Provincial Park		1 transect—running from Kananaskis River to center of park at Many Springs Pond	
Kananaskis Golf Course		1 transect—running from clearcuts east of Boundary Ranch to powerline through Golf Course	

Study Areas and Methods

We tested predictions by evaluating elk use (indexed by pellet counts) and browsing effects in aspen stands and adjacent grasslands and forests on five valley-bottom elk winter range areas of the Canadian Rockies in Alberta (table 3). The Jasper-Willow Creek area is a ≈30 km^2 area in Jasper National Park where wolf predation on elk has been frequently observed (Carbyn 1974; Dekker et al. 1995). In 1999, about 20 to 40 elk utilized the area during winter (Bradford, personal communication). These elk may periodically leave the park onto Alberta provincial lands where they are hunted during fall hunting seasons or year-round by Treaty Indians (Dekker et al. 1995). The Ya Ha Tinda Ranch is a ≈100 km^2 area along the Red Deer River adjacent to Banff National Park where approximately 1,000 to 2,000 elk winter on grasslands within 3 to 5 km of the ranch buildings (Morgantini 1995). During the study, wolf use was relatively high in areas farther away from the ranch and bull elk were hunted during a fall rifle-hunting season. Three study areas (Kananskis Golf Course, Bow Valley Provincial Park, Banff-Bow Valley) were in the lower Bow Valley on Alberta provincial lands and in Banff National Park. The Bow Valley has several areas of different wolf and human predation rates on elk (Paquet et al. 1996). The ≈100 km^2 Banff-Bow Valley area is bisected by a fenced highway and provides habitat for over 500 elk. Near Banff townsite, human-caused mortality rates on elk (from roads and the railroad) were 2% per year on roads and the railroad, and wolves took <4% per year (Paquet et al. 1996; Woods et al. 1996). Elk also concentrated on unhunted zones in Bow Valley Provincial Park, 50 km east of Banff, and the Kananaskis Golf Course complex, 60 km southwest of Banff (Alberta Environment Protection files, Canmore Office).

All study areas are in the montane or lower subalpine ecoregions of the Canadian Rockies (Strong 1992). Vegetation cover is predominantly lodgepole pine (*Pinus contorta*) forests interspersed with stands of trembling aspen, Douglas-fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and grass meadows with shrub birch (*Betula* spp.) and willow (*Salix* spp.) shrublands (Achuff and Corns 1982; Archibald et al. 1996; Beckingham et al. 1996). The study areas have a continental climate with peak precipitation in June and winter snow depths generally less than 50 cm (Holland and Coen 1982).

Ungulate and Wolf Habitat Use

We used pellet and scat counts on belt transects to index relative winter habitat use by wolves and ungulates (Neff 1968; Edge and Marcum 1989). Elk defecate most frequently when active, so pellet counts are likely biased toward areas where elk are feeding or moving as opposed to bedding (Collins and Urness 1979). Transects were measured in April and May, immediately after the winter snowpack melted. We evaluated wolf and elk habitat use by cover type and distance from trails and roads (table 3) at Jasper-Willow Creek (low human use, high wolf use, low elk density) and Banff-Bow Valley area (high human use, low wolf use, high elk density). From air photographs, we identified five transect locations (figure 3) perpendicular to the main valley bottom trails (Jasper area) and the Trans Canada Highway (Banff area) where a mix of aspen, conifer, and grassland habitat patches was found at 10 to 100 m, 100 to 500 m, and 500 to 1,000 m from the road or trail. Aspect and elevation were relatively similar along the transect. On the air photographs, we selected locations for five 2 x 50 m plots in each cover type at each of the three distances from the trail or road for each transect. All scats and ungulate pellet groups with centers within plots were counted by species.

We used a factorial analysis (2 study areas x 3 cover types [grass, aspen, conifer] x 3 distances from trail/road [close, moderate, far]) to test for main and interaction effects on the elk pellet group counts. Although frequency count data typically follow a negative binomial distribution, simulations by White and Bennetts (1996) showed that analysis with ANOVA is relatively robust to violations of normality. We minimized the effects of violations of parametric assumptions (normal distribution and equal variance) by balancing sample sizes for groups (Underwood 1997), comparing results of alternative data transformations of pellet counts on normal probability plots (Zar 1996), and using the square root transformation ($\sqrt{[\text{count} + .5]}$).

We tallied all wolf scats within 1 m of the main trail centers in the Willow Creek area of Jasper National Park for 3 years (1997, 1998, 1999), on side trails in Willow Creek for 1 year (1999), and on side trails near the Trans Canada Highway in the Banff-Bow Valley for 2 years (1998, 1999). Each trail was surveyed once in April or May, immediately after snowmelt. Trail distances by cover type were measured by wheel-odometer.

To evaluate effects of aspen stand structure and predation risk on elk habitat use (table 2), we identified five transects (table 3) across areas where elk likely had well-defined and rapid increases in risk (<2,000 meters across). For example, the elk predation risk from wolves likely decreased farther from wolf-used trails in the Jasper-Willow Creek area, or the predation risk from humans decreased when entering national or provincial parks in the Bow watershed from hunted, multiple use lands. Along each transect, we located three risk level zones (high, moderate, and low risk of predation or hunting) to approximate Point A, the 30% twigs browsed isoline, and Point C respectively in figure 1. At five sample points in each zone, we counted pellet groups on a 2 x 50 m plot in the interior of an aspen stand paired to a stand edge plot in grasslands 10 to 30 m away. Where possible, aspen interior plots were established in thickets, defined as a dense stand (<1 meter spacing, >50 stems/100 m^2) of stems predominantly 2 to 6 meters in height. Where no thickets were found (low risk-high elk density areas), we paired edge plots to plots in the interior of aspen stands with the highest stem densities in the area. The moderate risk zone on each transect was recognized as the zone where saplings were relatively dense in and near aspen stands but rare in adjacent grasslands. Predictions of elk use of aspen patches versus adjacent grassland patches at three risk levels (table 3) were tested with a one-way analysis of variance of the ratio of paired values (aspen stand interior/ edge of stand) of elk pellet group counts.

Elk Browsing Effects on Aspen

We estimated elk-aspen browsing levels on aspen at five points (10 m spacing) within each of the five 2 x 50 m paired plots at the low, moderate, and high risk points along each risk transect (see above). At each point, the nearest two aspen stems in each of three height classes (suckers [0 to 1 m], tall suckers [1 to 2 m], and saplings [2 to 6 m]) were tallied by live or dead condition and four browsing classes: <20% twigs browsed and/or stem debarked (BC1); 20 to 50% twigs browsed and/or stem debarked (BC2); 50 to 80% twigs browsed and/or stem debarked (BC3); and >80% twigs browsed and/or stem debarked. For analysis, an overall browsing index was calculated for saplings from the midpoint of each browse class, weighted by the number of stems in each class (BC 1 to BC4), and divided by the total number of stems (n), with the equation:

$$B = (0.1{*}BC1 + 0.35{*}BC2 + .65{*}BC3 + 0.9{*}BC4)/n$$

Predictions (table 2) of elk browsing intensity of aspen stems inside patches versus stems adjacent to grassland patches at three risk levels were tested with a one-way analysis of variance of the ratio of paired values (interior of aspen stand/ edge of stand) of browse index values.

Few aspen thickets of stems 2 to 6 m in height occurred at the high elk density and low predation/hunting risk end of transects. To evaluate over-winter elk herbivory effects on sapling stands under these conditions, we constructed five artificial sapling thickets in the Banff-Bow Valley area (table 3). Methods followed Lundberg and Dannell (1990) and Edenius (1991). Unbrowsed aspen stems were cut during winter dormancy in December and early January from the nearby fenced highway wildlife exclosure. Each artificial thicket consisted of 36 stems (2 to 5 m in height) set 20 cm into frozen ground to form a thicket 4 x 4 meters (approximately 0.75 m spacing between stems). Ten stems were placed farther out, spaced 5 m apart, in the grassland area around the thicket. Thickets were built around one to three mature, single aspen stems (>5 m height). We measured the browsing condition class (see above) for each stem every 8 to 12 days after construction (early January 1999) until spring (late March). For analysis of browsing effects, the browsing index (see above) was calculated for each sample date for stems grouped as open (in the meadow), edge (on edge of thicket), interior (0.5 to 1 m inside the thicket), and core (center of thicket).

Results

Wolf scat abundance on main and side trails was different between the Banff-Bow and the Jasper-Willow Creek areas (table 4). Fencing prevents wolves from using the Trans Canada Highway in the Bow-Banff area, and wolf use, as indexed by scat counts, was relatively low along side trails within 1.5 km of the fenced highway. For the Jasper area, wolf scats were abundant on the main valley bottom trail and less common on side trails.

Factorial analysis results of elk pellet counts (table 5, figure 4) showed significant main effects of landscape area (Banff or Jasper), distance from trail or road, and patch type. Banff had higher pellet group counts than Jasper. For both areas, the pattern of elk pellet counts was grass > aspen > conifer. The interaction effect between landscape area and distance from trail or road was significant, demonstrating an opposite pattern of elk use in Banff and Jasper corridors near roads and trails. In Banff, elk use was highest near the highway, with consistently less elk use in all patch types with increasing distance classes. In Jasper, elk use was lowest near the trail but was more variable with distance from the trail (table 6). Contrary to predictions, there was no significant interaction between landscape, distance from trail or road, and patch type. The relative number of pellet groups within grass, aspen, and conifer patches was fairly consistent within distance and landscape area (figure 4).

Elk pellet group counts and browsing index values for paired aspen stand interior and edge plots varied significantly between plots that had different predation and hunting risk (figure 5). There were few elk pellets in both edge

Table 4—Trail and highway distances sampled and mean spring (May, June) wolf scat counts by cover type on trails for the Banff townsite area, Banff National Park, and Willow Creek area, Jasper National Park.

		Jasper-Willow Creek			Banff-Bow Valley		
Type	Attribute patch type	Grass	Aspen	Conifer	Grass	Aspen	Conifer
Main trail or highway	Distance (km)	9.5	0.6	12.5			
	Scat count	46	1	62		Fenced	
	Scats/km	4.8	1.6	5.0			
Side trail	Distance (km)	1.7	.4	2.3	7.9	1.2	21.2
	Scat count	8	0	1	5	0	13
	Scats/km	4.7	0	.4	0.63	0.0	0.61

Table 5—Results of the analysis of variance of the effects of landscape area (Banff-Bow Valley, Jasper-Willow Creek), distance from road or trail (near, moderate, and far), and patch type (grass, aspen, and conifer), on the square-root transformation of elk pellet group counts (mulitiple $R = 0.745$, multiple $R^2 = 0.555$).

Source of variation	SS	Df	MS	*F*-ratio	*P*
Landscape	390.66	1	390.66	387.81	0.000
Distance from road/trail	50.63	2	25.32	25.13	0.000
Patch type	202.86	2	101.43	100.69	0.000
Landscape x Distance	68.34	2	34.17	33.92	0.000
Landscape x Patch	6.81	2	1.70	1.69	0.151
Distance x Patch	53.48	4	26.74	26.55	0.000
Landscape x Distance x Patch	5.42	4	1.36	1.35	0.252
Transect (area)	95.20	8	11.90	11.81	0.000
Error	427.11	424	1.01		

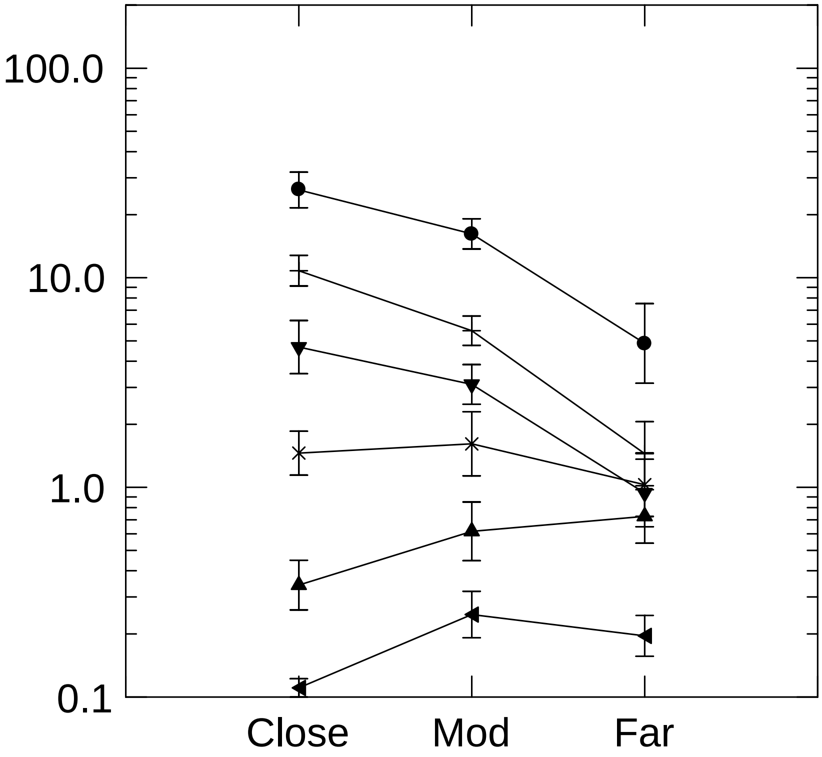

Figure 4—Geometric means ± SEM of elk pellet group counts for grass (G), aspen (A), and conifer (C) cover types at 3 distances from trails or roads in the Banff (B) and Jasper (J) study areas. The 1 pellet group/100 m^2 threshold line indicates the level above which aspen saplings are rare (C. White, personal observation). For each sample, *n* = 25.

Table 6—Mean pellet group counts/100 m^2 with standard error on mean for cover types within study areas. Column means with different superscript letters within areas and row means with different superscript numbers are significantly different (see text) at $p<0.05$ (Bonferroni test on square root of elk pellet counts). Sample sizes are $n = 25$ for plots grouped by landscape, distance, and patch type; $n = 75$ for plots grouped by patch types; $n = 225$ for each landscape, all distances and patches; $n = 150$ for plots grouped by cover for all distances; and $n = 450$ for all plots.

Landscape	Distance from trail or road	Patch type			For all patches	For all distances
		Grass	Aspen	Conifer		
Banff-Bow Valley	Close	38.6 ± 6.3	14.2 ± .0	7.9 ± 1.4	20.3 ± 2.8^{a}	12.7 ± 1.2
	Moderate	19.6 ± 3.0	7.5 ± 1.0	4.7 ± 1.0	11.2 ± 1.5^{b}	
	Far	13.9 ± 2.8	3.5 ± 0.7	2.7 ± 0.7	6.7 ± 1.1^{c}	
Jasper-Willow Creek	Close	2.2 ± 0.4	0.6 ± 0.2	0.0 ± 0.0	1.0 ± 0.2^{d}	1.4 ± 0.1
	Moderate	3.9 ± 0.7	1.4 ± 0.3	0.4 ± 0.1	2.0 ± 0.3^{e}	
	Far	2.4 ± 0.5	1.3 ± 0.2	0.3 ± 0.1	1.3 ± 0.2^{d}	
For both landscapes	All distances	13.7 ± 1.7^{1}	4.7 ± 0.6^{2}	2.7 ± 0.4^{3}	—	7.0±0.6

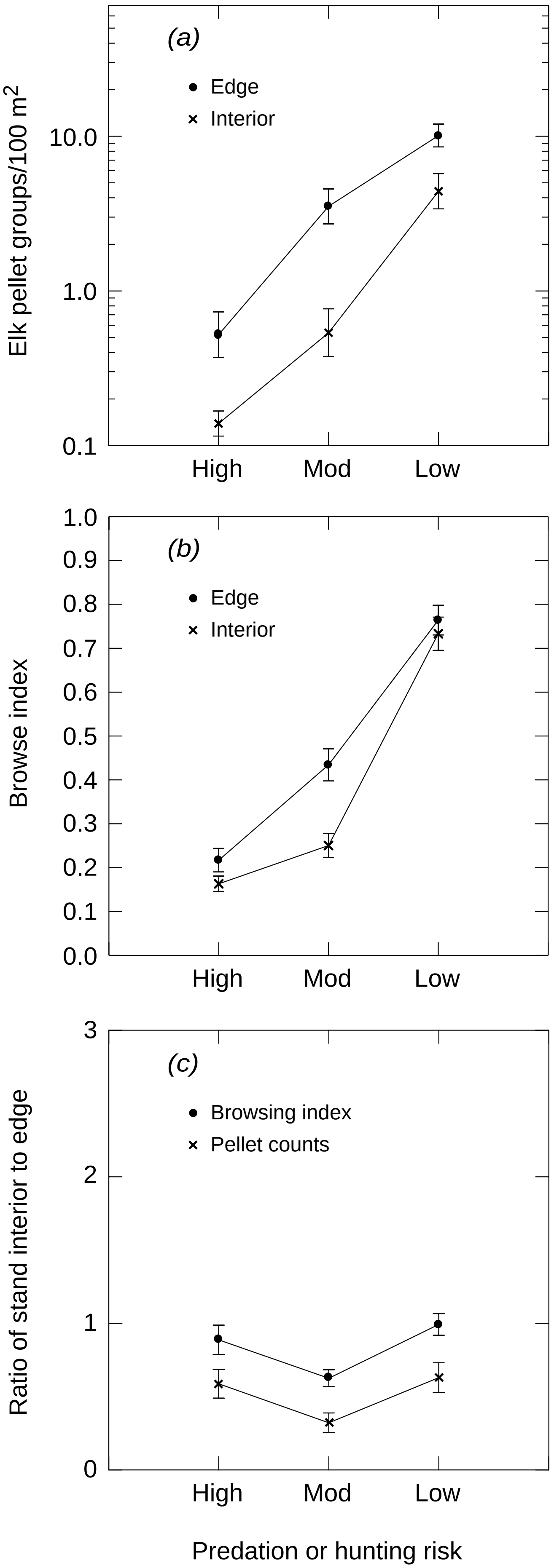

Figure 5—Means ± SEM of pellet group counts (*a*) and browsing index values (*b*) for paired plots on the edge and in the interior of aspen stands on transects from high to low predation or hunting risk to elk, and the ratio of interior to edge pellet count and browse index values (*c*). For each sample, *n* = 25.

and aspen interior plots in high-risk areas. Pellet numbers increased more rapidly in edge plots than aspen interior plots as risk decreased (figure 5a). Areas at moderate risk had a statistically significantly lower ($p = 0.03$, Bonferroni adjusted) ratio of interior to edge pellet group counts (figure 4c) than did low risk areas. Aspen sapling browsing index values had a corresponding pattern (figure 5b). The stand interior to edge ratio of browsing (figure 5c) was significantly lower in moderate than in high risk areas ($p = 0.04$, Bonferroni adjusted) and low risk areas ($p = 0.001$, Bonferroni adjusted). These use patterns corresponded with changing aspen stand structure. Aspen stands in moderate and high risk areas were dense and multi-aged (figure 6a). However, in lower risk areas where pellet counts were >1 group/100 m^2, stands had low sapling densities and were much more open (figure 6b).

Over-winter (approximately January 10 to March 20) browsing by elk was intense on the model aspen stands constructed in the Banff-Bow area. Browsing index values decreased for stem placements in the following order: isolated stems in open areas, stems on the edge of 4 x 4 m thickets, stems 1 m in from thicket edge, and stems in center of thickets (figure 7). By the end of winter, the mean browsing index was greater than 0.7 for all stem placements.

Discussion

Effects of Patch Type and Travel Corridors Used by Predators and Humans

General elk use by patch type (grass > aspen > conifer), as indexed by pellet group counts (figure 4, table 6), was consistent for the Jasper and Banff areas. High elk use of grass and short shrub habitat patches has been reported for numerous Rocky Mountain areas including northern British Columbia (Peck and Peek 1991), Alberta National Parks (Cowan 1947; Flook 1964), Montana (Jenkins and Wright 1988), Yellowstone National Park (Houston 1982; Coughenour and Singer 1996), and lodgepole pine and meadow areas in Utah (Collins and Urness 1979). Pellet group counts were comparable to earlier research (1975 to 1980) in the montane ecoregion in Banff and Jasper National Parks where means of 10 to 15 groups/100 m^2 for grassland types and 2 to 4 groups/100 m^2 for forest types were reported (Holroyd and Van Tighem (1983: 412).

The different patterns of elk pellet groups near valley bottom trails in a wilderness area of Jasper National Park in contrast to near a busy four-lane highway in Banff National Park (figure 4) were in accordance with predictions (table 1). In the Banff area, there was consistently fewer elk pellet groups as the distance from the highway increased (table 6). This may be the result of predator avoidance (Dekker et al. 1995). In Banff, wolves cannot use the highway as a valley-bottom travel vector due to highway fencing (table 4), and only infrequently use areas near the fence due to high traffic volume. Paquet et al. (1996) found from tracking and radio telemetry studies that wolves avoided areas within 500 m of the highway in Banff. Dekker et al. (1995) described a similar pattern of relatively low wolf use and high elk use near the main highway in the Athabasca Valley in Jasper National Park. However, in the Athabasca Valley, elk could also be attracted to the highway right-of-ways because of tree clearing and agricultural grass cover (Holroyd and Van Tighem 1983). In the Banff area, highway fencing blocks elk use on most of the right-of-way area (Woods 1990), thus reducing the effect of this confounding factor.

Figure 6—Dense stand of aspen saplings near a trail heavily used by wolves at Willow Creek in Jasper National Park, Alberta (a, upper photo), and heavily browsed, low stem-density stand approximately 500 m from the trail (b, lower photo).

In the Jasper-Willow Creek area, the valley bottom trail was a main winter travel vector for wolves (table 4). This corroborated the findings of several other studies of wolf movements in undeveloped areas of the Rocky Mountains (Carbyn 1974; Paquet et al. 1996; Kunkel 1997). In winter at Willow Creek, wolves maintain runways through snow along trails by repeatedly using the same route (Carbyn 1974). In addition, Jasper National Park wardens make infrequent winter patrols on the main trail by snow machine (G. Antoniuk, personal communication). Trails where the snow is packed, but are only lightly

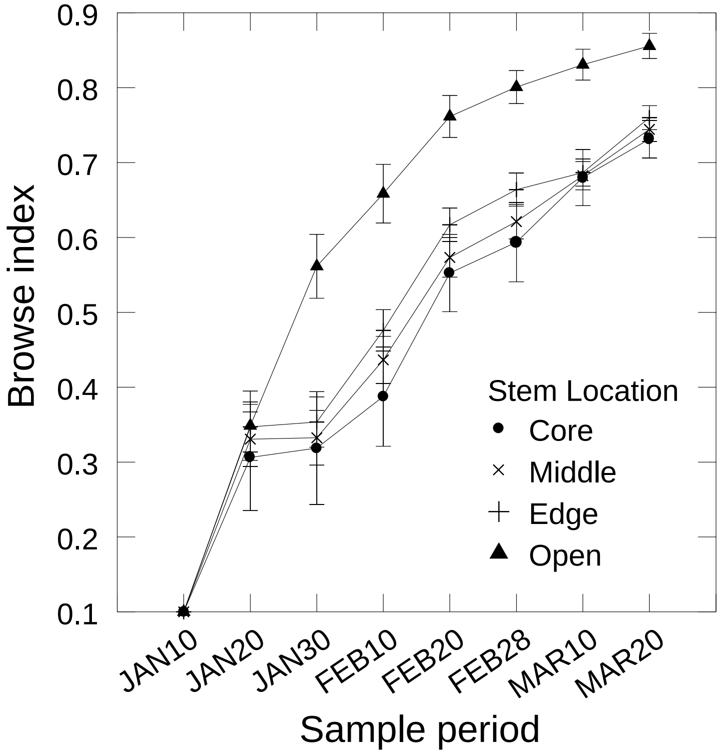

Figure 7—Mean ± SEM of browsing index values of aspen stems in and near model thickets. See text for location of stems. Sample sizes are open stems (*n* = 50), edge stems (*n* = 100), interior stems (*n* = 60), and core stems (*n* = 20).

used by people, are often preferred winter travel routes for wolves (Paquet et al. 1996). There was significantly less elk use within 100 m of the Jasper trail, but elk use was more variable with distance than in Banff (figure 4, table 6). In contrast to Banff where wolves predictably avoid areas close to the highway (Paquet et al. 1996), Jasper wolves may use main trails heavily but they still utilize side trails and areas away from trails (table 4). Further, predators such as cougar, black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*) are likely more common at all distances from trails in the remote Jasper area compared to near the highway in the busy Banff area (Banff Bow Valley Study 1996).

Contrary to predictions for an interaction effect on elk habitat use that included distance from trail or road (figure 4, table 2), there appeared to be similar relative elk use patterns for patch types (e.g., grass >> aspen > conifer for Banff, grass > aspen >> conifer for Jasper) for all distances within landscapes. Possibly, elk use of adjacent patches types as sampled with our methods was not independent. Elk often forage in grass patches, but may seek hiding cover in adjacent conifer patches when resting (Lyon 1979; Lyon and Ward 1982; Thomas et al. 1988). However, the low number of pellet groups in the aspen and conifer types closer to trails in the Jasper-Willow Creek area (table 6) suggested that elk avoided forest cover here when foraging or traveling.

The overall patterns of elk use with landscape, distance from trail or road, and patch type had important biological significance for aspen regeneration. In Jasper, aspen saplings within aspen and conifer patches near the trail were often unbrowsed (figure 6a). However, in all patch types at all distances from the road in Banff, Jasper aspen patches >500 m from the trail, and all Jasper grasslands, pellet group counts exceeded the threshold of ≈1 group/100 m^2 (C. White, personal observation) where aspen saplings are completely browsed off (figures 4, 6b).

Effects of Aspen Stand Structure and Predation Risk

Elk pellet group and browsing index values for paired aspen interior and grassland edge across predation and hunting risk gradients (figure 5) followed the predictions from risk-sensitive foraging (table 2). These results support the hypothesis that the Type 2 functional response observed for aspen sapling-elk interaction (figure 2) is at least partially caused by relatively less time spent by elk in dense-stemmed aspen patches. Along risk gradients (figure 5), this interaction was most clearly manifested at intermediate risk levels. At high risk, elk densities were low and elk browsing was low in both the edge of and inside adjacent aspen thickets (figure 6a). At low risk, elk were at higher densities and over time killed aspen saplings (figure 6b). The remaining open-grown stands were again more equitably used by elk in comparison to adjacent grasslands (figure 5c). At intermediate risk, elk densities were moderate in grasslands, but they most clearly avoided using aspen thickets. Further evidence of this fine-scale elk-foraging pattern was provided by browsing over time in the model thickets built in the Banff's Bow Valley. Elk browsed sapling stems in open grasslands near stand edges preferentially (figure 7). However, in this high elk density situation, even stems at the core of aspen thickets were heavily browsed within 90 days of stand construction. Shepperd and Fairweather (1994) observed comparably high elk browsing rates when fences protecting sapling stands in Arizona were removed.

The relatively low rates of browsing of aspen suckers and saplings in multi-aged, high stem density stands compared to more open aspen stands has been recognized by previous researchers (DeByle 1985a,b). The low elk use of dense aspen stands we observed could be the result of an interrelated suite of factors. Dense stands may have better cover for stalking predators such as cougars (Kunkel et al. 1999), increased snow depths (Telfer 1978), and decreased forage availability (Bailey and Wroe 1974). In contrast, adjacent open grassland areas provide elk with ease of escape from predators (Geist 1982), and when elk numbers are low, open grasslands provide a high availability of palatable grasses (Willoughby et al. 1997).

Plant structural characteristics such as thorns, spine, tough leaves, and prickles may reduce herbivore use (Harper 1977; Cooper and Owen-Smith 1986; Pollard 1992). But intuitively, increasing density of highly palatable forage such as aspen saplings would result in higher herbivore use of patches, not lower, if no other factors were operative. However, aspen communities exist in montane landscapes that historically included not just plants and herbivores, but also predators—humans, wolves, cougars, and black and grizzly bears (Mattson 1997; Kay 1998; White et al. 1998a; Kunkel et al. 1999). In three-level trophic systems, the interaction between vegetation structure, predator hunting behavior, and herbivore response to predation risk is likely profound, variable, and complex (Lima and Dill 1990; Hunter and Price 1992; Lima 1998; Kie 1999). Results of the present study suggest the hypothesis that aspen's dense-stemmed thicket trait confers increased fitness to aspen clones in predator-rich environments but could be detrimental in herbivore-rich situations. This requires further investigation.

Integration of Risk-Sensitive Foraging Patterns and Aspen Stand Structure

The three spatial scales of elk density and risk-sensitive foraging patterns (figure 3) evaluated here (regional, near trails and roads, and habitat patch level) appear to be associated with major structural differences in aspen stands. At the regional level in high-predation risk areas, such as Jasper's Willow Creek where elk densities were low (<1 pellet group/100 m^2; figure 4), aspen were often multi-aged and dense (figure 6a). In low-predation and hunting-risk areas, such as in Banff, elk densities were usually high (>3 to 5 pellet groups/100 m^2; figure 4). Under these conditions, all aspen stands were heavily browsed, and dense multi-aged stands did not occur.

At intermediate spatial scales, human and predator travel routes had completely different effects under different risk situations. In high-predation risk ecosystems with low human use, valley-bottom trails were frequented by wolves (table 4). Elk were not attracted to these trails, and may even have avoided some areas near them (figure 4). As a result, in the Jasper Willow-Creek area, aspen stands were multi-aged and most dense near the main trail, and more heavily browsed at increased distances from the trail (figure 6). In low-predation risk areas (e.g., near busy national park roadways) the opposite effect occurred. Elk may be attracted to valley bottom travel routes and facilities heavily used by humans but avoided by wolves (Paquet et al. 1996). This resulted in very high elk densities in aspen stands (e.g., >10 pellet group/100 m^2) such as observed in this study for the Banff's Bow Valley (figure 4). This "reversed" pattern of elk use in modern park landscapes makes herbivory impacts acute for aspen stands in valley-bottom areas once heavily used, but now avoided, by predators (Ripple and Larsen 2000).

At the finest scale of the habitat patch, structural conditions of aspen (low density stands versus dense, multi-aged stands) further affected elk foraging behavior. In a high-predator risk region, particularly near routes frequented by predators, aspen stands had high stem densities with low browsing rates (figures 5b, 6a). In contrast, a positive feedback mechanism occurred when elk densities were high—browsing reduced stem density, which increased elk habitat use and browsing rates. Most aspen stands in low-predation risk and high elk density areas in the Rocky Mountains are currently in this condition (Kay 1997a). From 1940 to 1970, several national parks including Jasper, Banff, Yellowstone, and Rocky Mountain culled elk but achieved no significant response from aspen (White et al. 1998a), even when elk populations were reduced to levels where aspen regeneration had previously occurred (Houston 1982; Huff and Varley 1999). This led to alternative hypotheses that fire suppression or climate change were important causes of aspen decline (Houston 1982; Romme et al. 1995). However, results of our study suggest that aspen regeneration would not be expected at the same elk densities at which it initially declined due to different elk behavioral patterns in remnant open stands (figure 2). Only a major decrease in elk density would re-create the dense multi-aged stands that are more resistant to herbivory.

Historically, spatial factors that affected predation on herbivores—such as predator travel routes (Carbyn 1974), wolf pack buffer zones (Mech 1977), and denning locations (Dekker et al. 1995) or First Nation intertribal warfare areas (Kay 1994; Martin and Szuter 1999)—likely shifted with time. The resulting spatially dynamic, risk-sensitive foraging patterns of elk would often provide conditions favorable for creating dense aspen stands that would be resistant to periodic higher densities of elk if predation risk declined. In contrast, many current risk zones (e.g., park boundaries) are spatially fixed and may result in long-term high elk density in some areas (White et al. 1998a).

The landscape analysis, or "natural experiment" technique, used here to evaluate hypotheses for risk-sensitive foraging by elk on aspen did not control for the relative effects of predation risk versus elk competition for food. For example, in all analyses, areas of higher risk had lower densities of elk, as indexed by pellet groups (figures 4, 5b; table 6). Relatively low browsing rates on aspen in these areas could be more related to the higher availability of preferred foods (e.g., some grass species) in low elk density areas than risk-driven avoidance of aspen stands. However, reductions in elk density at local or regional levels, through behavioral or demographic effects, may be a relatively consistent result of increased carnivore predation or human hunting rates (Lyon and Ward 1982; Dekker et al. 1995; Paquet et al. 1996; Kunkel and Pletscher 1999).

Conclusion

Patterns of elk herbivory on aspen result from multi-scale factors that include not just general elk density, but varying risk-sensitive foraging patterns resulting from predator habitat use (Ripple and Larsen 2000) and aspen stem-density conditions. In national parks of the Canadian Rockies that are heavily used by people, the current pattern is one of high-density elk populations attracted to valley bottoms and intense elk foraging on low stem-density aspen stands. This is the opposite of historical conditions throughout the Rockies and of the current situation in more remote areas, where elk have lower densities and are not attracted to valley bottom travel routes that are heavily used by wolves or human hunters. Low herbivory results in dense, multi-aged aspen stands that are resistant to periodically higher browsing rates by fluctuating populations of elk. This condition is likely similar to the long-term spatially dynamic conditions that maintained aspen in valley-bottom areas.

Elk-aspen foraging patterns result from complex interactions between predators, herbivores, and vegetation. As predicted by Hunter and Price (1992), these interactions are highly influenced by heterogeneity in more natural systems where predators still occur. Neither “top-down” nor “bottom-up” influences necessarily prevail. However, reductions in elk density at local or regional levels, through behavioral or demographic effects, may be a consistent result of maintaining the historical range of variability of carnivore predation or human hunting rates. Therefore, it may be difficult to isolate the effects of predation from reduced elk competition for food in future research on aspen herbivory. Results of this study suggest the hypothesis that aspen’s dense-stemmed thicket trait confers increased fitness to aspen clones when interactions occur between the behavior of predators and herbivores and the density of vegetation.

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Ecology and Management of Aspen: A Lake States Perspective

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***Abstract**—Aspen has been an ecologically important, though relatively minor, component of the Lake States (Michigan, Wisconsin, and Minnesota) forests for millennia. General Land Office records from the 1800s indicate that aspen comprised a small fraction of the region's eastern forests, but was more extensive on the western edge. Then Euro-American settlement in the 1800s brought land clearing, timber harvesting, and subsequent widespread wildfires that increased aspen-birch acreages considerably. Although aspen-birch acreage has declined since the 1930s, it remains the region's second most prevalent forest type. Aspen management is probably the most contentious issue confronting forest managers in the Lake States.*

Concerns regarding the status of early successional forest communities have emerged nationally. Across the United States, many disturbance-dependent ecosystems including prairies, savannahs, barrens, and early successional forests have declined in recent decades. These declines are due in part to nearly a century of fire suppression, as well as land conversion, rural development, and grazing. However, loss of late successional communities is also of national concern. Thus, both ends of the successional spectrum, young early successional forests and old late successional forests, have declined due to human activities.

Quaking aspen (*Populus tremuloides*) and bigtooth aspen (*Populus grandidentata*) are among the premier early successional species in the United States. Quaking aspen is the most widely distributed tree in North America (figure 1), whereas the distribution of bigtooth aspen is confined primarily to the northeastern United States and the Great Lakes Region (figure 2). These two species, and their less common eastern associates, paper and gray birch (*Betula papyrifera* and *B. populifolia*), are often characterized as the aspen-birch forest type.

Aspen and aspen-birch forests occur in 27 states within the United States, extending from Alaska to New Mexico in the west and from Maine to West Virginia in the east. The greatest acreage occurs in the eastern states of Minnesota, Wisconsin, Michigan, and Maine, and in the intermountain and mountain states of Utah and Colorado. Combined, these six states have 86% of the aspen and aspen-birch acreage in the lower 48 states. Based on the most recent Forest Inventory and Analysis (FIA) inventories, there are approximately 20.3 million acres of aspen and aspen-birch forest types (predominantly aspen) in the lower 48 states. These types comprise 7% of the nation's forest lands (298.1 million acres of land stocked at least ⅙ with trees) and 10% of the nation's timberland (198.1 million acres of more productive forest land; Powell et al. 1993). The Lake States (Michigan, Wisconsin, and Minnesota) are notably the stronghold of the aspen-birch forest type, with 12.9 million acres, or 63%, of the total acreage, in the lower 48 states.

Within the Lake States, there are 51.9 million acres of forest lands, of which 49.0 million acres are considered timberland. Recent FIA data indicate that the aspen-birch forest type covers 6.3 million, 3.4 million, and 3.2 million acres of

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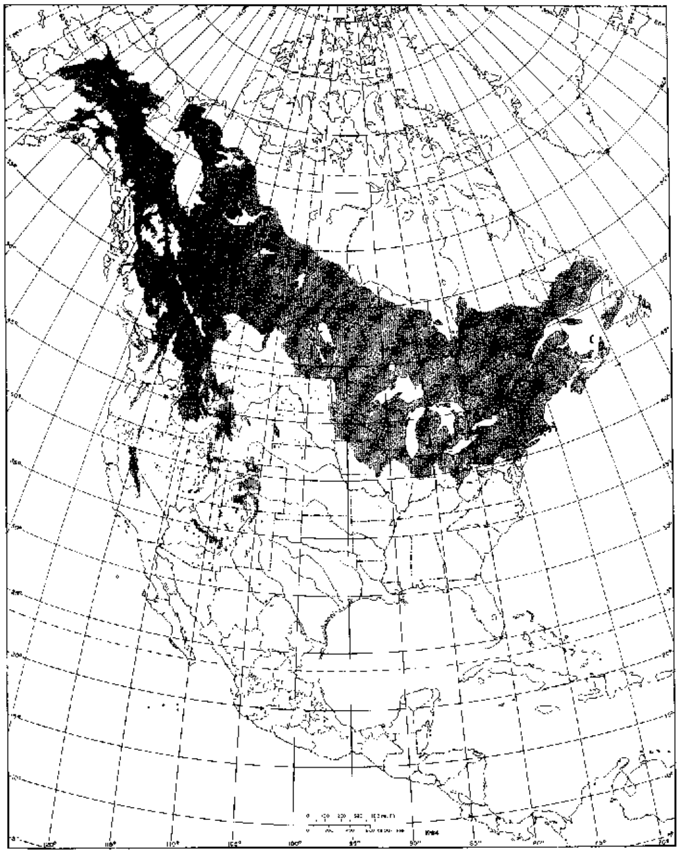

Figure 1—Range map for quaking aspen (*Populus tremuloides*) (source: Burns and Honkala 1990).

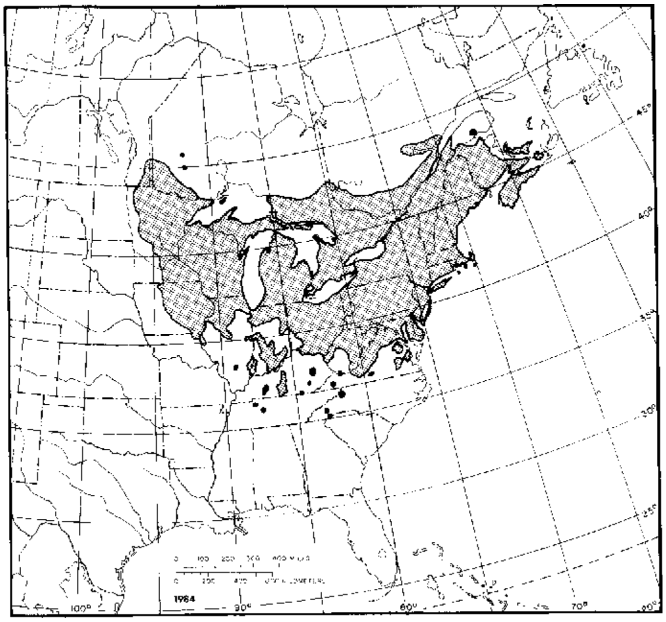

Figure 2—Range map for bigtooth aspen (*Populus grandidentata*) (source: Burns and Honkala 1990).)

Minnesota, Wisconsin, and Michigan, respectively (Leatherberry and Spencer 1996; Miles et al. 1995; Schmidt 1997). The extent of forests is important, but ownership patterns are as well—ownership provides insights regarding management options. In the Lake States, 62% of the timberlands are in private ownership, dominated by nonindustrial private landowners.

Public ownership is also important across the region, and each state's public ownership has evolved differently since the turn of the 20th century. "The lands nobody wanted" 100 years ago became the extensive Lake States public lands, intermixed with private lands (Shands and Healy 1977). Minnesota's public lands are, in descending order of magnitude, state forests, county and municipal forests, and national forests. Wisconsin's public lands are mostly county and municipal forests followed by national and state forests. In Michigan, state forests and national forests are the principal public ownerships; there are few county forests.

The purpose of this paper is to present a Lake States' perspective on aspen ecology and management, thereby providing a broader comparative context for conditions in the western United States. To this end, we describe the historical evolution of the aspen forests in the Lake States, contemporary aspen trends, and management options for aspen in a multiownership/multiobjective environment.

Historical Role of Aspen in the Lake States

Today's acreage of aspen in the Lake States is largely due to the extensive disturbance rendered by turn-of-the-century logging and fires, which greatly favored disturbance-dependent species. Understanding the ecological and social importance of aspen in the Lake States therefore requires a historical perspective.

Ecological Change

During the early part of the Holocene (ca. 10,000 YBP, years before present), following the last series of glacial advances and retreats, the forests of the Lake States underwent dynamic transformations in response to climate change and biological processes, including species migration and forest succession. Broad-scale changes occurred over thousands of years due to the long-term response of vegetation to variations in temperature, moisture, and air mass patterns (Webb et al. 1993). Most of the taxa present in the Lake States today had migrated into the region by 6,000 YBP, with virtually all taxa except hemlock established by 3,000 YBP (Brubaker 1975; Davis 1981; Davis et al. 1993; Frelich 1995; and Webb et al. 1993).

Although the migration of species into the region stabilized at least 3,000 years ago, species' distributions have continued to shift when viewed at a landscape scale (measured in tens of thousands of acres). The nature and rate of these changes have been regulated by interactions of minor climatic fluctuations like the Little Ice Age (600–150 YBP), natural disturbance regimes, insect and disease outbreaks, landform-controlled soil, topographic and hydrologic conditions (Host et al. 1987), and species-specific reproductive strategies and life expectancy.

Mesophilic, wind-driven ecosystems primarily supporting long-lived tree species (e.g., sugar maple, yellow birch, hemlock) historically changed slowly over centuries due to fine-scale blow-downs and relatively rare broad-scale catastrophic storms [Canham and Loucks 1984; Frelich and Lorimer 1991; Runkle 1982]). These "asbestos" forests seldom burned, and exhibited a repeating yet shifting steady state of fine-scaled mosaics of species whose overall proportions remained essentially constant (Borman and Likens 1979). These unevenaged, mesic forests were characterized by supercanopies of trees that were centuries old.

The age and landscape structure of mesophylic forests contrasted with fire-dependent ecosystems, such as spruce-fir, aspen-birch, and red or jack pine forests. These pyrophilic ecosystems were typically evenaged, and were composed of both long-lived tree species (e.g., white and red pine) and short-lived species (e.g., jack pine, aspen, white birch). Locations and sizes of forest patches changed over time due to disturbances from wildfire and burning by indigenous people; changes were more frequent and dramatic than in the mesic hemlock-hardwood forests. Cover types were replaced in patches of hundreds to thousands of acres within several decades to a century or more. Vegetation types were variously savannas, barrens, or dense coniferous forest, depending on fire frequency and extent. Thus, age classes and patch configurations of mesophilic and pyrophilic forests generally followed an ecosystem-dependent periodicity and spatial pattern associated with particular natural disturbance regimes.

While it is commonly accepted that wind and fire disturbance altered local and landscape ecosystems, minor climatic fluctuations did not result in major changes at any scale (Frelich 1995). Pielou (1991) explains this relative stability in the face of climate change with the concept of ecological inertia. She defined ecological inertia as the lag in forest change due to plant persistence, with established communities physically preventing encroachment by invading species that were better adapted to changed climatic conditions—species simply would not have time to migrate. This delayed response of vegetation to short-term climatic change may explain why the biogeography of forest trees changed steadily following Pleistocene glaciation, without any reversals in the direction of the change. She noted that, in addition to ecological inertia, natural selection for progeny adapted to changed conditions also resulted in stability.

Early Human Influences

Understanding the cause and rate of natural change that formerly influenced and distinguished the landscape and local ecosystems of the Lake States, technically termed the dynamics of homeorhetic stability (O'Neill et al. 1986; Reice 1994), requires consideration of biological processes, the physical environment, and disturbance regimes. Human influences have long been integral to these processes, although the extent of early influences remains a matter of debate.

Hunter (1996) makes the point that although the "overall ecological impact of Native Americans was much less than that of Europeans, it was significant in certain times and places." We know that pre-European contact indigenous populations in North America were a very small fraction of modern human populations. Denevan (1992) estimated there were 53.9 million Native Americans in the "New World" in 1492, with 3.8 million in North America. He asserted that "the Indian impact was neither benign nor localized." All ecosystems in the Lake States were not equally susceptible to fire, and burning by indigenous people would have primarily affected systems prone to burn, such as barrens, savannas, upland mixed conifer and oak forests, and other fire-dependent systems. Thus, the overall impact within pyrophilic ecosystems would have been large. This was not the case, however, in fire-intolerant, mesic hardwood forests that occurred throughout much of the Lake States at the time of European settlement.

Stearns (1949) noted that “in the virgin hardwood timber, fire is in the opinion of the writer rarely of much importance as the initial agent of catastrophe although it often follows windfall.” He observed that “hot slash fires have burned on the cutover hardwood land. Although these fires burned to the edge of the virgin stand they did not penetrate into it more than a few rods.” Even the sweeping wildfires that occurred following the turn-of-the-century logging did not fully consume the advanced regeneration of fire-intolerant hardwood species such as sugar maple in the moraines, loamy glacial lakebeds, and other mesic landforms of the Lake States. The flora of the “asbestos” forests in many cases simply would not burn, probably due to the high moisture content and low fine-fuel loading of the forest floor, and the “inability of the vegetation comprising the understory or residual tree sapling and pole strata to carry fire” (Whitney 1986, 1987). Hence, fire seldom affected mesic hardwood ecosystems, and burning by indigenous people would likely have had minimal impact on them.

Early Records of Lake States Forest Conditions

The original land survey by the General Land Office (GLO) is the earliest systematically recorded information on forest composition in the Lake States. The GLO surveys began in 1826 in Michigan, 1832 in Wisconsin, and 1847 in Minnesota (Stearns 1995). GLO surveyors noted tree species and their diameters along section lines, providing a grid of transects approximately 1 mile apart. Locations of recently burned areas, windthrows, beaver impoundments, rivers and streams, wetlands, existing settlements, trails and roads, and agricultural potential of soils were recorded, and generalized maps of timber types and soil quality were prepared. Pre-European settlement forest land conditions have been mapped by scientists using land survey notes in each of the three Lake States (Comer et al. 1995; Finley 1976; Marschner 1974). All of these maps were developed subjectively to some degree.

General Land Office data and related maps provide insights regarding the pre-European extent of aspen, which was probably an order of magnitude less in the historic forests in Michigan and Wisconsin than today. In northern Minnesota, 13% of all bearing trees recorded by the surveyors were aspen (Almendinger 1997), and nearly 30% of the forest land was composed of mixed communities that included aspen as a component. The situation then (and to a lesser degree now) was that extensive areas of mixed conifer-aspen, aspen-birch, and aspen-oak forests were present in Minnesota, each typified by high densities of aspen stems. Northern Wisconsin and northern Michigan had much smaller aspen components—approximately 300,000 acres in each (Comer et al. 1995; Finley 1976).

Ostensibly, maps generated from GLO notes only provide a single measurement of forest conditions during the early to mid-nineteenth century. As noted, climate change, disturbance regimes, and physical substrates must be considered when interpreting the meaning and utility of maps of historic forests relative to changes in forest ecosystems. Contemporary forests, where aspen is much more prevalent, have undergone tremendous change when compared to these earlier forests. And people set the stage.

The Root of the Aspen Boom

Although aspen had played a significant though minor role in the pre-European settlement forest of the northern Lake States, that situation began to change during the mid-19th century. At that time, prime timber in the northeastern United States was nearly gone. Furthermore, good farmland was scarce for young people starting out on their own and for immigrants just off the boat from Europe. So naturally eyes began to turn toward the virgin pinelands of the Great Lakes—"The West," as it was then known. The timber was magnificent, land was cheap, and state and federal governments vigorously promoted settlement. Furthermore, the then guiding principle of Manifest Destiny deemed that the wilderness had to be tamed so people could settle and farm the land. What happened in the next 80 years was indeed settlement on a grand scale, but it also turned into a rampant human-caused disaster and an ecological disruption seldom rivaled. It couldn't have been better for aspen.

Beginning in about 1850 in the Saginaw River Valley of Michigan, then spreading north and west through the Lower and Upper Peninsulas of Michigan, Wisconsin, and Minnesota, the timber barons and their legions of shanty boys went to work on the timber. Pine was on the top of their priority list, but hemlock, cedar, and hardwoods were exploited when the pine was gone. By 1930 most of the virgin timber in the Lake States had been felled. Today, remnant old-growth forests are virtually nonexistent in Michigan and Wisconsin, although some large tracts still exist in extreme northern Minnesota, principally in the Boundary Waters Canoe Area. What amounted to the clearcut of three states would have bode well enough for the future of aspen, but what usually followed logging suited this "Phoenix tree" even better (Graham et al. 1963).

Disastrous wildfires regularly ripped through the cut-over forest lands, usually in late summer or autumn following periods of extreme drought (Haines and Sando 1969). Consuming both people and pine reproduction without partiality, these fires created in their aftermath ideal conditions for aspen regeneration. The deadliest fires have become part of the lore of American forestry (Holbrook 1944). October 8, 1871, for example, was the worst day of wildfire in recorded history. The Peshtigo and Great Michigan Fires roared through Wisconsin and Michigan, killing nearly 1,500 people and blackening well over 3 million acres. On that same day The Great Chicago Fire burned most of that city to the ground, and thousands of acres of midwestern prairies were ablaze. Other wildfires achieved great notoriety: the 1881 Thumb and 1908 Metz Fires in Michigan; the 1894 fires that consumed much of northwest Wisconsin; and the 1894 Hinckley, 1910 Baudette, and 1918 Cloquet Fires in Minnesota. These fires often reburned land that had previously been scorched, creating an ecologically ideal situation for aspen by diminishing tree competition, creating an optimal seedbed, and stimulating sucker regrowth.

Michigan provides the extreme case study of wildfire's effect on aspen—of the three northern Great Lakes States, none was hit harder by 19th and early 20th century wildfires. Extensive areas were converted from pine to aspen. The area burned during the 60-year period beginning in 1871 is staggering—nearly 11 million acres, most in the northern part of the state (Mitchell and Robson 1950) (figure 3). Three caveats regarding these data, however, need to be emphasized. First, prior to 1930 the perimeters of large fires rarely were carefully measured, so their areas are only rough estimates. An exception was the disastrous 1881 Thumb Fire, the extent of which was carefully documented by Sgt. William O. Bailey of the U.S. Signal Service (Bailey 1882). Second, many smaller fires were not reported, much less known about, so yearly areas actually burned prior to 1930 probably exceed the recorded estimates, in some case by a considerable extent. Third, wildfires frequently reburned areas consumed in previous conflagrations, often repeatedly. Thus, the yearly burn estimates cannot be viewed as a continually expanding cumulative area of the state.

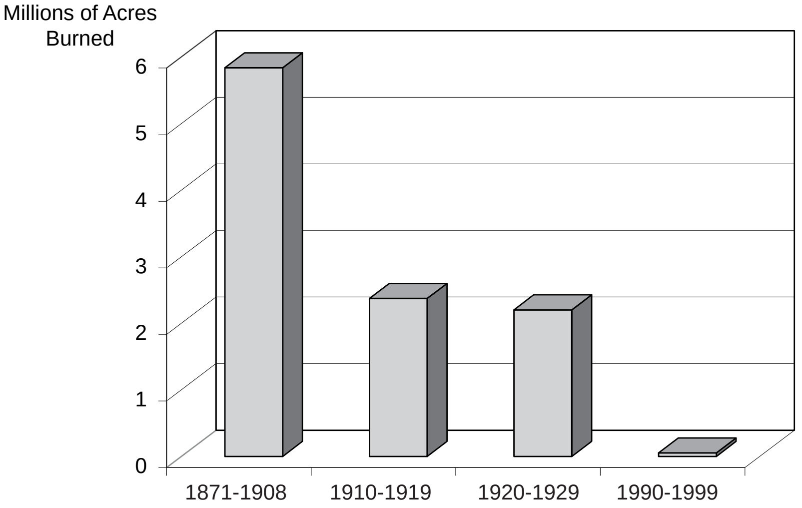

Figure 3—Estimated areas burned by wildfires during three early periods of Michigan history and the last decade of the 20th century. Areas are likely to be underestimated prior to 1930 (sources: Mitchell and Robson 1950; U.S. Forest Service; Michigan Department of Natural Resources).

Due to the combined effects of logging and wildfires, between a fifth and a quarter of northern Michigan was transformed into conditions favoring the establishment of aspen. Similar situations occurred in Wisconsin and Minnesota. This was a monumental ecological event and led to what is probably the largest human-caused forest type conversion in history. The irony of these profound events is that while their intent was to clear the land for the establishment of a vast agricultural enterprise, they instead led to a 20th century timber boom that mirrored the shanty boys' efforts from the previous century. However, the latter-day boom fed on aspen fiber, rather than pine lumber.

In contrast to the pre-1930s situation, wildfire currently plays a minor role in the regeneration ecology of aspen. Fire prevention and suppression efforts have reduced the millions of acres burned before and after the turn of the 20th century to a negligible amount—e.g., 51,630 acres in Michigan in the decade from 1990 to 1999. Wisconsin and Minnesota experienced similar success in taming wildfire. Thus, aspen's future in the northern Lake States depends on continued harvesting of mature stands to promote sucker regrowth and silvicultural practices aimed at natural seed regeneration or planting on carefully prepared sites. Notwithstanding these efforts, the over 17 million acres of aspen that once occupied the cut-over, burned-over lands of these three states will likely never be seen again, or at least never on such a grand scale. The relevant followup question, then, becomes—Why is this a problem?

FIA Records of Change: From the 1930s to Present

The aftermath of logging and burning had social as well as ecological impacts. The rotating ownership of denuded lands eventually gave way to a pattern of private and public ownership across the three-state region. Fire control became commonplace. And slowly, the forests grew, increasing in quality and extent.

Cunningham and Moser (1938a) noted that "…forests originally occupied 80% of all the land in the three States…", and in the 1930s that there was "…a large volume of wood of inferior quality and inferior species available for immediate use…". Over 11 million acres of previous forest land was still deforested in the mid-1930s—a target for planting by the Civilian Conservation Corps.

Although sample methods and definitions have evolved over the 60+ years of FIA inventories, these data provide the best measures we have of forest changes over the Lake States region. Since its recorded peak in the Lake States in the 1930s, aspen-birch acreage has decreased by 24% based on five FIA forest surveys/cycles (Chase et al. 1970; Cunningham et al. 1958; Cunningham and Moser 1938a,b; Findell et al. 1960; Guilkey et al. 1954; Jakes 1980; Lake States Forest Experiment Station 1936; Leatherberry and Spencer 1996; Miles et al. 1995; Raille 1985; Raile and Smith 1983; Schmidt 1997; Spencer and Thorne 1972; Stone 1966; Stone and Thorne 1961). The absolute acreage and rate of decline has varied by state, however (figure 4). Over a 58-year period in Michigan (1935 to 1993) and a 61-year period in Wisconsin (1935 to 1996), aspen-birch acreage declined by 37 and 36%, respectively. Over a 55-year period in Minnesota (1935 to 1990), aspen-birch acreage declined by only 6%.

The decrease in aspen-birch acreage in Wisconsin was relatively constant over this 61-year period, ranging from 0.6 to 0.9% per year. In Michigan, the decrease between 1935 and 1966 was also relatively constant, about 0.2% per year. Between 1966 and 1980, this rate increased seven-fold to 1.4% per year, dropping to 1.0% per year between 1980 and 1993. In Minnesota, a different trend has occurred. Aspen-birch declined initially, but then expanded modestly. The area of aspen-birch declined between 1977 and 1990 by 6%, or 0.4% per year. The end result of these declines creates a greatly reduced aspen-birch resource in Michigan and Wisconsin, and a slightly reduced area in Minnesota, where aspen-birch management has been more intensive.

Contemporary Aspen Trends in the Lake States

While acreages have declined since the 1930s, aspen-birch remains the second most prevalent forest type in the Lake States, representing 26% of the region's 49.0 million acres of timberland and 25% of the region's 51.9 million acres of forest lands. Only northern hardwoods (maple-beech-birch) have a greater acreage, comprising 28% of the region's timberlands and 27% of the forest lands.

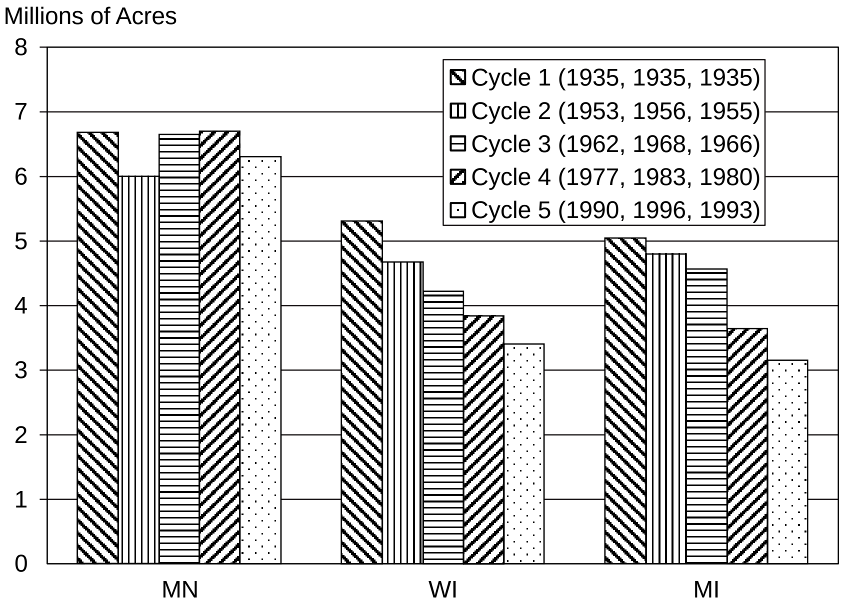

Figure 4—Area of aspen-birch in the Lake States over the five FIA forest survey cycles (cycle year in parentheses for Minnesota, Wisconsin, and Michigan, respectively (source: USDA Forest Service Lake States Forest Experiment Station and North Central Forest Experiment Station).

As we see in the long-term trends, intensive management/disturbance will be required to maintain or expand aspen area. Otherwise, the regional decline in the aspen-birch forest type will continue (e.g., there was a 1.3 million acre decline between the most recent forest inventory cycles). Indications that contemporary management is intensifying are reflected in (1) changes in aspen size classes, (2) forest type transitions identified in recent FIA surveys, and (3) reported production, sales, and stumpage prices.

The last two FIA survey cycles (4 and 5) spanned 13 years for Minnesota (1977, 1990), Wisconsin (1983, 1996), and Michigan (1980, 1993) (Jakes 1980; Leatherberry and Spencer 1996; Miles et al. 1995; Raille 1985; Raile and Smith 1983; Schmidt 1997). During this time, aspen (rather than aspen-birch) area declined by 5, 11, and 21% in Minnesota, Wisconsin, and Michigan, respectively (figure 5). However, several patterns indicating intensive management have appeared. In Wisconsin and Minnesota, acreage of aspen seedling-sapling increased from 39 to 55% and 28 to 34%, respectively, of the total acreage in this forest type. In Michigan, total acres of aspen seedling-sapling decreased, but the proportions remained relatively constant (40–41%). Across the three-state region, the area of aspen seedling-sapling increased from 34 to 41% of the total acreage in this forest type. In Minnesota, seedling-sapling and sawtimber area increased, but there was a substantial decline in poletimber (1.2 million acres). Wisconsin had declines in area of poletimber and sawtimber stands. Michigan's poletimber area declined, too, but the sawtimber area increased.

Ingrowth and conversions into and out of aspen also influence the long-term composition of the Lake States forests. Remeasured FIA plots were examined to identify transitions from aspen to other types between cycle 4 and 5 (figure 6). In Minnesota, a high percentage of plots that were aspen in cycle 4 remained as aspen in cycle 5. This percentage declined to the east. The increasing transition from aspen to maple-beech-birch is evident from west to east. Of course, there also are transitions into aspen—the major source of new aspen acreage is from various softwood forest types. But overall, more land is converting from aspen to more tolerant species than to aspen.

Estimates of current net annual growth versus current annual removals provide another indication of intensity of aspen harvest. Based on the most recent FIA reports, removals exceed net growth by 8% in Minnesota and 45%

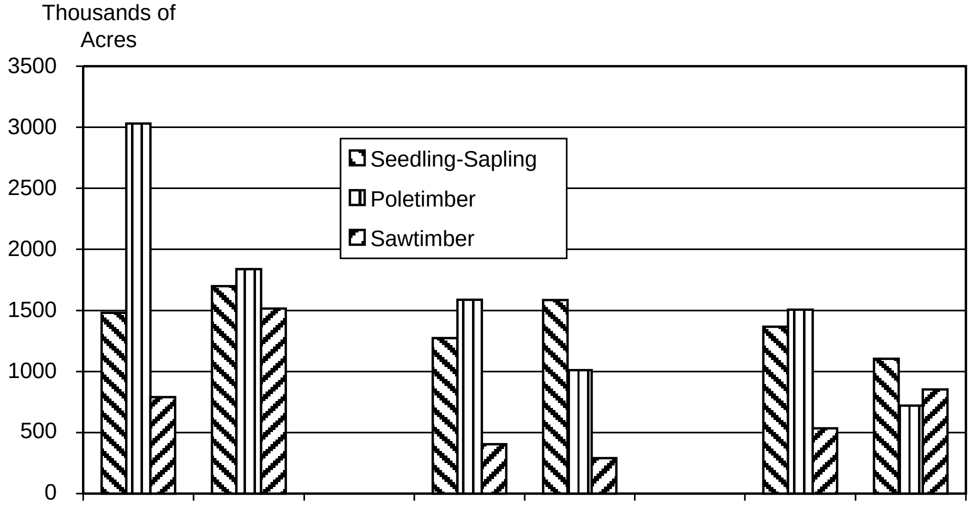

Figure 5—Size class distribution for aspen forest type over last two survey cycles (4 and 5) for Minnesota (1977, 1990), Wisconsin (1983, 1996), and Michigan (1980, 1993) (source: USDA Forest Service North Central Forest Experiment Station).

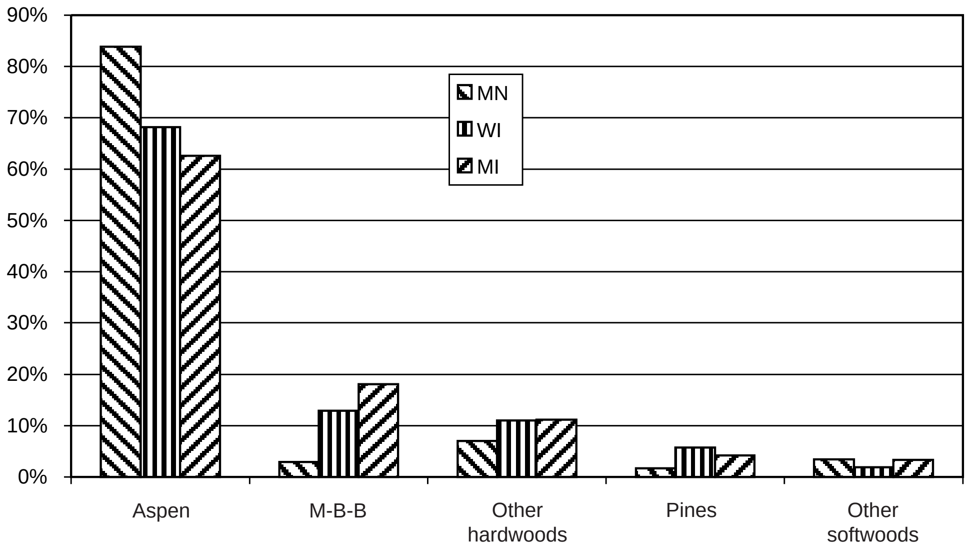

Figure 6—Percentage of area based on remeasured FIA plots that were aspen in cycle 4, and aspen and other types in cycle 5 (source: USDA Forest Service Eastwide Forest Inventory Data Base).

in Wisconsin. Removals are slightly less than net growth (98%) in Michigan. This is an indication of very intensive harvesting, particularly considering the questionable availability of private nonindustrial lands for timber production and the declining availability of federal lands.

Aspen has not always been a popular commodity. Holcomb and Jones (1938) wrote:

> As the supply of other material becomes scarcer and the aspen reached favorable size, several industries began to use it. Many thousands of cords are now consumed annually for excelsior, paper, box shooks, fuel wood, and even fence posts.
>
> It must be remembered, though, that aspen is serving as a nurse crop on depleted soil and much of it will give way to better soil demanding and more permanent species as the soil regains its former productivity.

Later, Spencer and Thorne (1972) emphasized that "[a]spen, one of the postfire species, was especially prolific and was considered a virtually useless weed species by many until recently."

It is no longer a weed tree. The level of aspen pulpwood production has increased substantially in the past 20 years, with Minnesota responsible for most of the growth (figure 7)—this mirrors the higher level of aspen area retention

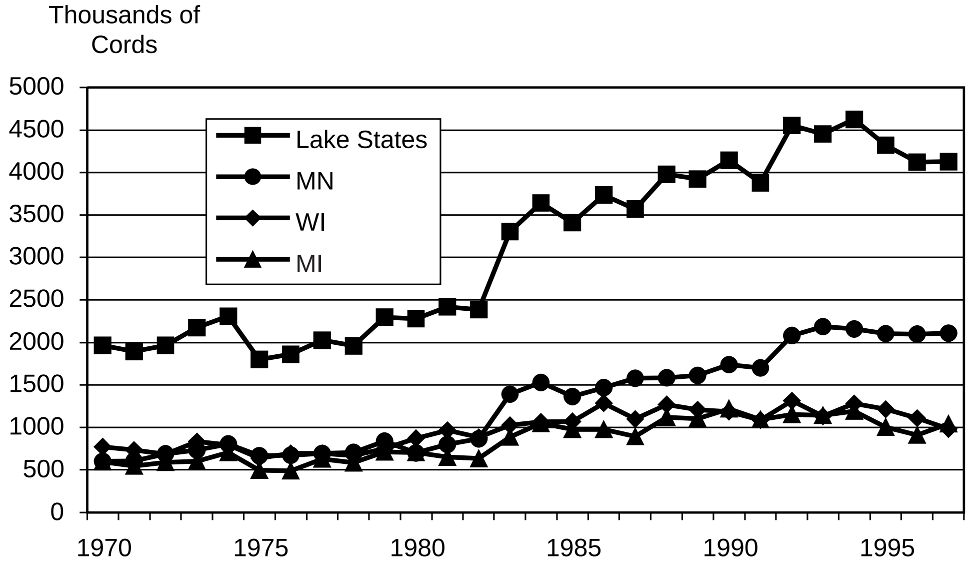

Figure 7—Aspen pulpwood production in the Lake States, 1970-1997 (source: USDA Forest Service North Central Forest Experiment Station).

in Minnesota. While overall aspen production is up, the role of the national forests has diminished (figure 8). Increasing prices for aspen stumpage provide an incentive for many landowners to harvest their timber.

In addition to its role in the timber market economy, the aspen forest type is synonymous with two popular game species in the Lake States—white-tailed deer and ruffed grouse. Hundreds of thousands of hunters wander the north woods with hopes of a successful encounter with these species. But there is much more to aspen in terms of habitat than simply white-tailed deer and ruffed grouse. Beyer (1983), for example, identified 60 bird species and 111 species of vegetation on his aspen study sites—all associated with timber harvesting. Older aspen can provide essential cavities for birds, and decaying aspen contributes to the dynamics of forest death and rebirth.

Based on indicators of changes in acres in aspen size classes and percent of growth harvested, aspen is being managed intensively in the Lake States. So the question again—Why is this a problem?

Management Options for Aspen

The Lake States, like most regions, has many people with different views on the appropriate use of forest lands. Some would have the forest protected from harvest, perceived as exploitation. Others would have them managed even more intensively. Many fall somewhere between the extremes—this creates the root of the problem, what to do with the aspen forests?

Aspen management has given rise to a number of contentious issues. Perhaps foremost are concerns regarding biodiversity, and the effects of aspen management on forest fragmentation and loss of interior habitats needed for area-sensitive species. And although aspen provides critical habitat for many species such as the ruffed grouse, it also helps support enormous deer populations. Overpopulation by deer has led to tens of thousands of car-deer collisions annually in each of the Lake States, has resulted in excessive browsing of tree seedlings and ground flora in general, and according to the National Center for Infectious Diseases in Atlanta, Georgia, has contributed to Wisconsin and Minnesota ranking seventh and tenth in incidence of lyme disease per capita in

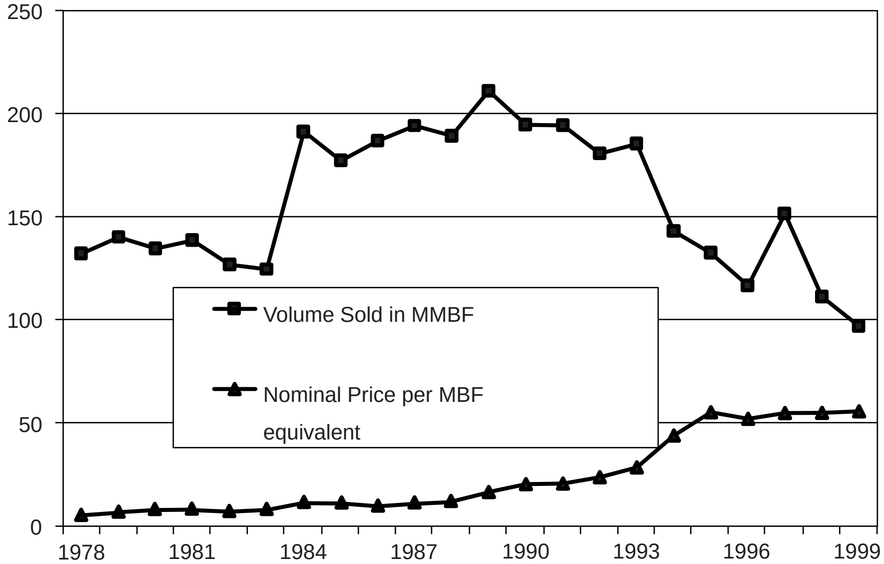

Figure 8—Aspen volume sold and nominal price per MBF equivalent from the Lake States National Forests, 1978-1999 (source: USDA Forest Service; Cut & Sold Reports).

the United States. Thus, management options for aspen are influenced by both social and ecological considerations. Rather than prescribe a social fix, we present a number of options for managing a resilient aspen resource.

The silvicultural prescription for aspen retention on a site has been traditionally viewed by Great Lakes foresters in a rather simplistic way—clearcut a mature stand, stand back and let suckers retake the site, wait, and then clearcut again when the stand matures. No site preparation, no cleaning, no thinning, no pest control, little thinking. Whereas this prescription has worked well in many situations and represents a viable silvicultural option for aspen, the more complex objectives of modern forest management dictate that additional pages be added to the active prescription manual for aspen (Perala 1977). This need is particularly acute for managers of public lands. The traditional approach also does not take into account ecological situations that might call for promoting succession out of aspen, or deterring aspen suckering, e.g., a dense understory of desirable trees and shrubs. Table 1 summarizes the palate of silvicultural options that are available to managers, depending on their management objectives. Our table extends the decision tree for management of mature Lake States aspen proposed by Stone (1997).

Management for timber represents the most straightforward approach to aspen silviculture, especially on forest industry lands. In this case the overriding objective is to maintain a continual supply of aspen raw material to the mill, so rapid growth, yield per acre, wood uniformity, and sustainability are paramount concerns. For pulpwood, oriented strandboard, or solid wood products, the conventional clearcut-coppice prescription works fine in most situations, with rotation length determined by culmination of mean annual increment or a diminishing economic rate of return. But other options are available, e.g., selective or strip thinning of sapling through pole-size stands (Brinkman and Roe 1975). Thinning has been demonstrated to reduce the length of pulpwood rotations (Jones et al. 1990), increase net volume increment (Weingartner and Doucet 1990), and increase sawtimber output up to 40% and veneer output up to 140% (Perala 1977). Thinning also can be an effective means of eliminating poor clones from a stand, provided residual densities are heavy enough to retard suckering. Blandin Paper Company in Grand Rapids, Minnesota, has mechanically thinned about 6,500 ha in the past decade. Their prescription for 8- to 10-year-old aspen sapling stands calls for flattening 2 to 2.5 m wide strips at a spacing of 2 to 3 m (Zasada et al. 2000).

An argument against thinning has been that low stand densities promote infection by *Hypoxylon mammatum* (Anderson and Martin 1981), especially in the very susceptible quaking aspen. Because considerable interclonal variation in canker incidence exists in quaking aspen (Ostry and Anderson 1990), thinning can be a viable option if it is restricted to the most resistant clones. Another option would be to delay thinning of dense stands until the lower branches have naturally pruned, since branches are a major entry point of *Hypoxylon* infection.

On the other end of the scale of management complexity from forest industry are public land agencies—in particular the USDA Forest Service and the state Departments of Natural Resources. Here, timber is just one of many management objectives (table 1), and in some cases a minor one. Aspen's vital role as habitat for game and nongame wildlife, its role as a component of old-growth systems or landscape diversity, and its aesthetic appeal presents a spectrum of management options for public land managers (Brinkman and Roe 1975). Therefore, silvicultural prescriptions—in addition to the traditional clearcut-coppice approach—could be designed to develop a multiage-class

Table 1—Alternative silvicultural approaches to management of Lake States aspen. In all cases the main objective is the retention of aspen as a component of the stand.

Stand silviculture	Management objective				
	Timber	Wildlife habitat	Old growth or aesthetics	Diversity	Conversion to aspen
Harvest	Clearcut commercially mature stands	Clearcut or variable retention of other desirable species	None[a], variable aspen retention, clearcut, or burn as stand breaks up	Clearcut or burn as necessary to maintain aspen type	Clearcut existing stand—hardwood or conifer
Size of harvest units	Generally large (40+ acres) or entire stand	10-100+ acres depending on habitat objectives	<5 acres to entire stand	Extremely variable	ca. 40 acres maximum for seed regeneration[b]
Rotation or cutting cycle	30-70 years[c], depending on site and clone	20-80+ years depending on area age class distribution	60-120+ years	35-70+ years	Variable depending on existing forest type
Site preparation	None[d], except where a dense understory of tolerant trees requires cutting, burning, or herbicide treatment	None[d]	None[d]	None[d]	Burn, scarify, herbicides, or a combination to reduce competition and create a seedbed
Tending	Precommercial or commercial thinning optional for dense stands or to expand desirable clones	Generally none	Optional; thinning will produce large-diameter trees more quickly	Generally none	Cleaning may be necessary in the first or second year after establishment of aspen regeneration
Overstory composition	Pure stands preferred	Pure or mixed species, multistoried stands depending on habitat objectives	Pure or mixed species, multistoried stands	Both pure and mixed stands	Pure or mixed stands; subsequent clearcut harvests can increase aspen component

[a] No harvest or disturbance means succession to a vegetation type devoid of aspen.
[b] Mature aspen seed trees must be upwind of harvest unit; larger sites may be planted.
[c] Very short rotations (<20 years) may lead to deterioration of aspen root systems.
[d] Provided adequate potential for sucker reproduction exists.

distribution across a local administrative district or area; promote mixed, vertically stratified stands with aspen as a major or minor component; grow large-diameter old-growth trees; produce standing or down dead aspen stems; and create vistas where the beauty of aspen and other forest types can be viewed by the public. To meet these objectives, creative application of clearcuts of varying size, thinnings from above or below, dispersed or aggregated partial harvest cuttings, and prescribed burning can be employed (Perala 1977; Weingartner and Doucet 1990).

Retention of aspen or other species on a harvest unit offers a range of creative options to produce stands that meet multiple objectives. Dispersed retention of trees, however, reduces sucker density and growth compared to a complete clearcut, especially if the residuals are aspen (Perala 1977). Nonetheless, residual basal areas as high as 14 m^2 per ha still can produce adequate aspen stocking, although the resulting regeneration will likely be mixed in composition (Doucet 1989). Recent work in the southeastern and western boreal forest has shown that quaking aspen will reproduce in gaps of various sizes that develop in a mature overstory (Cumming et al. 2000; Kneeshaw and Bergeron 1998). Thus, pure or mixed aspen stands could even be managed under an uneven-aged system, at least until tolerant species begin to dominate the understory. Retention of pines, spruces, oaks, black cherry, and other desirable species on harvest units can produce mixed aspen stands with improved wildlife habitat, diversity, or visual qualities. Aggregated retention provides another means to a similar end, without the penalty of reduced aspen stocking on the harvested areas. Groups from <1 ha to several ha in size of mature aspen or associated species can be left on an otherwise clearcut harvest unit to create patches of old growth or for other values.

Burning is another silvicultural approach that could be employed on a wider scale by public land managers in the Lake States. In this case the prescription would be to let fire be the selective agent, creating an unpredictable but nonetheless very natural mosaic within the burn unit. Aspen is uniquely adapted ecologically to recapture a site following fire (Perala 1995). Fire also can increase understory diversity and biomass in stands of sucker regeneration (Brown and DeByle 1989). Burning could be especially useful in the management of wilderness areas where timber harvesting is prohibited or in old-growth units. Private organizations like The Nature Conservancy also could utilize more fully the use of fire in managing aspen on their lands.

Other ownership categories fall somewhere between timber industry and public land agencies in the range of silvicultural options of choice. Organizations that promote game habitat—like the Ruffed Grouse Society or hunting clubs—may have habitat enhancement and diversity as their overriding objectives. In many cases dispersal of small clearcuts across their ownership provides the diversity of age classes needed to support high animal densities. In some cases partial cuttings or fire also may be employed. Still other land managers may choose to reduce aspen clearcutting to reduce fragmentation. One means would be to aggregate compatible land uses, concentrate aspen management in large blocks where possible, and avoid management in areas adjacent to continuous forest lands. Another means would be to selectively thin aspen, leaving residual trees and advanced regeneration composed of later successional species. Retention of some aspen trees may reduce sucker density because sprouting is hormonally controlled, and is suppressed by auxin transported from the stem to the roots (Schier et al. 1985).

In any discussion of ownership management options, the nonindustrial private forest land (NIPF) owners are the wild card. Ranging from complete unawareness of or disinterest in management in any form to sophisticated tree farm operations, the pervasive NIPFs could choose any or all of the options presented in table 1. Education always is of paramount importance when dealing with NIPFs, and in the context of this discussion perhaps the major task facing extension or service foresters is to convince NIPFs that doing nothing means the eventual loss of aspen. This fact has and will continue to come as an unpleasant surprise for many of these owners, especially if their prize aspen stand already has gone around the bend and broken up. On the other hand, the revelation that mature aspen can be sold at an excellent price, with little danger of regeneration failure, may strike other owners as a deal too good to pass up.

A final topic needs particular emphasis—aspen can be regenerated by seed (Zasada et al. 2000). Death and breakup of existing stands, therefore, does not necessarily mean inevitable reduction of the aspen component in a particular landscape. Three factors must come together, however, to get an adequate catch of aspen seedlings on a clearcut or shelterwood harvest area (Brinkman and Roe 1975). First, an adequate rain of seed must occur, which will occur in most years, particularly if aspen seed trees border the harvest unit. Second, a receptive seedbed must be prepared, either by scarification to expose mineral soil or by a hot fire. Third, seedfall must be followed by cool, moist conditions until seedlings are well established. While the last factor is not controllable by silviculturists, proper attention to the first two will produce a likelihood of success that does not differ appreciably from natural regeneration of most Lake States tree species.

Conclusions

Aspen has declined in the Lake States over the past 70 years, although the baseline for these losses was established immediately following a time and a human-caused series of disturbances with no historical precedent. The species and its minor associates remain the second most dominant forest type in the region, and increases in market prices and harvest intensity suggest that aggressive management will continue. As Hunter (1999) pointed out, "Aspen forests in the Lake States, which originated after severe, repeated fires following logging of the old-growth pine, are now valuable enough that foresters consciously perpetuate a severe disturbance regime that was quite uncommon before exploitation." It appears that the aspen forest type is secure for now in the Lake States, although additional loss of acreage, particularly from unmanaged private lands, is almost certain in some areas.

Questions of balance remain, however. Simultaneously meeting production and conservation goals of sustainable forest management remains an unmet national and international challenge. Blending aspen management with other ecosystem and species maintenance and restoration needs is probably the greatest challenge confronting forest managers in the Lake States. A potential exists to increase aspen productivity through even more intensive management. There is also considerable potential to supplement current supply by increasing the use of fast-growing hybrid aspens or poplars in reforesting poorly stocked forest lands and abandoned agricultural lands. The potential also exists to reduce adverse effects of aspen management by assessing resource conditions and trends across broad geographic areas, identifying opportunities and limitations for multiple-use management that features both conservation and production emphases, and engaging in collaborative resource education, planning, management, and monitoring. In other words, engaging in a voluntary multiownership adaptive management strategy that accommodates desired outcomes among cooperating parties. Under this scenario, the rights and choices of private citizens and landowners, goals of industrial interests, and mandates of government agencies might all be honored while resource production and conservation are achieved.

By acknowledging feasible options and mimicking natural disturbances while maintaining or restoring forest composition and age-class structures at landscape and local levels, we believe conservation goals can be achieved. In cases where we choose to depart from natural conditions and processes (e.g., high levels of aspen and plantation management), aggregating compatible uses to minimize adverse effects is warranted.

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Aspen Restoration in the Blue Mountains of Northeast Oregon

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Abstract—*In the Blue Mountains of northeast Oregon, quaking aspen is on the western fringe of its range. It exists as small, scattered, remnant stands of rapidly declining trees. Although little is known about the historic distribution of aspen in Oregon, it is believed that stands were once larger and more widely distributed. Decline of the species is attributed to fire suppression and browsing pressure from large ungulates. A landscape approach to restoring aspen is taken using a variety of techniques. Among these are construction of large herbivore exclosures, prescribed fire, establishment of new aspen stands using containerized planting stock, simulation of natural refugia, and use of genetic variation data to guide management decisions. Questions are raised on the social and economic costs of recovery efforts.*

Introduction

In the Blue Mountains of northeast Oregon, quaking aspen (*Populus tremuloides*) is on the western fringe of its range. It is most often found growing along stream corridors although it is occasionally seen on steep, rock outcrops and, to a much lesser extent, on dry, upland sites.

In the past decade, there has been increasing concern about the lack of successful regeneration in aspen stands. This has been attributed largely to fire suppression efforts as well as browsing pressure from both domestic livestock and large native ungulates, specifically both whitetail and mule deer (*Odocileus virginianus columbianus* and *Odocileus hemionus hemionus*) and elk (*Cervus elaphus nelsoni*).

The Role of Fire

Fire is an important component in both establishing new stands of aspen and in assisting aspen in maintaining its position on the landscape (Jones and DeByle 1985). Aspen seeds require exacting conditions for successful germination (McDonough 1985). These conditions include a mineral soil seedbed and an extended interval of optimum soil moisture. Fire exposes mineral soil by consuming forest floor litter and reducing or eliminating competing vegetation. Suppression of fires has limited the areas where new stands of aspen may become established.

Aspen is considered a shade-intolerant species (Baker 1949). In the Blue Mountains, conifers growing in the understory of aspen stands will eventually overtop the aspen canopy in the absence of fire or some other disturbance. In time, aspen will disappear from that location on the landscape. If, however, fire should consume both the conifer and aspen overstory, the aspen root system will often survive. Upon release from the apical dominance of the overstory trees, the root system responds by sending up thousands of suckers to reoccupy the site. The rapid initial growth rate of aspen, along with a fully established root system, allows it to outcompete other colonizing tree species for light, moisture, and

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nutrients. In this manner, a particular stand of aspen can maintain its position upon the landscape.

The Fall and Rise of Big Game Herds in Northeast Oregon

Browsing by large ungulates has contributed to the demise of aspen regeneration in many areas of the western United States (Bartos et al. 1991; DeByle 1985; Kay 1990; Kay and Bartos 2000; Smith et al. 1972). This may be due, in part, to a dramatic increase in herd size from pre-European settlement to the present (Kay 1994). The first homesteaders began settling northeast Oregon in the mid-1800s. Although no numbers are available for that period, game was said to have been "plentiful" (Hug 1961). However, Native Americans hunted herds for subsistence, and wild predators such as the wolf (*Canus lupus*) and the cougar (*Puma concolor*) also killed their share. One early settler in Union County, Oregon, was quoted as saying, "The Indian had his own game conservation programs that were effective, but white men paid little attention to them." As settlements grew, so did the hunting pressure. By the turn of the century, big game numbers had dwindled alarmingly. By 1909, elk were so scarce that the Oregon State Legislature put a ban on hunting elk that lasted until 1932 (Oregon Department of Fish and Wildlife 1992). In 1912 and 1913, 30 elk from Jackson Hole, Wyoming, were brought in to supplement the herd (Bailey 1936). These elk were placed in a protective enclosure known as "Billy Meadows" on the Imnaha National Forest where they thrived and grew in number.

With legislated protection from hunting, both introduced and native herds grew quickly. In 1916, elk only numbered in the hundreds on the Umatilla National Forest. By 1933, their numbers were estimated at 3,080 on the forest. During this same year, hunting of elk was reestablished due to complaints about competition between elk and domestic livestock. In spring of 2000, the Forest Service reported between 12,000 and 15,000 elk on the Umatilla National Forest (Charlie Gobar, Forest Biologist, personal communication).

Domestic Livestock

While deer and elk were struggling for their existence, domestic livestock numbers were on the rise. In the period between 1890 and 1912, rangelands were reported as being overgrazed by cattle and sheep (Hug 1961). This is not surprising considering that sheep flocks reached a peak population of 240,000 in Umatilla County alone (Bureau of the Census 1912). As cattle numbers increased, bands of sheep were eventually displaced from rangelands.

As native ungulate herds recovered, the addition of domestic livestock onto the landscape contributed to a level of browse pressure that aspen stands may never have experienced before in their life history. Add to this the reduction of fire in the ecosystem and you have an environment that is hostile to the regeneration of aspen. This article addresses the aspen restoration work completed to date on the North Fork John Day Ranger District of the Umatilla National Forest.

Existing Conditions

The North Fork John Day Ranger Station, located in Ukiah, Oregon, lies at an elevation of 3,350 feet. Situated in a somewhat dry valley bottom, most of the area is used as pasture for cattle and horses. Powell (2000) describes this as the valley grasslands zone. An occasional clump of aspen may be found growing along stream courses that have been heavily degraded by livestock. As the elevation increases to 3,500 feet (these elevation bands are not absolute and vary across the Blue Mountains and within the District), open stands of ponderosa pine (*Pinus ponderosa*), juniper (*Juniperus communis*), and sagebrush (*Artimesia* spp.) are encountered (the woodlands/shrublands zone). Above this elevation, the land is primarily forested, the species composition being dictated by aspect and elevation. South and west aspects, between 3,500 and 5,000 feet, support dry forest stands of ponderosa pine (the dry forest zone). Western larch *(Larix occidentalis*) often grows on south exposures within volcanic ash inclusions. Douglas-fir (*Psuedotsuga menziesii*) and grand fir (*Abies grandis*) invade these sites in the absence of disturbance. On east and north faces within the same elevation band, mixed conifer stands of western larch, Douglas-fir, grand fir, lodgepole pine (*Pinus contorta),* western white pine (*Pinus monticola*), smaller amounts of ponderosa pine, and Engelmann spruce (*Picea engelmannii*) are found. Engelmann spruce is limited to stream corridors and areas of high water tables. These constitute the moist forest zone.

Above 5,500 feet, in the cold forest zone, subalpine fir (*Abies lasiocarpa*), Engelmann spruce, lodgepole pine, and occasionally whitebark pine (*Pinus albicaulis*) are the dominant tree species. Quaking aspen occurs throughout the elevation gradient, 3,300–6,000 feet, growing wherever adequate moisture exists, primarily along stream channels.

Aspen does not appear to be restricted to any particular plant association or soil type. It is found growing adjacent to arid scab flats, warm pine sites, stands of mixed conifers, cool spruce-fir forests, or interspersed with lodgepole pine. Most stands have a significant component of conifers. No stand of aspen is larger than 20 acres, the majority being less than an acre in size.

Although aspen seedlings have been found recently inside of the 1996 Bull and Tower Fire perimeters, most regeneration observed to date has been from root suckering. While root suckers are usually numerous beneath stands, very few are recruited into the sapling size class, or larger, due to herbivory from large ungulates. Cattle are responsible for browsing a portion of the suckers from June through September. However, the most intensive browsing occurs after the cattle have been removed from grazing allotments in late September. By this time of year, grasses have cured out and the tender leaves, as well as the protein-rich buds, of aspen are especially appealing to deer and elk. By mid-October, it becomes increasingly difficult to find a sucker that has not been browsed. In fact, many suckers have been observed with multiple years of browse damage. These seldom reach more than two feet high and eventually die out. As a result, stands have failed to successfully regenerate.

The overstories of most aspen stands on the District are even-aged. Nearly all mature trees have stem decays, making accurate age determination difficult. However, survey results estimate stands to range in age from 80 to 150 years. This would place initiation of most of the overstories somewhere between the mid-1800s to early 1900s, when overhunting was decimating native elk herds and possibly before livestock numbers had peaked. While aspen root systems may persist for thousands of years, aspen trees have an average lifespan of between 100 and 150 years in the Rocky Mountains, although stands occasionally survive beyond 200 years (Burns and Hondkala 1990; Jones and Schier 1985). If the same holds true for aspen in the Blue Mountains, then most of our aspen overstories are approaching the end of their natural life cycles. Several stands still appear to be vigorous but most are rapidly declining. Natural mortality from a wide host of insects and diseases, overtopping by conifers, and windthrow have contributed to the steady shrinking, or elimination, of stands across the district.

Restoration Efforts

Exclosures

In the late 1980s, district wildlife biologists became increasingly concerned with the loss of aspen habitat. They responded by building a number of livestock exclosures, constructed of native lodgepole pine, using a buck-and-pole design. The results were encouraging. Inside exclosures, suckers were released from browse pressure and exhibited rapid height growth (figure 1).

Believing that cattle grazing was the primary problem, the District experimented with the use of single-strand electric fencing. The fences were disassembled after cattle were removed from allotments in late September. This form of protection proved ineffective, indicating that aspen needed to be protected from native ungulates as well as cattle (Randy Fitzgerald, former District Range Conservationist, personal communication).

As a result, buck-and-pole fences evolved from an early 4-rail design to the current 6- or 7-rail design used today (figure 2). These fences are close to 7 feet tall and allow no more than 12 inches between rails, with no more than 8 inches between the ground and bottom rails. (Fence design specifications are available from the author at http://www.fs.fed.us/r6/uma/aspen.) This design has proved effective in deterring not only livestock but deer and elk as well. By contrast, it still allows smaller animals to move freely through the fenceline.

We recommend that exclosures be kept small—less than 0.5 acres is optimum, as animals tend to walk around small exclosures but often break down portions of large ones. We believe this happens most often during the winter when an animal would have to expend more energy walking through deep snow around the exclosure rather than through it.

Figure 1—Buck-and-pole livestock exclosure made from native lodgepole pine. Note the successful aspen regeneration inside the exclosure.

Figure 2—A large ungulate exclosure on Morsay Creek using the 6-rail design.

Prescribed Fire

Aspen often show a strong suckering response following prescribed or natural fires (Jones and DeByle 1985). In 1991, a prescribed fire was planned for a 20-acre stand of aspen that was heavily encroached upon by conifers. The conifers were felled the previous season to allow them to cure. The prescription aimed for a 60% kill of the aspen overstory. Leave trees were protected with heat-reflecting fire shelters and debris was pulled back from their bases. Ignition took place in the fall of 1991 because this area was too wet to burn in the spring. A positive suckering response was observed in 1992 followed by heavy herbivory that fall (Lea Baxter, District Silviculturist, personal communication). Within 2 years, nearly all of the suckers were eliminated. This indicated to us that aspen on the North Fork John Day Ranger District could not successfully regenerate without some form of protection from ungulate browsing.

Aspen Management Plan

In 1995, the members of a tri-forest Aspen Network met to discuss their successes and failures with aspen management. This group included biologists, silviculturists, range managers, reforestation technicians, botanists, and fire managers from the Malheur, Umatilla, and Wallowa-Whitman National Forests. They concluded that management plans were needed to focus aspen restoration efforts on individual districts.

The North Fork John Day Ranger District developed a plan that began by mapping and inventorying all stands and then using this information to prioritize stands for treatment (see figure 3). Accessible stands in the poorest condition were rated the highest priority for treatment. In addition to protecting existing stands, we are also interested in increasing their perimeters and establishing new sites. Monitoring the condition of all stands, as well as the success of applied treatments, is also of great importance.

Inventory results indicate that we have at least 300 small stands on the district. Clearly, not all these stands can be protected from loss, whether from natural decline, excessive browsing, or natural or prescribed fires. Therefore,

I. Inventory
  - mapping
  - surveys
  - database development

II. Protection
  - prioritize stands
  - construct exclosures

III. Enhancement
  - collect root segments for propagation
  - select sites for introduction of new stands
  - increase perimeters of existing stands
  - establish clone bank

IV. Monitoring

V. Education and Partnerships

Figure 3—The North Fork John Day Ranger District Aspen Management Plan.

another key element in the management plan is to establish a clone bank as a reservoir of genetic material. This will require collecting root sections from as many stands as is reasonable for propagation of containerized aspen. The containerized stock will be planted at the National Forest Native Hardwood Propagation Area in Clarno, Oregon.

Genetic Evaluation of Aspen Stands

Surveys of aspen stands across the district stimulated several questions about the historic distribution of aspen and relatedness of neighboring stands. In an attempt to answer some of these questions, we conducted a genetic study in 1997. Leaf samples taken from root suckers were randomly collected along linear transects within stands. However, clumps of aspen within a stand that appeared to be phenotypically unique were sampled even when it necessitated deviating from the transect. Samples were collected from 45 aspen stands within 20 drainages across the district. A total of 150 samples were sent to the National Forest Electrophoresis Laboratory in Placerville, California. These samples were prepared and analyzed following standard isozyme analysis procedures (Conkle et. al. 1982; Wendel and Wendel 1989). Samples were tested for genetic variation at 18 loci. The results are displayed in a series of dendrograms in figures 4–6.

For stands to be considered highly related, they need to have 94% of the sampled genes in common. The stands on the eastern portion of the district (figure 4) were not highly related. This was not surprising since most of these stands are isolated geographically. Stands that were located somewhat near to one another, such as Park Creek and Howard Creek, were found to share a larger proportion of genes in common.

Most of the aspen stands are situated on the western half of our district, referred to as the Western Route. Stands located within drainages on the

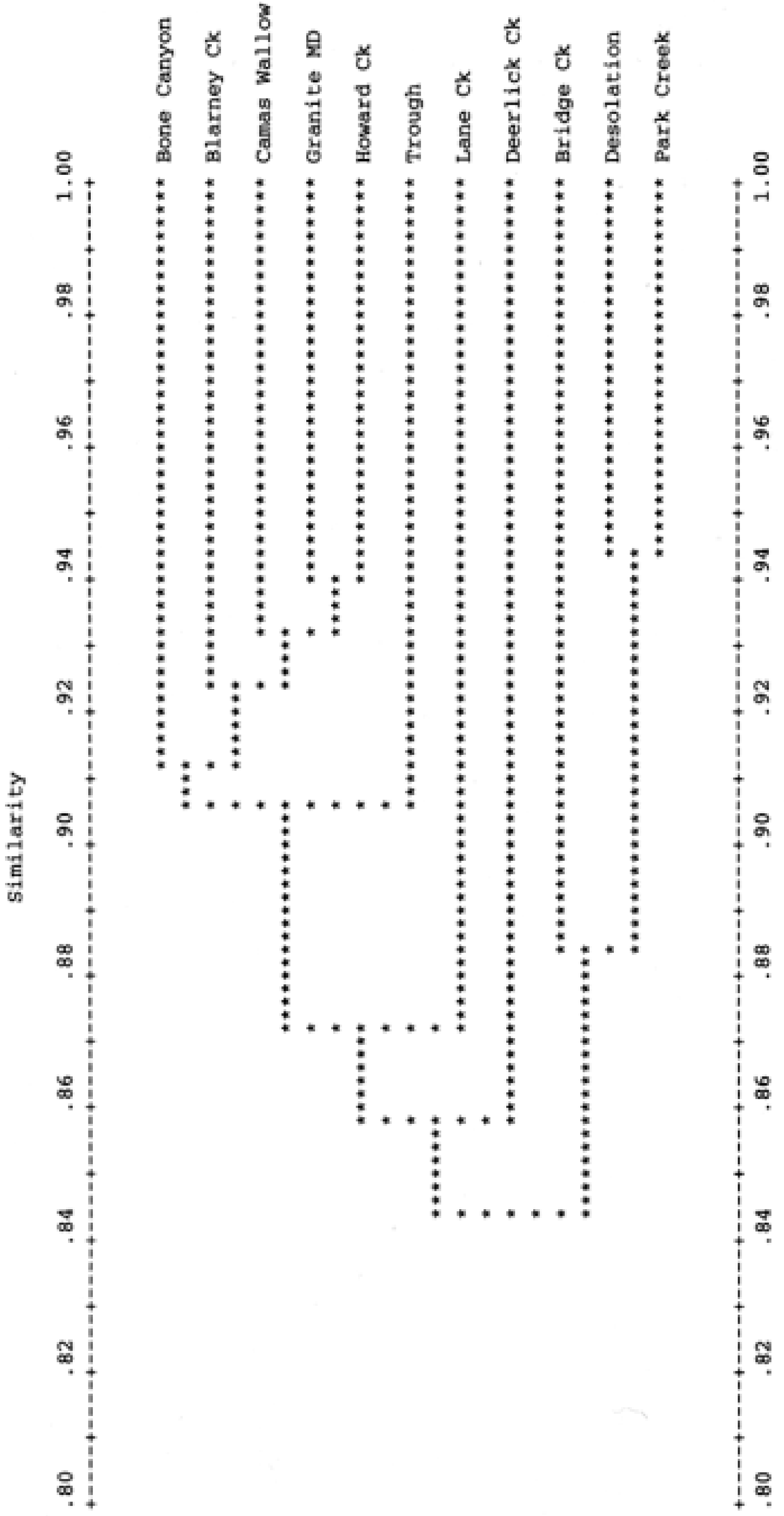

Figure 4—A dendrogram showing the results of isozyme analysis on aspen stands on the eastern half of the North Fork John Day Ranger District.

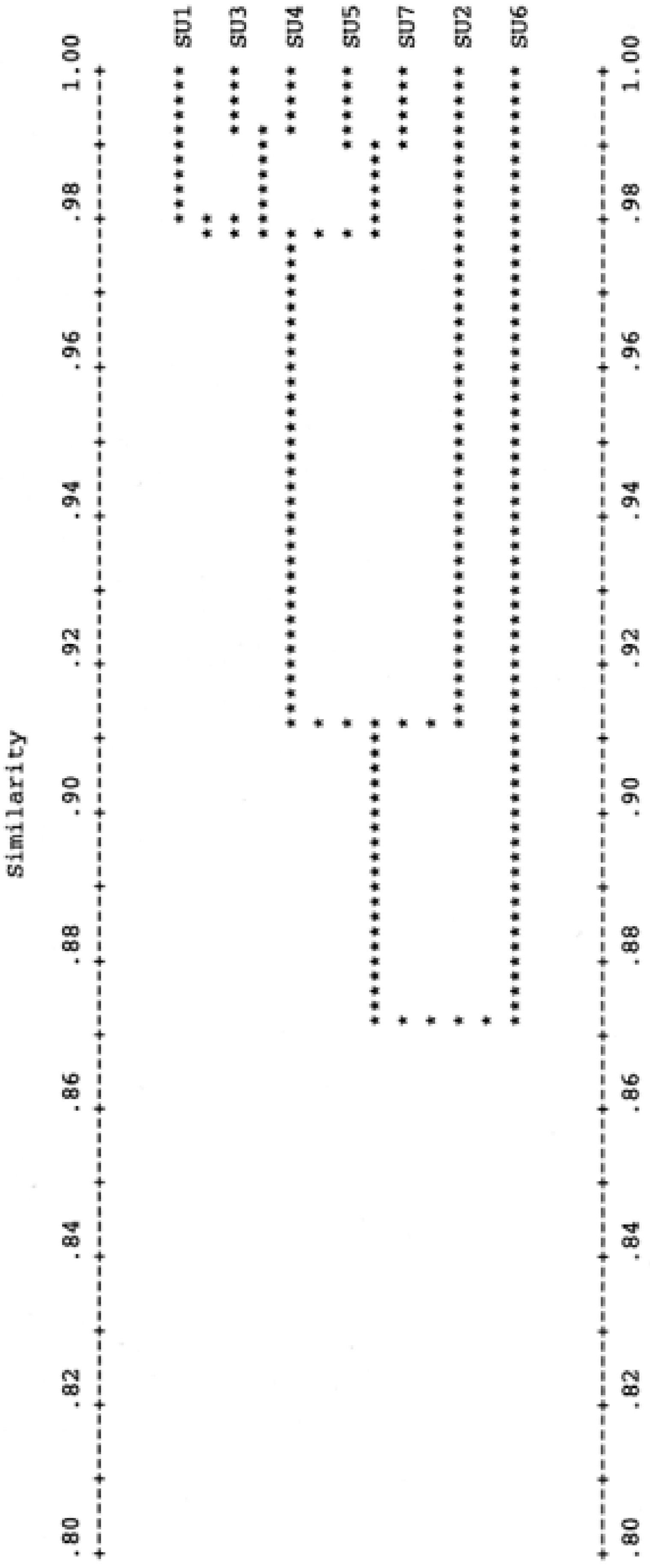

Figure 5—A dendrogram showing the results of isozyme analysis on aspen stands sampled along Sugarbowl Creek.

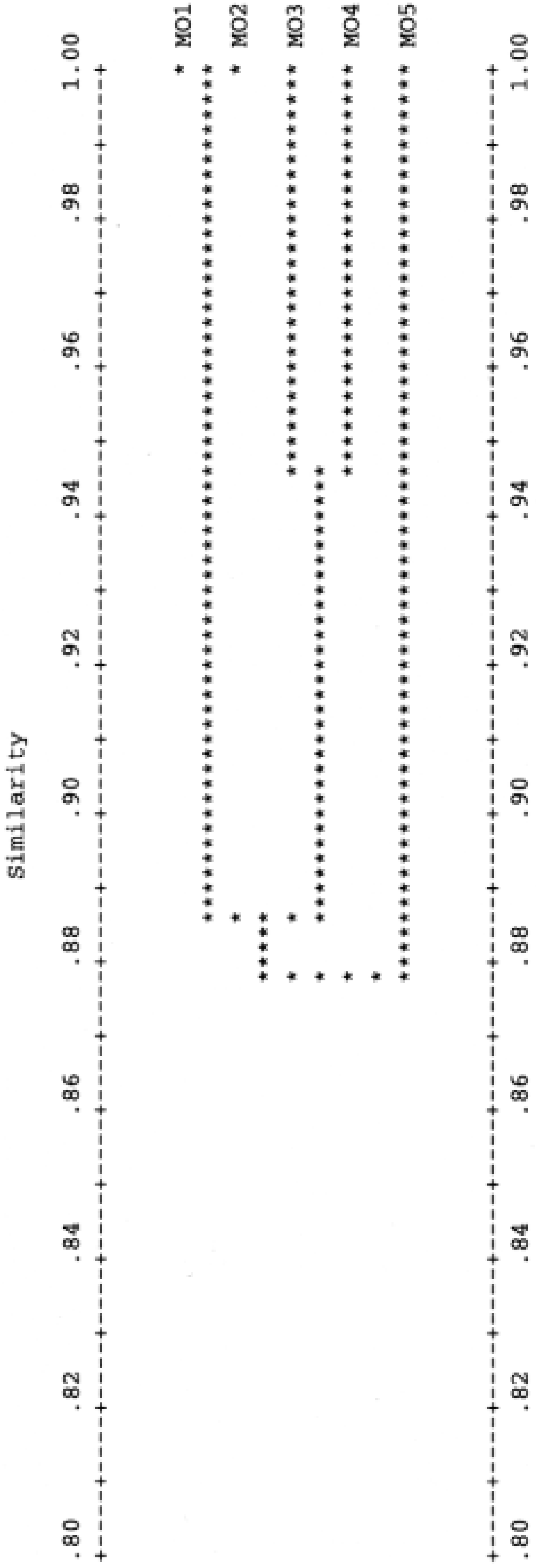

Figure 6—A dendrogram showing the results of isozyme analysis on aspen stands sampled along Morsay Creek.

Western Route generally showed a high degree of relatedness. In the Sugarbowl drainage, several stands were tightly clustered (figure 5). Sugarbowl aspen stands 1–4 (SU1-SU4), although not genetically identical, shared more than 94% of the genes sampled. This suggests that these stands are strongly related and may have sprouted from seed during the same establishment event. By contrast, SU6 was highly unique. Managers can use this information to allocate limited resources to protecting those stands that will maximize genetic diversity across the landscape.

Figure 6 illustrates the relatedness of stands in the Morsay drainage. Of notable interest is that Morsay 1 (MO1) and Morsay 2 (MO2) shared 100% of their sampled genes, indicating that these stands are, in fact, the same clone. Looking at a map of the Morsay drainage (figure 7), one can see that the clone consists of four fragmented stands. This suggests that at one time, these stands comprised one very large clone, derived from an extensive root system. This is probably an ancient clone, existing perhaps for thousands of years, with high reproductive success and the potential to be a reservoir for somatic mutations (Tuskan et al. 1996). This would also be a stand prioritized for restoration efforts. However, one could protect only one of the four stands sampled and still protect the genetic material contained within all.

While most stands proved to be a single clone, numerous stands contained multiple clones, adding a level of diversity we had not expected to find.

Isozyme analysis was found to be a useful tool for determining both landscape distribution patterns and relatedness of aspen. The analysis is also useful for assisting a manager in allocating resources for preserving genetic diversity.

Aspen Propagation

In 1998, the district began efforts to artificially regenerate aspen. In the fall of 1998, root segments 0.5 to 1.0 inch in diameter were collected from dormant

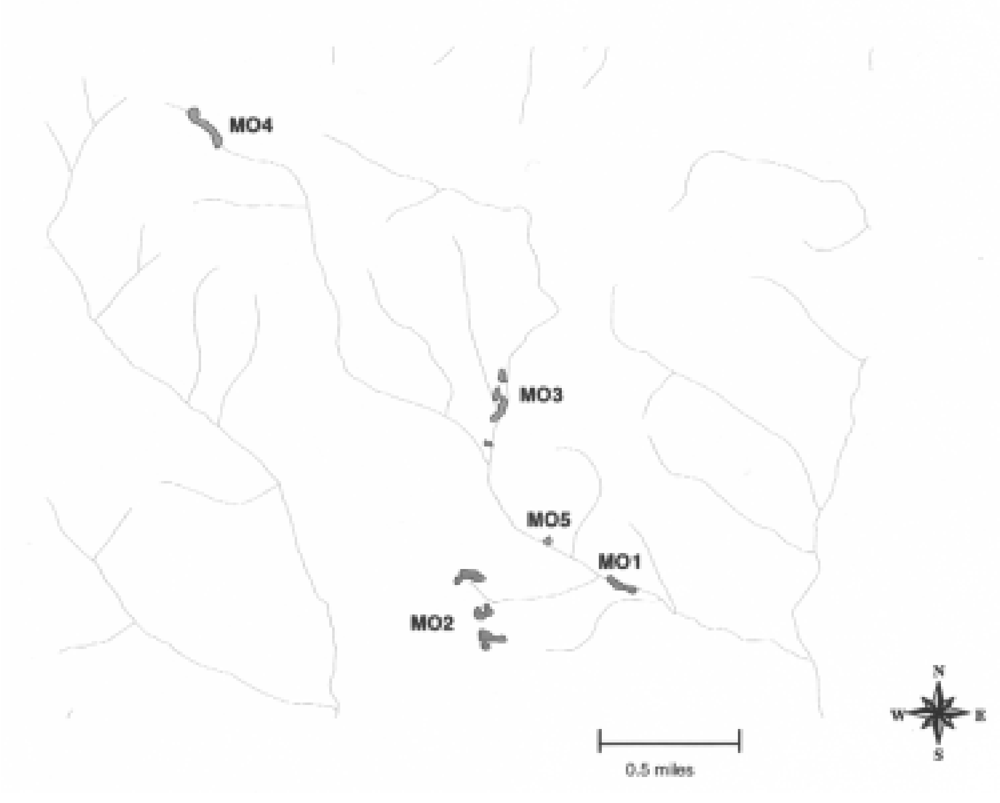

Figure 7—A map of the aspen stands sampled along Morsay Creek. Stands that are related are displayed in the same color.

aspen and sent to the J. Herbert Stone Nursery in Medford, Oregon. Root segments were washed in a large tub containing a 10% alcohol solution, wrapped in Kimwipes, and stored under refrigeration (Johann Visser, Culturist, personal communication). In February 1999, root segments were placed in wooden containers measuring 2 feet x 3 feet x 6 inches. Drainage holes were drilled into the base of the containers. The containers were then filled with a 1-inch layer of pure perlite, followed by a 3- to 4-inch layer comprised of 40% peat, 40% vermiculite, and 20% perlite. Root segments were placed on top of the latter layer and covered with approximately a quarter-inch of the same. The containers were placed in a greenhouse maintained at 70 to 75 °F. Sprouting took place within 10 days to 2 weeks. As root suckers emerged, they were excised, dipped in a commercial rooting enhancer containing IBA (indole butyric acid), and placed in individual D-40 (40 cubic inches) containers or in 1-gallon pots. These were grown in a mist chamber under a 24-hour photoperiod (during the day a layer of shade cloth was placed over the chamber to reduce sunlight by 50%), at 90% relative humidity and 78 °F. Suckers were fertilized with a solution containing a 21-5-20 formulation of nitrogen, phosphorous, and potash and trace amounts of micronutrients. When suckers appeared to be growing vigorously, they were placed in a greenhouse and grown for 2–3 weeks, or until approximately 10 inches tall. After the danger of hard frosts had passed, containers were moved outside for the remainder of the growing season. Once suckers had completely hardened off and entered dormancy in late fall, containers were moved into freezer storage until they were needed for outplanting the following spring.

In May 2000, the containerized aspen were planted in three types of locations: (1) in unoccupied portions of aspen exclosures to increase the perimeter of the existing stand, (2) between existing aspen stands within a drainage to encourage connectivity, or (3) where no aspen stands were known to previously exist. For the most part, a given genotype was planted back into the same drainage from which it was collected. However, some areas were planted with a mix of clones from neighboring drainages to increase diversity as well as the potential for sexual reproduction.

Sugarbowl Creek Aspen Restoration Project

The Sugarbowl drainage contains a string of remnant stands of aspen as well as the skeletons of former stands, noted by down or standing dead aspen trees. Sugarbowl Creek is heavily degraded by livestock use. Stream banks are severely eroded and support few native hardwoods or aquatic plants. The Sugarbowl Creek Aspen Restoration project has two objectives: (1) restore aspen stands to improve wildlife habitat and (2) improve stream bank stabilization. Several management strategies are in place to achieve these ends (figure 8). First, a series of exclosures were built to protect existing stands. The fences were constructed of lodgepole pine using the buck-and-pole design or with black plastic deer-deterrent fencing. The latter is attached to existing lodgepole pine, used as living fenceposts, wherever possible. Competing conifers have been felled and piled, or lopped and scattered, within protected aspen stands. Burning these felled conifers may encourage root suckering (Maini and Horton 1966), however, it is not our intention to kill the overstory aspen. Between existing stands, aspen has been interplanted to encourage connectivity (stands identified as "IP" in figure 8). Buck-and-pole fences were constructed around these new sites during the summer of 2000. Root ripping in stands that are reluctant to sucker may also be attempted.

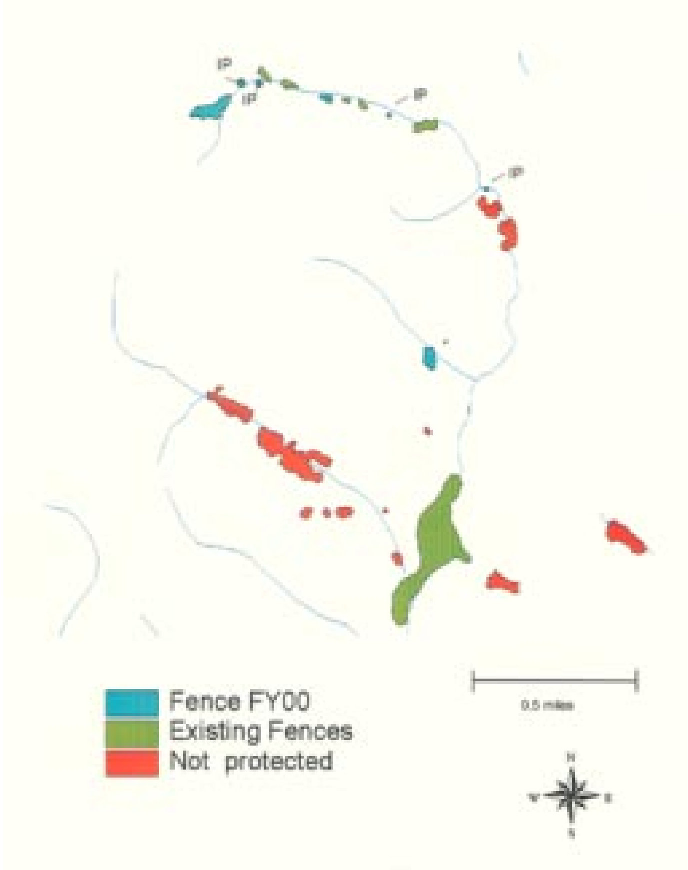

Figure 8—A map of the stands in the Sugarbowl Creek Aspen Restoration Project. Stands labeled with "IP" are areas interplanted with containerized aspen in May 2000 and fenced in July 2000.

Desolation Watershed Aspen Restoration Project

The Desolation Watershed Aspen Restoration project involves protection of existing stands as well as the establishment of aspen on a new site. In 1996, the Bull Fire burned a portion of the Skinner Creek drainage (figure 9). This drainage contained no stands of mature aspen. We postulated that if the aspen stands in surrounding areas were producing seed, the Skinner Creek drainage would be an ideal area for colonization of new aspen stands. In 1998, we selected a site for establishing a new stand using artificial regeneration. While laying out the proposed fence corridor, we actually located two new aspen seedlings within the selected site. Careful excavation of the root systems revealed that these seedlings were not attached to a pre-existing aspen root. This confirmed our theory that aspen seed would drift into this area following a fire.

Root segments were collected from the surrounding stands in Howard Creek and Bull Prairie in October 1998. These were used for the propagation of containerized aspen. In the fall of 1999, a buck-and-pole fence was constructed on the site on Skinner Creek (figure 10). In the spring of 2000, containerized aspen were planted inside of the exclosure. The success of this project will be closely monitored.

Natural Refugia

During the stand inventory process, it was noted that, on occasion, suckers grew into larger size classes whenever they could escape herbivory. Stands adjacent to heavily trafficked roads were often avoided by elk and, in these locations, clumps of sapling-sized aspen were observed. Areas of natural refugia include rock outcrops, piles of fallen trees, or jackstraw. This has also been observed by Ripple and Larsen (in press) in Yellowstone National Park.

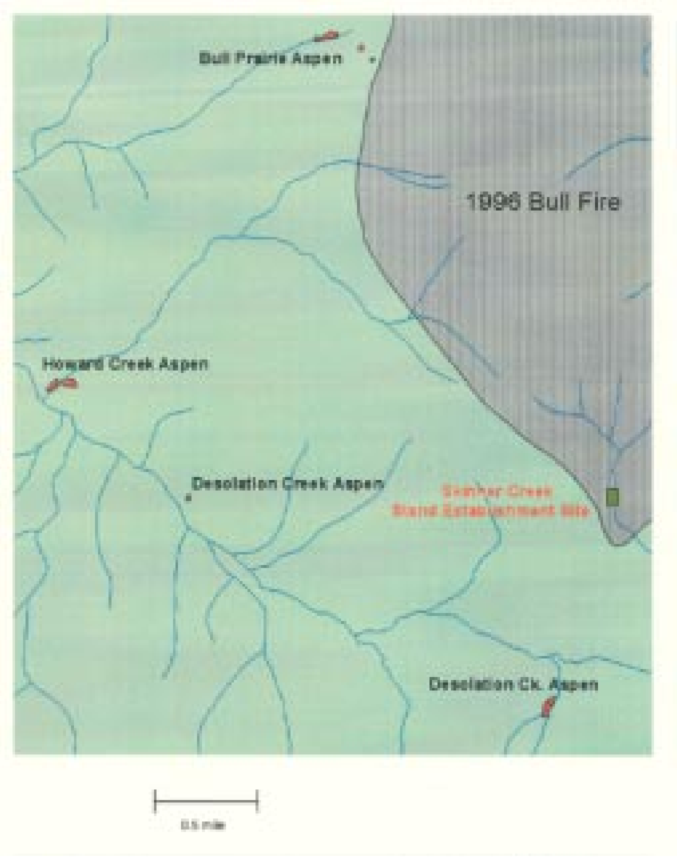

Figure 9—A map showing the aspen stands in the Desolation Watershed and the area burned by the 1996 Bull Fire. The location of the Skinner Creek aspen establishment site is highlighted in green.

In areas with difficult access, or where funds are lacking for fencing projects, we have attempted to simulate natural refugia by placing jackstrawed debris around existing aspen suckers. In a stand on Thompson Creek, we felled several conifers, at a stump height of 3.5 to 4.0 feet, leaving a hinge of holding wood to hang up the butt end of the tree. Wherever possible, we would fell four trees to form a box around the selected sucker. These resulting areas of jackstraw

Figure 10—The Skinner Creek exclosure located within the Bull Fire perimeter.

presented an obstacle approximately 6 to 12 feet on a side and 4 to 5 feet in height. In our experience, animals moving through a stand generally avoid small areas of jackstraw. This is not the case for extensive areas of jackstraw, which cannot be as easily avoided. In fact, large areas of jackstraw often attract large native ungulates, as they can provide desirable security habitat.

Conclusions

Without some sort of human intervention, aspen will quickly disappear from the landscape in the Blue Mountains of northeast Oregon. A number of techniques are available to the land manager to protect and enhance existing stands of aspen. However, they provide a "Band-Aid" approach to treating symptoms of a much larger, ecosystem-scale problem. The situation is much graver than merely the loss of aspen habitat. In fact, we are losing all of our native hardwoods from the landscape including black cottonwood (*Populus balsamifera*), mountain mahogany (*Cercocarpus ledifolius*), bitterbrush (*Purshia tridentata*), a multitude of willows (*Salix* spp.), and other woody vegetation.

Landscape-scale solutions are necessary. These include the reintroduction of fire, the careful management of livestock grazing within aspen stands, and a reduction in herd sizes of native ungulates. Not only are these solutions costly in economic terms, they are also politically sensitive issues.

It has been well established by the scientific community that wildfire is a natural and necessary part of ecosystem cycles (Agee 1993; Caraher et al. 1992; Gast et al. 1991; Powell 2000). The repercussions of the Yellowstone National Park (1988) and Los Alamos (2000) fires, however, are still with us. We can never guarantee the public that our prescribed fires, or the natural fires that we allow to burn, will not escape proposed control lines and threaten the public domain. Yet fire is a vital component in most ecosystem restoration plans.

Likewise, the sale of game tags provides an important source of revenue to state wildlife programs. People enjoy seeing abundant wildlife, especially deer and elk, when they recreate on public lands. Hunters desire successful hunts and prefer to bag trophy-size animals. There will always be tremendous opposition to restricting hunts or significantly reducing herd sizes.

The bottom line is that effective ecosystem restoration comes with a hefty price tag. Is society willing to pay that price?

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Prescribed Fire, Elk, and Aspen in Grand Teton National Park[1]

Ron Steffens[2] **and Diane Abendroth**[3]

Abstract—*In Grand Teton National Park, a landscape-scale assessment of regeneration in aspen has assisted park managers in identifying aspen stands that may be at risk due to a number of interrelated factors, including ungulate browsing and suppression of wildland fire. The initial aspen survey sampled an estimated 20 percent of the park's aspen stands. Assessment of these data indicate an aging stand structure plus a park-wide impact of elk and ungulate browsing on aspen regeneration less than 2 m tall. While the use of prescribed fire and wildland fire use actions may stimulate aspen regeneration, the continued impact of elk browsing may counteract the flush of post-burn regeneration. To monitor this dynamic, the Grand Teton National Park has inaugurated a fire effects monitoring program. This will be used to better understand the variables (such as aspect, habitat type, timing, and size of prescribed fire application) and spatial distribution that influence browsing pressure and aspen regeneration. A review of aspen burn prescriptions, both locally and regionally, will allow managers to refine the prescriptions and enhance project success.*

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[1] Authors chose to submit abstract in the place of full report.

[2] Southwestern Oregon Community College, Coos Bay, OR.

[3] Grand Teton National Park, Moose, WY.

Aspen Encroachment on Meadows of the North Rim, Grand Canyon National Park[1]

Margaret M. Moore[2] and David W. Huffman[2]

Abstract—*Composition and structure data were analyzed to determine the characteristics of trees encroaching on the montane meadows and subalpine grasslands of the North Rim, Grand Canyon National Park. Tree invasion in the 1900s showed a pattern of increasing establishment, with quaking aspen comprising the majority (52%) of encroaching trees. Most aspen established in the last 10–20 years, with a mean establishment date of 1982 (mean age = 10 years). Interestingly, meadow encroachment began as early as 1903, followed by a distinct lack of aspen establishment from 1913 to 1933. This 20-year gap in aspen regeneration corresponds with the widely known Kaibab Plateau mule deer population explosion that occurred in the mid 1920s. Meadow encroachment by aspen from 1930–1993 was estimated to be at an average rate of 1.17 m per year.*

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[1] Authors chose to submit abstract in the place of full report. Manuscript will be submitted to journal.

[2] School of Forestry, Northern Arizona University, Flagstaff, AZ.

Hydrologic Recovery of Aspen Clearcuts in Northwestern Alberta

R. H. Swanson and R. L. Rothwell[1]

Abstract—*A 3-year study of evapotranspiration from aspen clearcuts 1 to 14 years of age indicated the following: (1) The annual evapotranspiration from 1- to 5-year-old clearcuts ranges from 0 to 143 mm less than a mature forest on the same site. Evapotranspiration is highly dependent upon the amount of precipitation. (2) These effects can vanish in as few as 2 years with low precipitation (300 mm) or persist for 40 to 45 years with high precipitation (600 mm). These results were confirmed by data from the Spring Creek experimental watershed. Simulated water yield increase from the harvested catchment averaged 16 mm, compared with 16.3 mm estimated from the paired watershed data. In planning harvesting scenarios on flood-prone watersheds, full hydrologic recovery should be assumed to occur 45 years after harvest. Harvesting sequences designed using this approach should not cause a measurable increase in flooding levels or flood frequency.*

Introduction

Clearcutting generally increases water yield (Anderson et al. 1976; Hibbert 1967; Swanson and Hillman 1977; United States Environmental Protection Agency 1980). This is a logical consequence of the removal of trees and a reduction in water loss by transpiration. In windy environments, clearcutting can be accompanied by removal and rearrangement of the winter's snowpack (Tabler and Schmidt 1972; Troendle and Meiman 1984), which can alter the duration of snowmelt and the quantity of snowmelt water. In coniferous stands in the Rocky Mountains, the combined effects of these processes may last for 80 to 120 years (Leaf 1975). Similar effects on snow accumulation and melt have been noted in aspen stands (Swanson and Stevenson 1971). The duration of water yield increases from clearcuts in aspen stands is reportedly shorter, approximately 9 to 14 years (Verry 1987) and somewhat uncertain in Alberta (Swanson et al. 1998). Our purpose in the study reported here was to determine how long these processes were operating to affect water yields from aspen harvest on the Keg River watershed in northwestern Alberta, Canada.

Flooding of Homes and Fields

Forest clearcutting has generally been dismissed as a factor in major flooding events (Hewlett 1982), but there is some evidence to the contrary in the Keg River watershed in northwestern Alberta. About 13% of the Keg River watershed area was cleared for agriculture (Delta Environmental Management Group Ltd. 1989; W-E-R Engineering Ltd. 1990). The Keg River area was settled as a ranching community in the early 1930s. According to the Delta report, between 1957 and 1987, most of the coniferous timber stands from the Naylor Hills portion of the Keg River watershed were removed, with the result that yearly spring flooding and high water table levels are now a common hydrological feature of the area. According to the WER report, "Since

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settlement of the area, overbank flows along the Keg River and its tributaries have been a frequent occurrence. As a result, any activities in the watershed which may influence flood conditions in this area are of vital concerns to the local residents."

Much of the upper portions of the Keg River watershed contains mature deciduous forest. Daishowa Marubeni International, Ltd. (DMI), which has the cutting rights in this area, proposed to start harvesting aspen in the winter of 1991/1992. DMI has been sensitive to the concerns expressed by residents on farm and ranch lands downstream from their proposed harvests and commissioned the report by W-E-R Engineering Ltd. (1990) to evaluate the potential hydrologic impacts of their harvests. Their report concluded that the hydrologic effects of any single aspen harvest would essentially vanish in 2 to 3 years. To mitigate flooding concerns, the report recommended that "harvesting activities should be scheduled over two or more years in sub-watersheds which will be extensively harvested or where channel erosion is a significant concern."

DMI questioned the validity of the 2- to 3-year estimate for the effects of aspen harvesting to vanish. Verry (1987) reported a significant increase 14 years after aspen harvest in Minnesota. In southern Alberta, a harvest of aspen from 50% of the area above a small spring in the Streeter Basin experimental watershed produced increases in water yield greater than 25 mm for the 7 years of measurement following harvest (Swanson et al. 1986). (Water yield is defined as the depth that would result if all of the streamflow for a defined period and from a defined watershed were spread evenly over the watershed area. Water yield in millimeters equals streamflow volume in cubic decameters divided by watershed area in square kilometers.) Extrapolation of the Streeter results (figure 1) in time indicated that the effects of the harvest would vanish in about 30 years (Swanson et al. 1998). DMI chose to design its initial harvesting scenarios in accordance with the recommendation of the WER

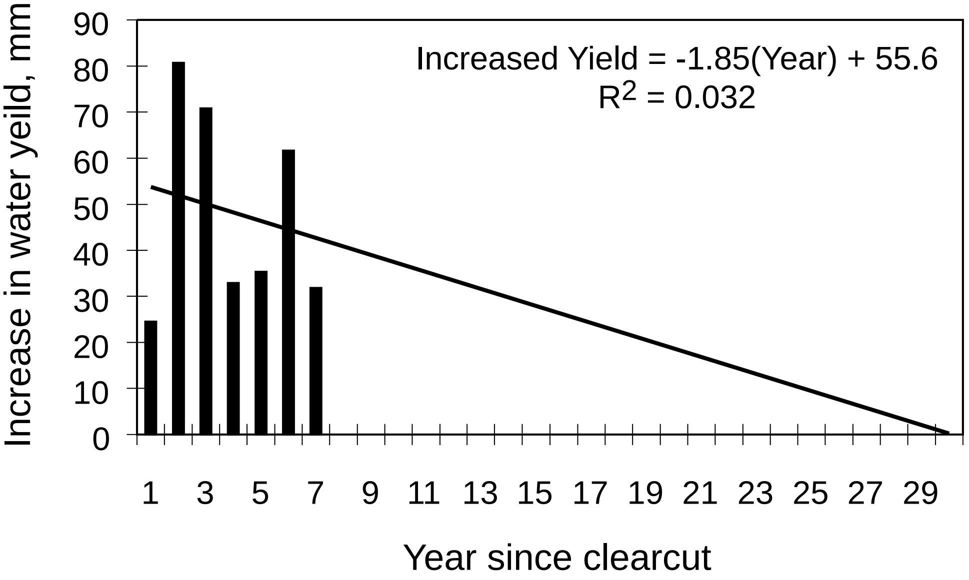

Figure 1—Decline in annual increases in generated runoff from an aspen watershed after clearcutting. Unpublished analysis of data from the Streeter Experimental Basin, Alberta. Aspen forest was harvested in 1976 and water yield data collected through 1982.

report but used simulations with the WrnsHyd[2] version of the WRENSS procedure (United States Environmental Protection Agency 1980) and the Streeter Basin results to ensure that water yield increases remained well within the 15% of average water yield bounds set by Alberta Environmental Protection (John Taggart, Alberta Environment, Edmonton, Alberta, personal communication). Because of the uncertainty in the length of the recovery period, the study reported here was funded by DMI and the Canadian Forestry Service's Partnership Agreements in Forestry program (in our case, a project funded jointly by the Government of Canada, the Province of Alberta, and DMI).

Objectives

Our first objective was to better define the period during which aspen clearcuts could significantly affect water yield and the potential for flooding. We assumed that: (1) a reduction in evapotranspiration (ET) would result in an increase in generated runoff[3] (GRO) of the same magnitude, and (2) annual increases of 10 mm or less in GRO would be considered insignificant.

Our second objective was to incorporate tree growth equations within the WRENSS procedure (United States Environmental Protection Agency 1980) so that it could be driven by forest inventory information and used by forest managers to relate cumulative areal and temporal harvests to water yield change. These would enable the use of the WRENSS procedure for evaluation of existing harvests and to plan future harvests in order to minimize any detrimental effects on water users, either instream or downstream.

Scope of Investigations

The study was to be conducted over 3 years commencing the first year after instrumentation was installed (1993). All of our investigations were conducted on existing harvested cut blocks 0 to 10 years old (in 1993), 20 to 40 ha in size, and in deciduous forests in northwestern Alberta. We initially sought all of our sites within the Keg River watershed. However, there was only one age class available, those harvested in the winter of 1991–1992 (our site Kg92). And, since aspen had not been harvested to any great extent in the past in Alberta, there were few sites to choose from anywhere in northwestern Alberta. Most of those in which aspen regeneration had occurred had been treated either mechanically or with herbicides to discourage deciduous growth and to favor that of coniferous plantings. We located 5- and 10-year-old sites (Gp88 and Gp83) south of Grande Prairie, Alberta, that were suitable. A mature and a second newly logged site (SpMat and Sp94) were found on the Spring Creek experimental watershed, near Valleyview, Alberta.

The Spring Creek experimental watershed was started in 1966 with stream gauges on all sub-basins and a comprehensive network of weather stations. The watershed study was deactivated in 1986 before any experimental treatment was done. Alberta Environment proposed reactivation of the watershed and that DMI harvest one of the sub-basins in 1994 to complete a portion of the original purpose of the experimental watershed. Alberta Environment reactivated the stream gauge on Bridle Bit Creek, the 21 km^2 control watershed, and on Rocky Creek, the 15.3 km^2 watershed that DMI would harvest. Sp94 was located on the Rocky Creek watershed. The two sub-basins, monitored since 1994, provided data for a paired watershed comparison. The Spring Creek paired watershed study serves an excellent complement to, and check on, the data derived from the evapotranspiration measurements and model simulations.

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[2] WrnsHyd is an MS-DOS implementation of the hydrology chapter on the WRENSS (United States Environmental Protection Agency 1980) handbook. WrnsHyd was programmed by the Canadian Forestry Service and made available to any interested user in 1990. It is currently available by ***email only*** (rswanson@expertcanmore.net), free of charge from R.H. Swanson.

[3] Generated runoff (GRO) is that increment of water added during a given time interval that will eventually leave a catchment. All onsite losses have been deducted but the water has not passed through the stream gauging point. It is correctly defined as precipitation-evapotranspiration. This definition is in agreement with that proposed by the U.S. Army Corps of Engineers (1956), which states that generated runoff is water in transitory storage in the soil, groundwater, or stream channel.

Plan of Attack

Our plan was to obtain the data necessary to estimate the change in generated runoff through time from new clearcuts in the Keg River watershed to mature aspen stands. Initially we thought that measured precipitation and the estimates of annual evapotranspiration from microclimate and soil moisture measurements obtained at each age might be sufficient to define an age:generated-runoff relationship. However, we soon realized that the sites had sufficiently different climates to render direct comparisons of evapotranspiration magnitude impossible. We anticipated this and planned to simulate generated runoff with a microclimate and vegetation model in addition to the direct measurements. The direct measurements of ET were to serve as control values for simulated ET on the same sites.

The BROOK90 model (Federer 1995) was used to integrate all of the site information including winter and summer precipitation and to simulate the change in generated runoff from the time of initial harvest to 60 years. The Spring Creek paired watershed results were used to verify the BROOK90 simulations of increased water yield from Sp94. The results obtained from the BROOK90 simulations were then incorporated into WrnsDmi, a version of the hydrology section of the WRENSS (United States Environmental Protection Agency 1980) procedure for use by DMI within its allotted area to evaluate existing harvests and prescribe future ones to maintain water yield increases within acceptable bounds, presently set by Alberta Environment at 15% of average annual yield. The value of 15% was chosen through unit hydrograph analysis, which indicated that increases in annual yields of this magnitude would not increase the magnitude of instantaneous or daily peak flows.

Measurements

The data necessary to calibrate and use the BROOK90 model (Federer 1995) to simulate change in generated runoff were taken at each site. The BROOK90 model requires daily values of air temperature, vapor pressure, solar radiation, wind speed, and precipitation. Leaf area index (LAI) and tree height (TH) are required to describe the vegetation on a site. Site latitude, initial water content of the snowpack, and the amount of water in groundwater storage are used to initialize a simulation run. Soil water can be drawn from one to 10 layers. Various combinations of output variables are available. We chose to view daily, monthly, and annual ET, generated runoff and soil moisture, and calibrated the model at each site on 1994 climate, LAI, TH, and soil moisture data. We did not attempt simulation of actual streamflow because the BROOK90 model does not include a storage routing routine or storage parameters. Spring Creek's streamflow is highly dependent upon withdrawals from and replenishment of soil, groundwater, and surface storage during years of low and high precipitation as is the streamflow of most watersheds in northwestern Alberta.

An instrument tower was installed at each site (10 m tall at Kg92 and Sp94, 15 m tall at Gp83 and Gp88, 30 m tall at SpMat). All were identically instrumented (table 1) with the wind sensors approximately 10 m above the canopy. Hourly-averaged climate data was collected at each site with a Campbell Scientific (CSI) CR10 data logger programmed to read all sensors at 1-second intervals. The soil moisture and soil temperature sensors were read every 4 hours. Both climate and soil moisture/temperature data were taken year-round.

Snow depth and density were measured at all sites in February or March 1994, 1995, and 1996. If available, an adjacent newly harvested clearcut and a mature stand were also sampled. No permanent snow courses were established.

Table 1—Aspen study sites in northwestern Alberta, locations, and instrumentation.

Location, harvesting, and instrumentation dates						
Nearest town	**Identifier**	**Latitude**	**Longitude**	**Elevation**	**Harvested**	**Instrumented**
				m	*Year*	*Mon/Year*
Keg River	Kg92	57:46:00N	117:55:00W	513	1992	04/1993
Grande Prairie	Gp83	54:54:50N	118:47:30W	610	1983	07/1993
	Gp88	54:54:45N	118:56:00W	610	1988	07/1993
Valleyview	Sp94	54:58:20N	117:45:00W	730	1994	03/1994
	SpMat	54:55:30N	117:42:45W	700	Unharvested	04/1993

Continuous observations taken at all above sites from 1994 through 1996			
Type of data			
Climate	Air temperature	CSI[a] HMP35C (Fenwal[b] UUT51J1 Thermistor sensor)	°C
	Relative humidity	CSI HMP35C (Vaisala[c] capacitor RH sensor)	%
	Short wave radiation	SKYE[d] SKS 1110 Pyranometer	W/m^2
	Wind speed	RM Young[e] 05103 Propeller Anemometer at 10 m.	km/h
	Wind direction	RM Young 05103 Potentiometer Vane at 10 m	0–360
	Soil mmoisture and temperature	MC363[f] Fibreglass Moisture and Temperature Cells at 15 and 40 cm depths (15 and 30 cm at Kg92)	mm & °C

Periodic observations taken at all sites from 1994 through 1996		
Rainfall 1 May to 31 October	CSI TE525MM Tipping Bucket	mm
Snow accumulation February to March	USDA-SCS snow tube, 10 point snow course approximately 100 m long.	mm SWE[g]
Bowen's Ratio 1 May to 31 October	Temperature Gradient. Unshielded 0.08 mm Chromel/Constantan Thermocouples, approximately 2 m separation, CSI 10TCRT Reference.	°C
	Vapor Pressure Gradient. Air was drawn over a centrally mounted Vaisala sensor alternating every 30 seconds between top and bottom vents collocated with the thermocouples.	kPa
	Net Solar Radiation. CSI Q-6 (REBS[h] Net Radiometer).	W/m^2
	Soil Heat Flux. CSI HFT3 (REBS soil heat flux sensor).	W/m^2

[a] Campbell Scientific (Canada) Corp., 11564–149 St., Edmonton, AB T5M 1W7.
[b] Fenwal Electronics Group, 500 Narragansett Park Drive, Pawtucket, RI 02861-4325.
[c] Vaisala, Inc., 100 Commerce Way, Woburn, MA 01801-1068.
[d] Skye Ltd., Unit 5, Ddole Industrial Estate, Llandrindod Wells, Powys, UK LD1 6DF.
[e] R.M. Young, 2801 Aero-park Drive, Traverse City, MI 49684.
[f] Hoskins Scientific Ltd., 239 East 6th Ave, Vancouver, BC V5T 1J7.
[g] SWE = Snow Water Equivalent.
[h] Radiation & Energy Balance Systems, Ins., P.O. Box 15512, Seattle, WA 98115-0512.

At each site a starting point at least 100 m from the forest edge was selected and 10 measurements made at 10 m intervals.

The soil moisture sensors at each depth (table 1) were calibrated against gravimetric measurements at those same depths during each month of the 1994 growing season (dry weight basis every month, volumetric measurements made in June only). The volumetric moisture contents were converted to mm of water in each soil layer.

The data to calculate Bowen's ratio were taken at periodic intervals in 1994 and continuously from 1 May to 31 October in 1995 and 1996. During 1994, we attempted to use the CSI Bowen Ratio instrumentation but it proved unsatisfactory for use over forest canopies because the length and construction of the sensor mounting arms made it almost impossible to move them or to repair or replace the thermocouple sensors while mounted on the towers.

We constructed Bowen's ratio apparatus that functioned similarly to CSI's using readily available 2-inch diameter white ABS pipe. Two 1 m lengths of pipe were fastened to opposite ends of a central chamber containing a CSI HMP35C sensor. The resulting rigid structure allowed easy mounting on a tower with supports placed at any convenient position on the tower. Thermocouple sensors (0.08 mm diameter) were mounted on 1 mm diameter 10 cm long ceramic arms extending outward near each air intake. The bottom sensor's temperature and the difference between the upper and lower sensors temperature were read at 1-second intervals and averaged over 30 or 60 minutes as desired. Vapor pressure gradient was obtained by drawing air over the HMP35C sensor alternately from the upper and lower vents. Air was drawn from the upper vent for 10 seconds to flush the central chamber, and then vapor pressure was recorded for 20 seconds. This procedure was then repeated with air drawn from the lower vent. This sequence was repeated every 60 seconds.

Leaf area indices and tree heights were obtained during 1993 and 1994 by harvesting all of the leaves from plots or representative trees (three each 9 m^2 plots at Kg92, four each 1 m^2 plots at Gp83 and Gp88, three representative trees at SpMat). Sampling was done in late June and July following full leaf expansion. The trees were felled and all green foliage collected and bagged for laboratory analysis. The area of 15 to 20 subsamples of the leaves from each site was measured. An equation was derived for leaf area as a function of oven dry weight (in a forced air oven at 40 °C for 24–48 hours). The total oven dry weight of all of the leaves was used to estimate total leaf area for the plot or tree(s). The LAI obtained by averaging the data from the plots was considered the LAI for that stand. The LAI from the individual trees at SpMat was scaled up by multiplying the average leaf area per tree by the number of trees per hectare in that stand. The heights and diameters of the trees at breast height and at the root collar were measured. Estimates of stocking (stems/ha and basal area) in the mature stand were obtained by counting all of the trees in two randomly established 0.01 ha plots. The heights of the trees in each plot or sample were averaged and considered representative of the stand from which they were obtained.

Results

Snow Accumulation

Snow accumulation in the clearcuts and in the uncut forest was approximately the same from 1994 through 1996. Average winter wind speed at 10 m at the Spring Creek or Keg River clearcut sites was generally less than 2 km/h, considerably less than the 24 km/h that Tabler and Schmidt (1972) indicate as the threshold velocity for transporting snow particles from a snowpack. In addition, the regeneration height in the clearcuts at the end of the first-year's growing season averaged 1 to 1.5 m, which provided sufficient aerodynamic roughness to protect the shallow snowpacks in these areas from wind erosion or transport (Swanson 1994).

Leaf Area Indices and Tree Heights

There were no replicates of age classes because of the lack of suitable sites, particularly in the 5- and 10-year age groups. The LAI's that we obtained were plotted against age (figure 2) and a logarithmic curve was fitted to the data (equation 1). The tree heights were plotted as a linear function of age (equation 2).

These equations were used to estimate the LAI's and tree heights at each age used in the BROOK90 simulations (table 2).

$$LAI = 1.665\mathrm{Ln}(Age) - 0.0712 \quad (1)$$

$$TH = 0.261(Age) + 0.88 \quad (2)$$

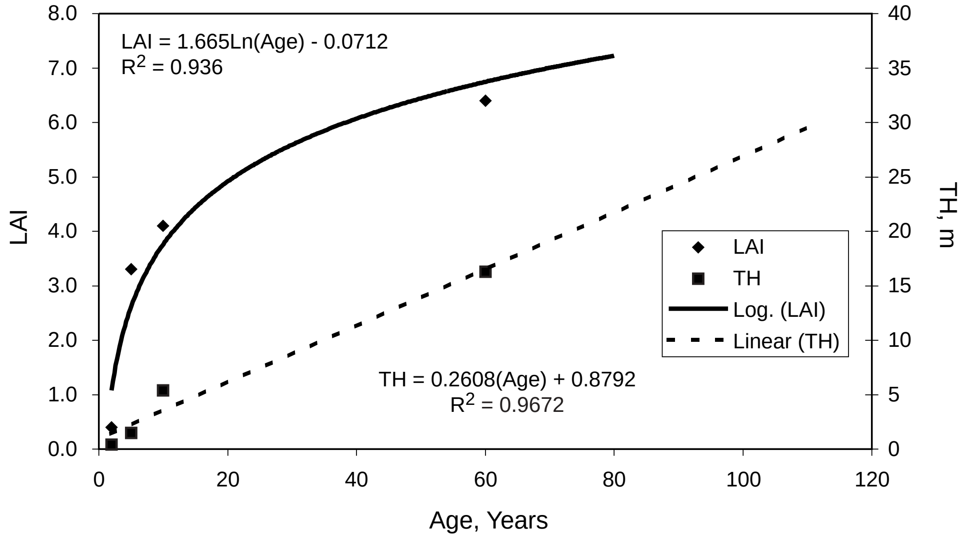

Figure 2—Leaf area index (LAI) and tree height (TH) as a function of aspen age in northwestern Alberta.

Table 2—Annual evapotranspiration as simulated with the BROOK90 model at LAI and tree height at site age versus that simulated using SpMat vegetation data (Age 60, LAI = 6.7, TH = 16.5 m) on the same site.

Age (year)	LAI at age	Height	Precipitation	ET (at age)	ET (mature)	ET (decrease)
	m^2/m^2	*m*		- - - - - *mm* - - - - -		
Gp88 Grande Prairie site, clearcut in 1988						
6 (1994)	2.9	2.4	507	412	445	33
7 (1995)	3.2	2.7	605	427	499	72
8 (1996)	3.4	3.0	591	410	447	37
Average			**568**	**416**	**464**	**47**
Gp83 Grande Prairie site, clearcut in 1983						
11 (1994)	3.9	3.7	507	377	421	44
12 (1995)	4.1	4.0	577	392	446	54
13 (1996)	4.2	4.3	677	428	496	68
Average			**587**	**399**	**454**	**55**
Kg92 Keg River site, clearcut in 1992						
3 (1994)	1.8	1.7	379	298	346	48
4 (1995)	2.2	1.9	312	277	277	0
5 (1996)	2.6	2.2	407	346	375	29
Average			**366**	**307**	**333**	**26**
Sp94 Spring Creek site, clearcut in 1994						
1 (1994)	.8	1.0	462	275	418	143
2 (1995)	1.1	1.4	457	307	373	66
3 (1996)	1.8	1.7	616	349	462	113
4 (1997)[a]	2.2	1.9	500	363	430	67
5 (1998)	2.6	2.2	387	307	320	13
Average			**484**	**320**	**401**	**80**
Average decrease in ET area-weighted over Rocky Creek watershed						**16**

[a] Temperature, vapor pressure, and solar radiation data from SpMat used for 1997 and 1998 simulations at Sp94.

Evapotranspiration Estimates From Soil Moisture Data

Evapotranspiration can be estimated from soil moisture changes over the growing season. The water balance equation (3) was used to make these ET estimates (Johnston et al. 1969):

$$Q = P - ET - I - \Delta G - \Delta S \qquad (3)$$

where Q = water yield, P = precipitation, ET = evapotranspiration, I = Interception, ΔG = change in groundwater storage, and ΔS = change in soil moisture storage.

$$ET = P - \Delta S \qquad (4)$$

To calculate ET from the soil moisture data collected during this study, we assumed that surface runoff, interception, and percolation to groundwater were negligible. Under these assumptions, calculations (table 3) with equation (4) indicate that during 1994–1996, the ET from the younger Gp88 site averaged 442 mm, 2 mm less than the 444 mm at the older Gp83 site. Evapotranspiration at Gp88 was higher than at Gp83 for 2 of the 3 years of data, which tends to confirm observations of DeByle (1985) that for stands reproduced from root suckers "within 10 or 20 years, the sprout stand will probably consume as much water as its parent trees did."

During this same time period, the ET at the newly clearcut site on Spring Creek (Sp94) averaged 318 mm, 64 mm less than the 382 mm at the mature Spring Creek (SpMat) site. Evapotranspiration at the Keg River site (Kg92) averaged 254 mm. We had no ET data from a mature site at Keg River to compare with that from the clearcut.

Evapotranspiration Estimates From Bowen's Ratio Data

The Bowen's ratio method uses a form of the energy balance equation (5) to estimate ET (Oke 1987).

$$Q^* = Q_H + Q_E + Q_G \qquad (5)$$

Table 3—Seasonal water use from aspen sites as estimated from soil moisture depletion and precipitation, 1 May to 30 September (Kg92, 1996, 1 May to 31 August).

Site	Age	Year	Precipitation	Water use
	years		----- *mm*	-----
Gp83	11	1994	328	390
	12	1995	394	472
	13	1996	474	473
Average				**444**
Gp88	6	1994	328	406
	7	1995	431	509
	8	1996	388	412
Average				**442**
Kg92	3	1994	212	244
	4	1995	196	220
	5	1996	239	297
Average				**254**
SpMat	60+	1994	293	368
	60+	1995	266	346
	60+	1996	421	431
Average				**382**
Sp94	1	1994	293	400
	2	1995	266	220
	3	1996	421	336
Average				**318**

where Q^* = net all wave solar radiation, Q_H = sensible heat, Q_E = latent heat, and Q_G = heat conduction to or from the underlying soil. The Bowen's ratio, b, equation (6) is defined as the ratio of sensible to latent heat (Oke 1987), where C_A is specific heat of air, L_V is latent heat of vaporization, and T_1, T_2, V_{P1}, and V_{P2} are air temperature and vapor pressure at levels 1 and 2, respectively.

$$\beta = Q_H / Q_E = C_A(T_1 - T_2)/L_V(V_{P1} - V_{P2}) \tag{6}$$

Evapotranspiration can be calculated with equation (7) by rearrangement of equation (5) and substitution of β.

$$ET = [(Q^* - Q_G)/(1 + \beta)]/L_V \tag{7}$$

Bowen's ratio can be determined with very accurate measures of air temperature and vapor pressure at two levels above the canopy. In order to meet all of the assumptions inherent in the derivation of Bowen's ratio, stringent fetch and height constraints must be met. In general, one can assume that the fetch requirement is met if the distance to the nearest obstacle to wind flow over the site is 40 times the height of the lowest air temperature and vapor pressure sensor set (measured from above the canopy). This fetch requirement was met at all but the Gp83 site.

The placement of the lower sensor cannot be specified exactly and will always involve some trial and error. In our case, we started with the lower sensor set 2 m above the tallest vegetation and with a 2 m separation between the lower and upper sensor sets. This spacing and placement appeared to give satisfactory readings. The spacing between the upper and lower sensors was not changed but at the three newest clearcut sites (Gp88, Kg92, and Sp94), the lower sensor was moved to 2 m above the canopy before leaf-out each year.

We found it difficult to maintain the complete Bowen's ratio measurements at all sites over a full growing season. Although the instruments were checked monthly, data logger program failures, broken temperature sensors, and holes pecked by birds in the shields of the net radiometers rendered much of the data suspect. The 1996 data sets at all sites are the most complete because all of the temperature and vapor pressure data were valid. However, birds were particularly bothersome in 1996 with the result that most of the net radiation data was unusable. Therefore, we estimated net radiation by subtracting a fixed value for albedo (0.18) from direct solar radiation readings.

The results for 1996 (table 4) indicate that growing season ET from the Sp94 site, where the regeneration was in its third year, was 410 mm, 40 mm less than that (450 mm) from the mature SpMat site. The monthly values of ET simulated by the BROOK90 model for 1996 are shown for comparison with the

Table 4—Monthly evapotranspiration in 1996 as estimated from Bowen's ratio data and BROOK90 simulations at one of the Grande Prairie sites, the two Spring Creek sites, and the Keg River site.

	Bowen's Ratio				BROOK90			
Site	**Sp94**	**Kg92**	**Gp88**	**SpMat**	**Sp94**	**Kg92**	**Gp88**	**SpMat**
Age, years	3	5	8	60+	3	5	8	60+
Month	mm	mm	mm	mm	mm	mm	mm	mm
May	29	31	31	53	23	26	34	30
June	101	101	112	87	84	76	112	86
July	120	114	142	126	93	100	128	108
August	120	91	132	136	91	86	59	98
September	41	—	49	49	44	—	61	54
Season	410	337	465	450	334	288	393	376

Bowen's ratio data. The Bowen's ratio ET show similar trends to those of the BROOK90 simulations, but their magnitudes were not sufficiently comparable to use as control data for the model.

Generated Runoff Estimates From Model Output

Complete data sets for the BROOK90 model were either taken or estimated for the years 1994 through 1996 for all five sites. The model was calibrated for each site on the soil moisture in the top 40 cm. (The data taken gravimetrically at monthly intervals from 26 April to 9 September 1994 at each depth [table 1] were depth-weighted and combined into one measurement for a 40 cm thick soil layer.) We considered the model to be calibrated for a particular site when it simulated the soil moisture within 5 mm of that measured on 1 May and 31 August with the 1994 weather data from that site. For all sites except Sp94, several months of weather data were available for 1993, and these data were used to initialize the contents of the storage compartments within the model for simulation of the 1994–1996 data sets. On Sp94, the 1994 data was entered twice and the model storage components initialized on 1994 data before simulation of the 1994–1996 data sets.

We used the watershed results from Spring Creek as a check on the simulated generated runoff change. Regression analysis of Rocky Creek versus the Bridle Bit Creek control indicated a high correlation ($R^2 = 0.9732$) between their flows during the pre-harvest period. Measured flows during the post-harvest period, 1994–1998, are consistently above the pre-harvest regression line (figure 3), even when the data from a storm on 28–31 May 1996[4] are left out. In 1999, the estimated change in water yield is on or slightly below the regression line for the first time.

The average water yield increase for 5 years, 1994–1998, obtained from the paired basin regression analysis was 16.3 mm. The increase in generated runoff simulated with the BROOK90 model for these same years for the clearcut and area-weighted with the uncut portion of Rocky Creek was 16 mm (table 2). We take this close correspondence for the years 1994–1998 as reasonable verification of the simulations with the BROOK90 model.

The increase in generated runoff from each site was simulated with LAI and TH as estimated for the years 1994 through 1996 (table 2). These simulations were compared with simulations as if trees at each site were the same as those at SpMat (LAI = 6.7, TH = 16.5 m) for each of those same years. The increase in GRO ranges from a low of 0 mm in 1995 at the Keg River site to a high of 143 mm in 1994 at the Spring Creek clearcut site. In general, greater increases in generated runoff occur in high precipitation years, e.g., 1996.

We simulated generated runoff increases at the Keg River and Spring Creek clearcut sites through 60 years using the highest and lowest precipitation that occurred during the period 1994 through 1996. The simulations for the Keg River site (figure 4) indicate that the effect of harvest on GRO increase would be insignificant (<10 mm) at 25 years with high precipitation and at 2 years with low precipitation. On the Spring Creek site where precipitation during the study years was higher than at Keg River, the effects of harvest on GRO increase would be about 10 mm at 40–45 and 25–30 years with high and low precipitation, respectively (figure 5).

Alberta Environment indicated that they could detect no change in peak flows following the harvest on Rocky Creek. This is consistent with similar findings for coniferous harvested areas on the Weldwood forest management area near Hinton, Alberta (RH Swanson & Associates 1997). Swanson estimated that the maximum change in any one-day's peak-generated runoff could

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[4] A beaver dam failed on 28 May 1996 resulting in the highest flow on record for Rocky Creek. Alberta Environment recommended that the streamflow from the entire month of May be excluded from the analysis of the harvest effect. We saw no reason not to include the streamflow data prior to the failure of the dam, nor for excluding that after the hydrograph returned to pre-failure level. We therefore excluded only the streamflow data for 28–31 May 1996 from both the control and treated watersheds. We also cannot rule out the possibility that the increased yield resulting from the harvest was a factor in the dam failure.

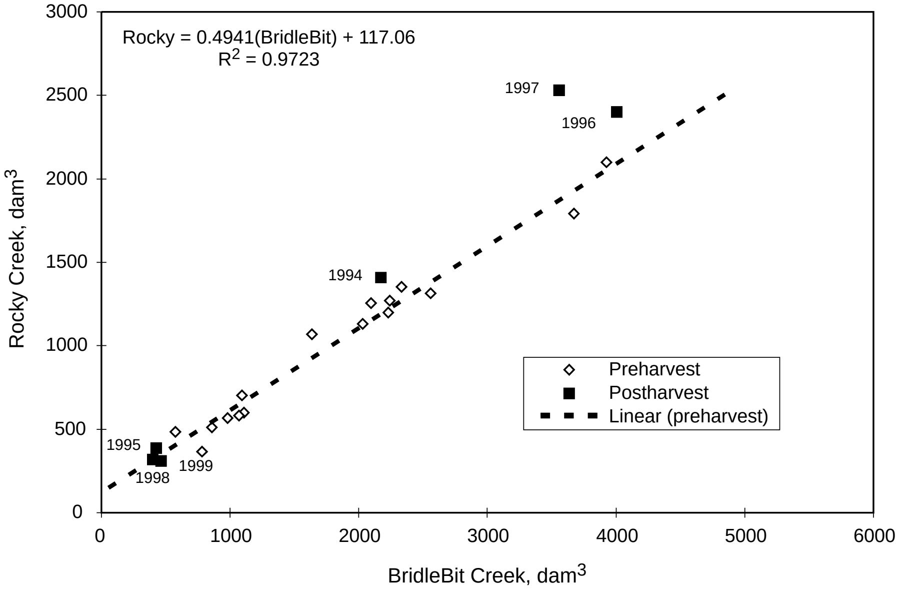

Figure 3—Effect of the 1994 clearcut harvest of approximately 20% of the area of Rocky Creek on annual water yield. Data for 1996 excludes the storm of 28–31 May; it could be somewhat higher because at least part of the runoff during that storm was due to the harvest. Note that the water yield for all of the years since harvest (except 1999) are above the pre-harvest regression of Rocky Creek on Bridle Bit Creek.

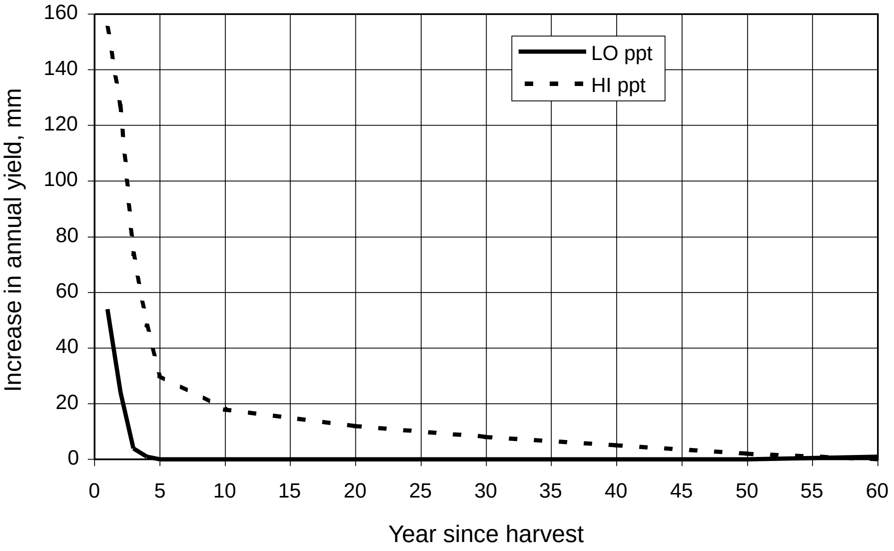

Figure 4—Change in annual generated runoff at Keg River with age of clearcut. Simulations with BROOK90 model using the climate data from the lowest (LO ppt; 312 mm) and highest (HI ppt; 407 mm) precipitation years that occurred from 1994–1996 at the Keg River site.

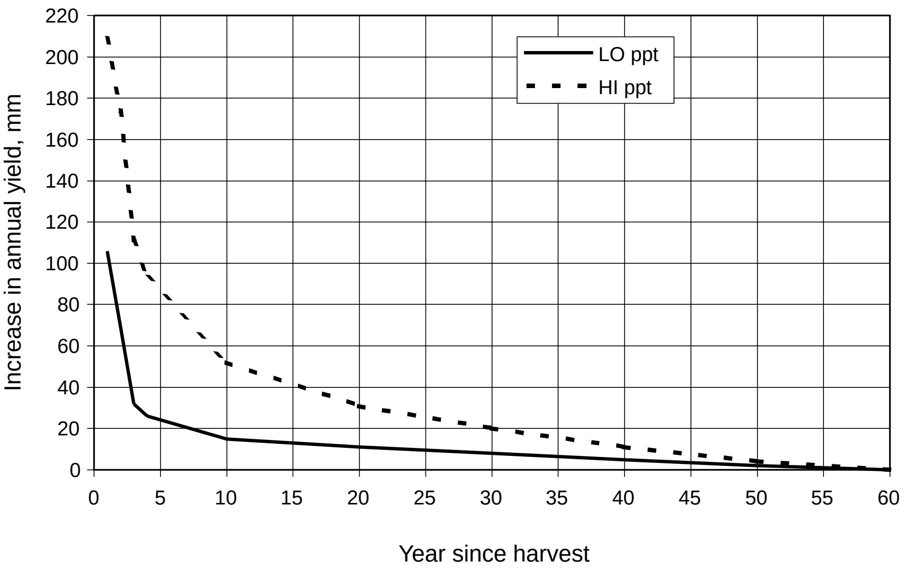

Figure 5—Change in annual generated runoff at Spring Creek with age of clearcut. Simulations with BROOK90 model using the climate data from the years with the lowest (LO ppt; 457 mm) and highest (HI ppt; 615 mm) precipitation at Spring Creek.

not exceed the potential evapotranspiration for that day. The maximum potential evapotranspiration for 1 day in this portion of Alberta is about 6 mm. If all 6 mm were added to a day's streamflow as a result of harvest, there would be a significant increase in peaks recurring at a frequency of every 2 years, but little or no change in the peak magnitude of those recurring at a frequency of 5 years or greater. We simulated daily additions to peaks with the BROOK90 model for 1996, the year with the highest precipitation at Rocky Creek, and found that the maximum increase in one day's generated runoff was 6.5 mm on the clearcut area (figure 6). This is approximately 1.3 mm when area weighted over the cut and uncut portions of the watershed. One should not expect to detect a change this small in maximum daily or instantaneous peak streamflow.

Interpretation of Results

The evapotranspiration values calculated from soil moisture or Bowen's ratio data were useful in a general sense in that they confirm that water yield increases cannot be reliably estimated solely from the age of a clearcut. Differences in precipitation masked the comparison of ET obtained from soil moisture at Gp88 and Gp83 or from Bowen's ratio data at Gp88 with that at the mature SpMat site. Both soil moisture data (64 mm difference over 3 years) and Bowen's ratio (42 mm difference during the 1996 growing season) at Sp94 and SpMat indicated higher values of evapotranspiration at the mature site and the decrease in ET on the clearcut site was reasonably comparable to GRO increases simulated with BROOK90. However, the soil moisture and Bowen's ratio data did not answer our question about how long it takes until the decrease in ET from aspen clearcuts becomes insignificant. The BROOK90 simulations gave us an answer, providing the duration of effects for use in the WrnsDmi procedure.

An increase in generated runoff in the hydrology section of WRENSS (United States Environmental Protection Agency 1980) is dependent upon the cover density of vegetation in a clearcut. In the hydrology section of the WRENSS procedure, the effect of any given clearcut generally vanishes when the cover density in that clearcut reaches half the maximum cover density anticipated for that particular stand. Cover density is defined in the hydrology section of WRENSS as an empirical function of basal area for each species in a WRENSS region (figure 7). Maximum cover density is assumed to occur at

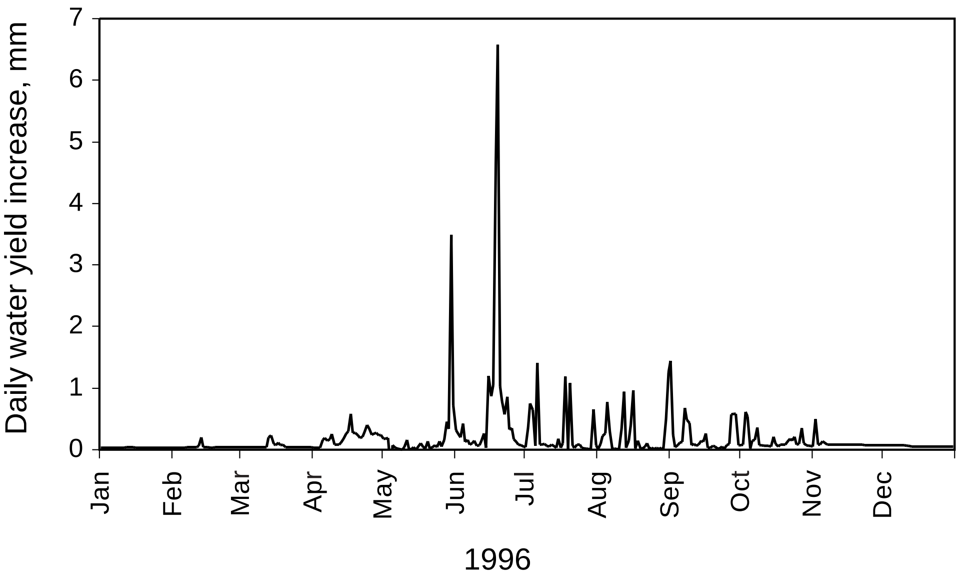

Figure 6—Simulated change in daily generated runoff for clearcut area. Maximum increase in one-day GRO is 6.5 mm on clearcut; area-weighted, 1.3 mm on watershed.

maximum basal area. WrnsDmi, our implementation of a computerized version of the hydrology section of the WRENSS procedure specific to the DMI forest management area in northwestern Alberta, contains basal area and tree height growth equations specific to deciduous stands in northwestern Alberta, considered by us to be in WRENSS region 1, “New England/Lake States” (figure 8). These growth equations are normalized curve shapes that can be programmed to reach a maximum value at any given stand age.

Prior to obtaining the results of this study, we assumed that the hydrologic effects of aspen harvest in northwestern Alberta would vanish at approximately 30 years (Swanson et al. 1998), so we programmed the aspen regrowth equations in WrnsDmi to reach maximum basal area at age 60 for “medium

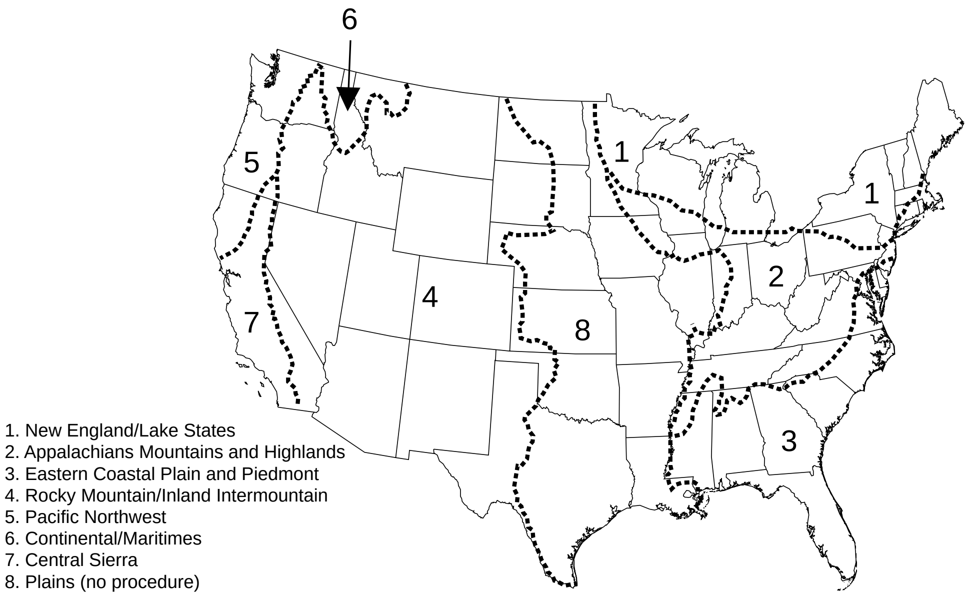

Figure 7—WRENSS regions of the United States.

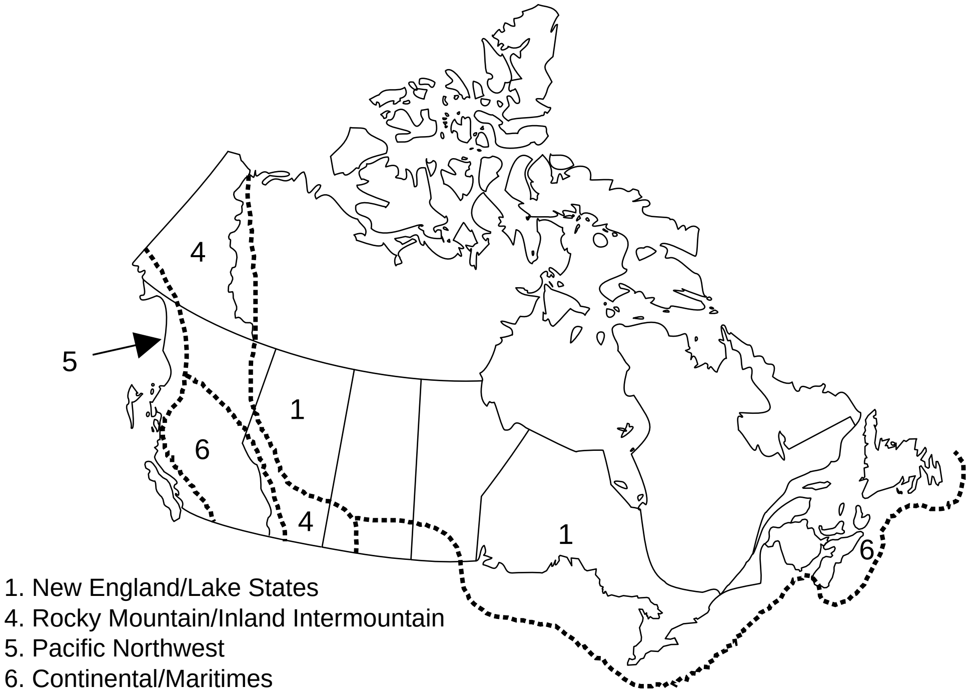

Figure 8—WRENSS regions extrapolated into Canada.

sites" (site index 16 m at 50 years, breast height age). Although 60 years was a reasonable approximation, our results from this study suggest a longer time in wetter years.

The precipitation measured at Kg92 during 1994 to 1996, and used to simulate the change in ET over 60 years, appears to be considerably lower than average. Annual precipitation from a nearby (57:45:00N, 117:37:00W, Elevation 405 m) Alberta Forest Service (AFS) weather station range from 376 to 670 mm (average 468 mm) during the period 1984 to 1997. The highest precipitation that we measured at Kg92 from 1994 to 1996 was 407 mm—less than the average at the AFS site.

The simulations of duration at the Spring Creek clearcut site (Sp94) for the year with 457 mm precipitation (slightly less than the average at the Keg River AFS site) indicate that the effect of harvest will be 10 mm or less at approximately 25 to 30 years and will not vanish until year 55 (figure 5). The simulations with 615 mm precipitation, which is closer to the maximum (670 mm) recorded at the Keg River AFS weather station, suggest a longer time period—i.e., an increase in GRO to less than 10 mm at 40 to 45 years and vanishing at 60 years (figure 5).

The results of this study were intended to be used to limit water yield increases in flood-prone areas. The water yield and any water yield increase caused by harvest is highest in years with most precipitation. Therefore, years with the highest precipitation are the most likely to be associated with flooding. We feel that the most conservative result we obtained should be used in planning harvesting sequences on flood-prone watersheds. In accordance with this conservative approach and our assumption that an increase in GRO of 10 mm or less is not significant, we recommend that the regrowth equations in WrnsDmi be programmed for full hydrologic recovery at 45 years, i.e., maximum cover density at 90 years after harvest. Harvesting sequences designed using this approach should not cause a measurable increase in flooding levels or flood frequency.

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Restoration of Aspen-Dominated Ecosystems in the Lake States

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***Abstract**—A reserve tree method (RTM) of harvesting was installed in six 70- to 75-year-old aspen-dominated stands to determine if retaining 10 to 15 dominant aspen per acre would decrease sucker density to facilitate restoration of a conifer component. A reserve shelterwood cut was applied to three additional stands to evaluate performance of white pine planted under 50% crown cover. After the first full growing season following harvest, 96% of the RTM harvested areas were stocked; sucker density averaged 27,000 (27 k) per acre versus 38.2 k per acre on a clearcut control, 41% greater. Basal diameter of dominant suckers averaged 0.45 inch, 28% greater than the control, and mean height was 60 inches, 33% greater. The control site had 3.1 k stems per acre of associated commercial species versus 5.8 k on the RTM sites, an 87% difference. Four of the nine stands have been planted; first-year survival ranged from 75% to near 100%. The RTM shows promise for reducing sucker density, increasing their early growth, maintaining species diversity, and providing abundant regeneration of commercial species on a high proportion of the areas harvested. Early results indicate that both the RTM and shelterwood methods can facilitate restoring a component of native conifer species in these ecosystems.*

Introduction

Throughout the northern Great Lakes region, most of the forest types are far different from those of a century ago. Depending on location, the presettlement species growing on well-drained, medium to fine-textured soils of northern Minnesota, Wisconsin, and Michigan were predominantly shade-tolerant conifers including white pine (see appendix for scientific names), eastern hemlock, and northern white-cedar; and tolerant hardwoods dominated by sugar maple, red maple, yellow birch, and basswood (Albert 199; Coffman et al. 1983; Kotar et al. 1988). White spruce, balsam fir, white ash, and American elm were common associates. Without stand-replacing disturbances (primarily fires), the aspens (trembling and bigtooth) occurred as minor associates (Braun 1950).

During the late 19th century, exploitative logging, initially of conifer species, created conditions for slash-fueled wildfires that swept over large areas of the region, destroyed advanced regeneration of the former species, and resulted in "brushlands" comprised predominantly of aspen suckers and stump sprouts of associated hardwood species (Graham et al. 1963). Effective fire control beginning in the 1920s permitted these stands to develop into the present-day second-growth forests dominated by aspen.

Throughout much of the region, present-day forests have an abundance of aspen that reduce the landscape diversity associated with a more natural, conifer-dominated landscape. Resource managers are seeking silvicultural alternatives to conventional clearcutting, and ecologically sound and cost-effective means to reestablish a component of native conifer species on some of these sites. By "ecosystem restoration" we mean reestablishing a component of native conifers

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in these ecosystems so that stand-level species composition is somewhat closer to that prior to the logging and wildfires of a century ago. We report data on aspen regeneration the first full growing season after harvesting six stands using a reserve tree method (RTM) on the Superior National Forest in northern Minnesota, and survival of white pine planted under three reserve shelterwood stands on the Ottawa National Forest in western upper Michigan.

Ecology and Management

The aspens are shade-intolerant, rapidly growing, short-lived species that regenerate by root suckers following removal of the parent stand (Perala and Russell 1983). Suckers exhibit more rapid early height growth than seedlings or sprouts of associated species, so they typically form the dominant overstory during the early and mid-stages of stand development. On medium and fine-textured soils, pure aspen stands are rare; most include a component of more tolerant, longer lived species typical of these sites in the absence of disturbance. On most commercial forest land in the Lake States, aspen is managed for wood products or for a combination of fiber and wildlife habitat. Where wood production is a primary objective, the stands normally are harvested by a complete clearcut of all species, and the aspen is regenerated from root suckers. Presumably, the procedure can be repeated and the aspen maintained indefinitely (Perala and Russell 1983), provided the root systems are not damaged by severe soil disturbance during logging (Stone and Elioff 2000).

The Problem

Clearcutting at frequent (40- to 50-year) intervals to maintain single species stands in an early successional state counters several of the objectives of ecosystem management (e.g., Irland 1994) by interrupting natural processes and “resetting the successional clock” (Mladnoff and Pastor 1993). Many stakeholders object to clearcutting and to single species management because of visual quality and aesthetic values. Extensive loss of the conifer component from much of the forest area of the Lake States region has caused concerns about ecosystem structure and function and the diversity and quality of wildlife habitat (Green 1995; Mladenoff and Pastor 1993). Ruark (1990) proposed a reserve shelterwood system to convert 30- to 35-year-old, even-aged aspen stands to two-aged stands, and to allocate limited site resources (sunlight, nutrients, water, and growing space) to fewer stems per unit area. The method had not been tested or validated, but offers several potential advantages at different spatial scales (Stone and Strand 1997).

A major objective of ecosystem management is maintenance or enhancement of species diversity (Kaufmann et al. 1994). Many resource managers are seeking ways to reestablish a component of native conifer species. Establishing these species on suitable sites would be a first step toward increasing stand-level species diversity. Moreover, total yields of mixed-species stands may well exceed those of aspen alone (Man and Lieffers 1999; Navratil et al. 1994; Perala 1977). Natural regeneration of most conifers on these sites usually is limited by lack of available seed sources. Development of planted seedlings frequently is hampered by competition from dense stands of aspen suckers, beaked hazel, mountain maple, and herbaceous species.

Approaches to Solution

As an alternative to conventional clearcutting, and to facilitate reestablishing a component of native conifer species on the Mighty Duck timber sale, the LaCroix District on the Superior National Forest decided to take an "adaptive management" approach and try a reserve tree method (RTM) to reduce the density of aspen suckers and to increase survival and growth of planted conifers. Similarly, the Ontonagon District on the Ottawa National Forest utilized a reserve shelterwood approach to protect advance regeneration of white spruce (Navratil et al. 1994), and underplanted white pine on three sites where it formerly was a major component of stands on clay soils. On both forests, the aspen was 65 to 75 years old, mature or overmature, and the stands were losing net volume from mortality due to stem decay. The residual aspen overstory will not be salvaged on either forest. Both forests contain inclusions of poorly drained soils occupied by black ash, red maple, and associated moist-site species; these were delineated on the ground during sale preparation and excluded from the sales.

Methods

LaCroix District

In each stand, 7 to 15 dominant or codominant aspen stems per acre were selected at a uniform spacing of 50 to 80 feet and marked with paint spots at the stump and at 6 to 8 feet. Prior to harvest, we established transects at 1.5 chain intervals across each stand, marked sample points every 1.0 chain along each line, measured the basal area of all living trees >4 inches d.b.h. with a 10-factor prism, and recorded all saplings and shrubs >6 inches high on a circular 5 m^2 (54 ft^2) plot at each sample point. Stand 9 included an intermittent drainage that served to separate the RTM portion from a control portion that received a silvicultural (complete) clearcut. Stands 1 and 7 were harvested during the summer (July 1997 and August 1998) and the other four during the winter. During September, after the first full growing season following harvest, we recorded the d.b.h and height of each reserve tree within 1.0 chain west or south of the transect lines. On each 5 m^2 regeneration plot, we recorded the number of stems of all commercial species >6 inches high, the basal diameter at 6 inches, and height of the dominant aspen sucker on each. Each regeneration plot was considered stocked if it included one (800 per acre) or more stems of aspen or other commercial species. The data were summarized and means calculated for each site.

Ontonagon District

The shelterwood stands were marked to remove the poor quality aspen and mature white spruce and balsam-fir, leaving about 50% crown cover of predominantly healthy aspen to provide high shade. The stands were commercially harvested using cut-to-length equipment. After logging, the sites were prepared by manually cutting the understory shrubs (predominantly hazel) to reduce root competition and low shade. During May, 1998, they were planted with 3-0 bare root, rust-resistant white pine seedlings at about 9 x 9 ft spacing (500 per acre). They will be manually released once or twice during the first 10 years. Breakup of the residual overstory will provide a final release.

Results and Discussion

LaCroix District

The density of reserve trees ranged from 7.3 to 15.3 per acre and averaged 11.6 per acre on the six sites (table 1). Site 1 was the first stand marked and fell below the desired 10 to 15 trees per acre. As the markers gained experience, their judgement of spacing distance improved and density on the other five sites was close to the objective. Except for the first stand, the reserved basal area was consistently between 10.5 and 12.2 ft^2 per acre, indicating that markers can produce uniform results with relatively little training and experience. Except for site 11, the d.b.h and height data indicate better-than-average site quality. However, the first-year regeneration data (table 2) suggest that this stand may have been younger than the others.

After the first full growing season following harvest, sucker density ranged from 18.3 k per acre to 33.4 k per acre and averaged 27.0 k per acre on the six RTM sites (table 2). Interestingly, the highest density occurred on a summer-logged site (1), and the lowest on a winter-logged site (13). However, the relatively low sucker density on site 13 most likely is because 40% of the initial basal area consisted of associated species, predominantly paper birch and red maple. Thus, in these areas there would be few, if any, aspen roots present to produce suckers.

During the public comment period on the environmental assessment of the timber sale, there were concerns that the RTM might severely reduce sucker density and growth. These data indicate clearly that this is not a problem.

Table 1—Characteristics of reserve trees on the Mighty Duck sale.

Site	Number	D.b.h.	Height	BA	Density
		inches	*feet*	*square feet per acre*	*number per acre*
1[a]	100	15.0	88	9.4	7.3
7[a]	150	11.5	66	12.2	15.0
9	108	13.5	80	10.7	10.0
11	150	10.6	56	10.5	15.3
13	129	12.2	67	11.8	12.8
17	171	15.2	93	12.2	9.3
Mean	135	13.0	75	11.1	11.6

[a] Summer logged.

Table 2—First-year regeneration on the Mighty Duck sale.

	Number	Aspen			ACS[a]	Total	Percent
Site	plots	Diameter	Height	Density	density	density	stocked
		- - - - *inches* - - - -		- - - - - - - *k per acre* - - - - - - -			
1[b]	138	—[c]	59	33.4	5.0	38.4	99.3
7[b]	101	0.38	46	21.8	5.5	27.3	90.1
9	109	0.40	49	31.4	5.0	36.4	95.4
11	98	0.56	76	29.7	7.5	37.2	99.0
13	102	0.37	50	18.3	7.4	25.7	95.1
17	187	0.58	80	27.4	4.4	31.8	95.7
Mean	122	0.45	60	27.0	5.8	32.8	95.8
Cont.	43	0.35	45	38.2	3.1	41.3	97.7

[a] Associated commercial species.
[b] Summer logged.
[c] Not measured.

Graham et al. (1963) considered a sucker density of 6 k per acre as minimum stocking and 12 k well-distributed suckers per acre as optimal; using these criteria, all six of the sites are more than fully stocked. A mean basal diameter of 0.45 inch and height of 60 inches is excellent first-year growth. Moreover, the greater diameter and height of suckers on the RTM sites suggest that carbohydrate and/or nutrient reserves in the parent root systems are indeed channeled to fewer suckers, thereby increasing their early growth as postulated by Ruark (1990). Site 1 was logged during August 1997, and planted with container-grown white pine in May 1998; first-year survival was near 100%.

An objective of ecosystem management is conservation or enhancement of species diversity (Kaufmann et al. 1994). Dense stands of aspen suckers and their rapid early height growth place the seedlings and sprouts of associated species at a competitive disadvantage. The nearly twofold difference in density of associated species on the RTM sites (table 2) suggests that reserving a portion of the overstory contributes, either directly or indirectly, e.g., less machine traffic, to maintaining stand-level species diversity. While this is a limited sample size, we have noted similar trends in other studies (unpublished data on file).

Each of these stands was commercially harvested using conventional logging equipment, i.e., mechanical fellers and grapple skidders. Except for the second summer-logged site (7), >95% of the regeneration plots were stocked with one or more stems of aspen and/or other commercial species (table 2). In related studies designed to monitor harvesting effects on site disturbance and regeneration, 10 to 20% (or more) of most sites are occupied by roads, skid trails, landings, or other heavily disturbed areas that remain nonstocked for several years following harvest (Stone and Elioff 2000). A significant difference between the contract for the Mighty Duck sale and other typical national forest timber sales was the inclusion of a clause specifying a $75 penalty for damage to each reserve tree. The damage clause was highly effective; except for an occasional broken live limb, we noted little logging damage to reserve trees. Operator awareness is critical to protecting advance regeneration (Navratil et al. 1994). Enhanced operator awareness also may have contributed to the relatively low amount of rutting and other severe site disturbance, and in turn, to the high proportion of the areas stocked with commercial species. Use of reserve tree, or other contract modifications, to increase operator awareness of site disturbance and silvicultural objectives merits serious consideration.

Ontonagon District

Shortwood harvesting of the shelterwood stands on the Ontonagon District provided lower sale volumes and required manual removal of the understory, but produced an overstory that probably will be more favorable for establishment and growth of the planted conifers. There has been no significant windthrow or stem breakage on any of the three sites. Despite an exceptionally dry summer, first-year survival of planted seedlings ranged from 75 to 88%.

Summary and Management Implications

Reserving 7 to 15 dominant aspen per acre in six commercially harvested stands resulted in: (1) little logging damage to the reserve trees; (2) regeneration of aspen and associated commercial species on 96% of the area; (3) first-year sucker density of 27.0 k per acre on the RTM sites versus 38.2 k per acre on the clearcut control; (4) mean sucker diameter of 0.45 inch and height of 60 inches;

and (5) 5.8 k stems per acre of associated commercial species versus 3.1 k on the control site. Of the four stands that have been planted, first-year survival ranged from 75 to near 100%. The RTM shows promise for reducing sucker density, increasing their early growth, maintaining species diversity, and providing abundant regeneration of commercial species on a high proportion of the areas harvested. These early results indicate that both the RTM and reserve shelterwood methods can provide stand conditions that are favorable for restoring a component of native conifer species in these ecosystems.

Application

From a landscape perspective, two-storied stands comprised of a mixture of species are aesthetically more appealing to many people than are clearcuts and single-species management. Maintaining partial stocking of the site can be less disruptive to normal hydrologic and nutrient cycling processes; this can be a critical factor on some sites. Two-storied, mixed-species stands provide structural diversity that benefits some wildlife species. The portion of the timber volume retained will reduce the sale volume per unit area, so the Allowable Sale Quantity can be distributed over a larger area. This will accelerate development of a more balanced age class distribution and reduce the eminent breakup of overmature stands. From a silvicultural and forest health viewpoint, this is especially important to those districts that are losing net volume from mortality due to stem decay.

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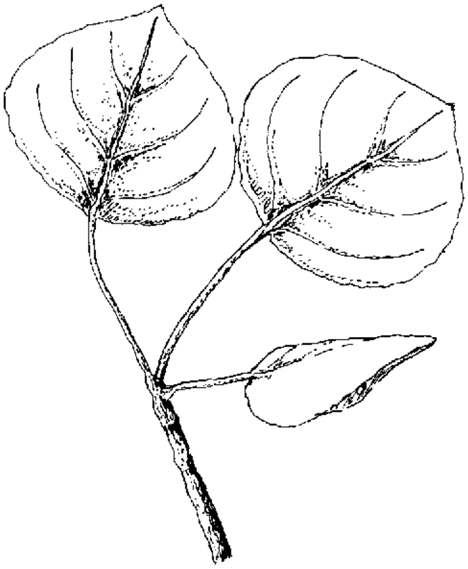
Appendix: Common and Scientific Names of Trees and Shrubs

Common name	Scientific name
Balsam fir	*Abies balsamea* (L.) Mill.
Red maple	*Acer rubrum* L.
Sugar maple	*Acer saccharum* Marsh.
Yellow birch	*Betula alleghaniensis* Britt.
Paper birch	*Betula papyrifera* Marsh.
White ash	*Fraxinus americana* L.
Black ash	*Fraxinus nigra* Marsh.
White spruce	*Picea glauca* (Moench) Voss
Eastern white pine	*Pinus strobus* L.
Bigtooth aspen	*Populus grandidentata* Michx.
Trembling aspen	*Populus tremuloides* Michx.
Northern white-cedar	*Thuja occidentalis* L.
Basswood	*Tilia americana* L.
Eastern hemlock	*Tsuga canadensis* (L.) Carr.
American elm	*Ulmus americana* L.
Mountain maple	*Acer spicatum* Lam.
Beaked hazel	*Corylus cornuta* Marsh.



Human Dimensions

Quaking Aspen and the Human Experience: Dimensions, Issues, and Challenges

Stephen F. McCool[1]

Abstract—*Humans assign four types of meanings to aspen landscapes: (1) instrumental meanings dealing with the attainment of a goal—such as production of pulp or provision of recreation opportunities; (2) aesthetic meanings; (3) cultural/symbolic meanings dealing with spiritual and social attachments to landscapes; and (4) individual/expressive meanings derived out of interactions with aspen landscapes at the personal level. The amount of knowledge available for each meaning varies, with most knowledge developed for instrumental meanings. Management of aspen occurs within a dynamic social and political context, with greater emphasis being placed on the latter two meanings, but without the empirical, positivist basis to support actions. Therefore, a change in the planning paradigm used to develop decisions is needed.*

> I wonder about the trees.
> Why do we wish to bear
> Forever the noise of these
> More than another noise
> So close to our Dwelling place?
> *Robert Frost, The Sound of the Trees*

Introduction

While the hike had been long, it had not been that arduous. The North Fork of the Sun River with its large meadows and hilly eastern skyline provided the beauty that overshadowed distance as the hikers moved toward their favorite campsite. It was a crisp and sparkling September day, the mountains were brilliant, with abundant herds of elk moving through the clones of yellowing aspen. A slight breeze fluttered the leaves, as if nature had to inform the hikers of the source of the aspen's scientific and common name. It was the time of the fall that the clones could be distinguished by variations in leaf color, and the view from a distance could only be termed magnificent. In a sense, the aspens here represented the oncoming of fall, the predecessor to those long Montana winters. Seeing the turning of colors provided some reassurance that nature was alive, dynamic, and aesthetic; yet as the hikers recollected previous winters, they remembered aspen as a kind of warning sign of what would be coming in very short order.

Their camp was not far from an aspen clone across the river, and it seemed to amplify and reflect the golden rays of the setting sun back to them. Bugling elk complemented the aspen as the hikers ate their dinner, suggesting not only a sense of remoteness, but also an impression of tranquility. Aspen, their color and trembling leaves, promoted a feeling of peacefulness, one that was consistent with a wilderness experience, one that was not only uplifting, but encouraging as well, and one that stimulated thought and introspection.

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As experienced hikers, they knew there was more to aspen than its use as pulp; it was not only essential to their experience, but as wildlife habitat as well. They felt that aspen must have played an important, if symbolic, role in Native American relationships with the land.

They understood that there were problems in the reproduction of aspen, and they felt that some type of action was needed. Their discussion around the campfire that night led them to a number of questions, most without easy answers. How is the condition of aspen related to larger scale biophysical processes? What factors are leading to declines in aspen stands, and how can managers influence them? How do these declines relate to the broad range of landscape values associated with aspen? How are these important values protected in a restoration strategy? What is the range of values? How are they mapped and measured? How do they differ in various regions of the mountains? What restoration practices are appropriate and where? Do land management agencies have the capacity to conduct comprehensive analyses of the values potentially compromised before restoration occurs? How adequate is the science supporting calls for more active management and restoration of aspen in the West?

The hikers knew that restoration of a system that has been damaged is a long-term process. Will the institutional and political systems that govern restoration practice tolerate experiments for which there may be few results in the short term? Will the biologists that design restoration initiatives be around in a decade or so to see what transpired? Will they establish monitoring programs that will demonstrate whether the restoration was successful?

These are profound questions—among many others—for today's land managers. They exist within a context of changing land management paradigms, decreased institutional capacity for management, a paradoxical increase in calls for both scientifically based decisions and public participation in them, and an increased demand for a widening array of goods and services from the nation's public lands.

Management of aspen could only be described as a messy problem—a situation where goals are vague (at best) or contested (at worst) and where our understanding of cause-effect relationships is incomplete. Human interactions with aspen—and the meanings that result from them—exist within and involve this dynamic context and are the subject of this paper. More specifically, this paper has three principal objectives. First, using a framework based on human-environment transactions and landscape meanings, I will present a classification of human dimensions of aspen. This discussion will help establish a foundation for understanding that there are multiple such dimensions that are often not subject to classical positivistic appraisal, yet fundamental to understanding the social benefits of aspen. Second, I will briefly examine some of the institutional issues associated with aspen management. This context is a vital component of management; how it is structured and how it operates influence management decisions. Finally, I review some of the challenges associated with management of aspen that arise in the social domain. This argument suggests that management and restoration practices based on limited, narrow definitions of the "aspen problem" incompletely specify the costs and benefits of aspen in the Western landscape and potentially marginalize the participation of important segments of the population in developing and implementing restoration practices.

Charting the Human Dimensions of Aspen in the Western Landscape

Aspen is a ubiquitous, highly visible attribute of the Rocky Mountain landscape. Understanding the human dimensions of aspen, as defined by people, is a vital component of any strategy to manage it. While aspen has important and well-known instrumental and aesthetic values, there may be others as well. In this section, I will present a framework based on the notions of environmental transaction and place meanings that suggest what those dimensions may be. I begin first with a general description of the framework and then move to a more specific discussion of how it applies to quaking aspen.

Human dimensions may be perceived as a set of meanings people place on the environment and its attributes. These meanings derive from the types of transactions between people and the environment that occur (Ittelson 1973). Meanings are influenced not only by the specific physical attributes of aspen, but also by the larger biophysical and cultural contexts, managerial settings in which they occur, and by the individual viewer's background characteristics (Ittelson 1973).

In the case of aspen, these transactions involve visual perception—the stem and leaf color and texture, stem density, clumpiness of clones, and the shimmering of leaves trembling in a breeze. Such transactions also include the sounds of leaves quaking in the breeze. These characteristics combine to provide a special sense of place as articulated in this comment by a naturalist in Montana: "There may be no finer place than an aspen grove in the fall," according to Ellen Horowitz. "Once you learn the sound of the aspens," she says, "you can go into the woods and close your eyes and be able to pick out the voices of the trees. Aspen groves are special places" (quoted by Jamison 1999).

At close distances, the special character of aspen clones, in terms of the density, size, color, and shape of individual sprouts within a forest context, help form meanings and expectations. This series of transactions occurs over time in a variety of settings, and over time people learn from these transactions. This learning leads to the sight of aspen symbolically representing certain specific meanings to an individual as well as a group. These meanings may vary spatially and temporally.

These meanings can be described by characteristics such as their tangibility, commonality, and emotionality (Fournier 1991). Tangibility refers to whether the meaning can be assessed objectively, measured according to some independent scale, or whether the meaning is held within the mind of the viewer. Thus, the cloning of aspen, and their distinction, particularly in early fall or spring, is a highly tangible characteristic. Commonality is a characteristic that indicates the extent to which a meaning is widely shared or, conversely, unique to an individual. The aesthetic value of aspen in the fall is not only tangible, but widely shared among many Americans. Emotionality refers to arousal or depth of attachment. A rural farm or home in the West may have an excellent view of a particular aspen clone. The family within that home may find itself deeply bonded to it.

Variations in such characteristics lead to spaces becoming places—spaces with social definitions. The meanings attached to places may be classified according to a typology put forth by Williams and Patterson (1999). They suggest four types of meanings: (1) instrumental; (2) aesthetic; (3) cultural/symbolic; and (4) individual/expressive. Instrumental definitions develop out of an environmental attribute's ability to promote a specific behavioral or economic objective. Environmental attributes "become" resources because of their utility for economic and production systems. The meanings here are tangible and widely held, yet they normally do not carry much emotional significance. Because of their relevance to the material needs of society, the mechanisms for measuring and understanding these definitions are well developed and fit nicely into scientific-based, expert-driven models of decisionmaking.

Aesthetic meanings reflect an emotional, somewhat tangible interpretation of the environment as scenic or beautiful. Interpretations of selected environmental settings as scenic, beautiful, or inspirational are widely held and often form the basis for much of the tourism industry, particularly in the Western United States and Canada. Such meanings are frequently expressed in artistic impressions— primarily through paintings and photography but also in poetry such as that of Robert Frost—of the environment. Systems for measuring and mapping aesthetic attractiveness and managing scenic beauty have been developed over the last 30 years and are integrated into federal public land management planning processes (Litton 1979; USDA Forest Service 1995).

Cultural/symbolic meanings attached to landscapes derive from transactions with landscapes at a group level. While these meanings may result from a significant cultural event—such as a battle or the birthplace of an important individual—they may derive from beliefs about the natural world, how it operates, and its influence over human life. Mythologies may be associated with specific biophysical characteristics or a unique site, such as Devil's Tower in Wyoming. Such meanings are not necessarily tangible, but are shared among individuals within a specific family, clan, tribe, community, or society. For example, Devil's Tower National Monument was established because it represents an outstanding and unique geological formation, clearly a meaning that is instrumental at its foundation. Early Western visitors often climbed to the top, beginning a tradition that has lasted over 75 years. Defining Devil's Tower as a place to climb represents an instrumental meaning. Yet, such climbers—and the managing agency—were unaware that to Native American tribes of the northern Great Plains, Devil's Tower represents an important environmental feature that is spiritually significant to those tribes. These two meanings came into conflict as Native Americans voiced their values and preferences and attempted to restore long-held spiritual practices at the monument, compelling the National Park Service to attempt to reduce climbing near the time of the summer solstice, and leading to a new management regime.

Cultural/symbolic meanings are emotionally arousing; Williams and Patterson (1999, page 148) state, "…emotion is a relatively enduring affection for a place built up through a history of experiences in the place. In this case, the emotion is not the result of any particular experience of the place, but involves some level of emotional investment in the place built up over time."

The move to ecosystem-based management has generally led to recognition that ecosystems provide a wider range of goods and services than the commodity-based, multiple-use approach of the past. The recognition that cultural/symbolic values exist is an important component of this new approach, but also one that is not easily linked to specific, spatially identifiable characteristics of landscapes. These meanings cannot be easily measured in the same sense as board feet of timber.

Individual/expressive meanings also derive from a socially constructed view of environmental values, but at the individual level. Such meanings are highly intangible, not shared—except perhaps within a family—and strongly emotional in character. To many people, landscapes help provide their sense of identity. Williams and Patterson (1999, page 148) suggest that such meanings attached to landscapes "help communicate…who we are." A favorite campsite located along a bubbling stream that has been the location for family reunions is an example of a place defined by individual/expressive mechanisms. A particular place evokes memories, recollections, and events that are specific to an individual. Because such meanings are expressive at the individual level, and thus idiosyncratic, they cannot be linked to spatially identifiable landscape characteristics.

This framework provides a policy-relevant approach to understanding human dimensions of aspen and its management. Enhancing our understanding of meanings can not only reduce conflict about how to manage places where aspen occurs, but also better understand the consequences of various management strategies and suggest ways in which meanings can be protected and enhanced. Unfortunately, the literature about the social meanings of quaking aspen is not only diminutive but varies considerably from category to category, so what follows may be more speculative and tentative than grounded in formalized research and technical analysis. Nevertheless, the discussion indicates that there is much we need to know about aspen before we make irreparable decisions about its management.

Instrumental meanings, such as the value of aspen for pulp, flakeboard, and furniture, tend to be tangible and widely shared, particularly in the north-central region of the United States. Aspen meanings, in fact, are usually defined and measured in purely instrumental terms. For example, Einspahr and Wyckoff (1990) define the "aspen wood resource" in such terms as cords per acre and billion cubic feet of volume. When discussing utilization, they refer solely to manufacturing wood products and pulp. They conclude that "Only a minor amount of the aspen resource in the western United States is being utilized" (page 169), when in fact, much of it is the source of noninstrumental utilization and meaning.

Aspen sometimes served as a source of medicine for Native Americans (Willard 1992). Preparations made from bark were often oriented toward relief of symptoms from fever, rheumatism, arthritis, colds, and other indications. Recreationists frequently camp in public campgrounds located within aspen clones; but the actual significance and preference for aspen-dependent experiences is not known.

Emerging instrumental meanings of aspen concern its utility for wildlife and the role of fire in maintaining the presence of aspen in the landscape; yet these meanings may be held only by a small group of scientists, with little emotional attachment to specific places containing aspen clones. Little is known about recreation as an instrumental meaning of aspen. Ways of measuring and mapping instrumental meanings of aspen are well developed in the literature and practice.

Aesthetic meanings of aspen are commonly held, relatively tangible, and probably evoke a moderate level of emotionality or attachment. Its visual appearance, clumpy distribution, and contrast with surrounding vegetation make aspen landscapes not only distinctive, but visually attractive, particularly during the autumn when colors of aspen clones differ from the surrounding landscape. Such values of aspen are frequently displayed in artistic photography, such as that by Ansel Adams. Adams was a master of understanding landscapes, of interpreting the aesthetic meaning of combinations of mountains and trees, water and ice, clouds and sky, sun and shadow. He was equally a master of the technical process of manipulating and displaying such images in print. Equipped with both skills, he captured these forms and patterns like no other on black and white film. His attention, while frequently focused on the mountains and forests of the Sierra Nevada, occasionally turned to other subjects and locations. For example, his image "Aspens, Northern New Mexico" emphasizes the pattern and form of aspen stems in the immediate foreground, bringing out in rich detail and contrast their aesthetic value. While Adams used black and white photography, a variety of others have attempted to capture aesthetics of aspen, particularly in two books by Colorado photographer John Fielder (*Colorado: Images of the Alpine Landscape* and *Colorado Aspens*). Fielder captured through color the full dimension of aspen aesthetics, less interpretive than Adams' approach, but just as dramatic.

The landscape dominance elements of form, line, color, and texture (Litton 1979; USDA Forest Service 1974) can be used to describe these aspen stands and may serve as the foundation for actions that reduce the visual intrusiveness of management. The aspen landscape occurs in a variety of forms: small independent clumps, a series of different clones juxtaposed, large portions of mountains covered with aspen, and a linear form found along streams of the Rocky Mountain Front in northern Montana. The seasonally dynamic character of aspen can also be described by these landscape dominance elements, as the color changes in their form become more recognizable; in the winter, the dominance element of line is more visible. This dynamic character of aspen suggests the basis for its aesthetic value changes over fairly short temporal scales.

High levels of aesthetic attachment to specific clones may exist for some small communities and families with aspen clones nearby that provide aesthetic values. The literature shows little research on aesthetic preferences for aspen, although the methodology for aesthetic mensuration is well developed in general.

Aesthetic meanings of aspen may lead to important economic benefits as tourists flock to communities adjacent to aspen stands during the fall, thus extending the tourism season. Frequent use of such aesthetic meanings may lead to new cultural/symbolic and instrumental meanings of aspen as communities exploit growing public interest in aesthetics to bolster their tourism industries. In urban and suburban settings, aesthetic meanings of aspen are identified through its frequent use as a horticultural element in commercial and residential landscaping.

Cultural/symbolic meanings derive out of transactions that interpret the meaning of specific environmental attributes to a group; as such, these meanings may vary from one group to another and are not necessarily shared among groups. Our knowledge about cultural/symbolic meanings of aspen are poorly developed and understood. In Western society, these meanings are often recognized through formalized boundary setting, as when Congress establishes a national monument or historic site. Aspen may have served as the basis for a variety of Native American tribal stories and mythologies, such as a Blackfoot story about how aspen came to tremble. Briefly,

> One day, the aspens got together and decided that Napi (the Blackfoot man/god/clownster) wasn't all that important, so they agree that they would not bow down for him, next time he was around. True to their word, the next day when Napi came walking by, they just stood there indignantly. Well of course Napi didn't like this. In a tantrum, he

> started throwing lightning bolts at them, almost scaring the leaves off their branches. To this very day, the aspens are so scared that every time they hear someone walking in the woods, they tremble their leaves in fear it might be Napi (Willard 1992, pages 65-66).

There may be other cultural/symbolic and individual/expressive meanings. For example, the turning of colors symbolizes the oncoming of fall and winter, serving to suggest that people have one more chance to engage the landscape on a personal level and then prepare for the difficulties of living in a northern climate. Returning to naturalist Horowitz: "When fall comes on, I want to put away some food, gather some wood; I want to get ready to winter well. That fall light still has a powerful pull on all of us. I can feel it all the way through" (Jamison 1999).

For others, aspen may represent the Western landscape. And there may be another symbolization that aspen serves particularly relevant to this conference. The fire exclusion and grazing that has left much of aspen territory without adequate reproduction may lead at least some people—particularly citizens, scientists, and managers interested in resource management in the West—to view aspen as a symbol of the continuing human interference in natural processes. Just as white bark pine tends to symbolize remote, rugged, and wild landscapes (McCool and Freimund 2000), aspen may come to represent landscapes where natural processes have been disturbed.

Meanings of aspen at the individual level contain high emotionality, low commonality, and low tangibility. Examples include use of individual clones for traditional family celebrations such as reunions, use for personal introspection, reflection, and prayer, and the view of a clone from a ranch house. Such attachments are difficult to describe and are not spatially differentiated across a landscape, leading such common analysis tools as geographic information systems to be inadequate. One of the paradoxes faced here is that while people may become attached to such clones, the dynamic character of landscapes means that such clones will eventually disappear as others appear. The relatively short life span of individual stems means that such changes may be visible within a human generation.

Place meanings may differ temporally (Lee 1972), with different groups assigning meanings to the same space over a day, season, or year. Different definitions of place may be the source of conflict over that place's disposition. For example, a campsite in an aspen stand that has long served as the location of family reunions over decades may be viewed by a biologist, not in individual/expressive terms, but in very instrumental ways, such as decadent and in need of restoration treatment. Thus, meanings of a specific space may differ from one group to another; the primary meaning is constructed by the dominant social group using a place.

Management and Restoration of Aspen: Institutional Issues Related to Social Uses, Values, and Processes

There apparently is no longer a question about the status of aspen in the Western landscape: it appears to be declining in its spatial distribution, although there is significant variation in the potential decline from one locale to another (Debyle 1990). The causes of such declines seem to be most frequently attributed to fire exclusion and grazing by both domestic livestock and wild ungulates, but definitive answers remain elusive. This decline seems to be widespread in the Western landscape, suggesting the temporal and spatial pervasiveness of these human-caused disturbances.

These findings suggest that aspen in the future may be a less common element of the landscape than it is now. Assuming a goal of sustaining aspen, at least in some type of dynamic way, what are the institutional issues associated with management and possible restoration actions? Such issues are important because institutions—laws, agencies, managerial cultures—associated with land management form a strong paradigm that determines what decisions will be made, how, and by whom. The management of aspen may be constrained or enhanced in this respect.

Natural resource planning is dominated by a rational-comprehensive or synoptic style of planning that places great emphasis on scientific expertise, establishment of goals, consideration of all possible alternatives, systematic evaluation of alternatives, and choice of a preferred course of action. This planning tradition emphasizes formalized information, quantitative modeling of biophysical systems, and assumes that problems are well defined and that planners will have perfect information and unlimited time in which to conduct analyses and recommend decisions (Forester 1989). Synoptic planning does well in situations where scientists agree on cause-effect relationships and the goals of management are left uncontested.

However, when these two contextualizing factors take on different characteristics, synoptic planning is ill-suited to its task. Such formalized planning systems neither represent the current situation in natural resource planning nor are they particularly well equipped to incorporate cultural/symbolic and individual/expressive landscape meanings. More typically, scientists disagree, and the public has not come to a consensus about goals. Often, conflicts in values (representing cultural and individual meanings) are at the heart of environmental disputes. Problems may not be well defined, or at least managers may be confronted with multiple and competing definitions. There may be structural distortions in access to information and decisionmakers. Political power is nonrandomly distributed.

The application of a synoptic planning process in such a setting miscasts the goal of planning. Rather than selecting the most efficient alternative to a given end, planning must be focused on determining which of several plausible futures are desirable and on understanding the relationships among various causal factors and their effects. This “messy” situation requires styles of planning that emphasize consensus building and learning, recognize various forms of knowledge as legitimate, understand that some values and uses cannot be directly measured and mapped, and incorporate a diversity of the affected publics so that consensus can be created. Thus, science helps to facilitate a decisionmaking process, just as the emotional and experiential knowledge of the public and the administrative experience of the manager does. Emotional and experiential forms of knowledge are particularly useful in identifying the cultural/symbolic and individual/expressive meanings for which synoptic style measures do not exist and cannot be spatially modeled.

These issues suggest that one needs to be careful not to underestimate the complexity of the aspen management question. A substantial argument can be mounted that the context within which management of aspen is ill-structured and messy, and that there may tendencies to define aspen restoration as “just like” the question of white bark pine restoration, a major issue across the West as well (McCool and Freimund 2000).

The types of meanings assigned to aspen carry significant ramifications for management. These implications involve (1) how such meanings are measured, mapped, and inventoried and (2) how they are evaluated and weighed in decisionmaking and incorporated into management actions for multiple-value settings. Inventory systems have been developed to identify, measure, and map aesthetic and various instrumental landscape meanings. A variety of scientists have contributed to increased understanding of the landscape elements that lead to evaluations of whether a particular place is scenically attractive. Management systems that protect or enhance scenery have been developed. These systems fit well into management because they are consistent with the positivist tradition of synoptic, scientific-based, expert-driven approaches to decisionmaking. However, cultural/symbolic and individual/expressive meanings are not easily measured and mapped, are identifiable generally through nonpositivistic approaches to landscape assessment, but yet may be the most significant meanings attached to a landscape feature and, therefore, those most affected by management actions. The state of knowledge of these values is limited, and their relationship to aspen is generally unknown.

Restoring Aspen: Challenges From the Social Domain

As a system that is potentially in decline, management of aspen represents a series of important, but thorny, human issues for restoration ecologists and land managers. It is not clear if there is unanimous agreement among scientists about the causes of aspen decline or how the decline should be addressed, nor is it clear that objectives for restoration and maintenance of aspen in the region are well accepted by affected publics. Given the variety of institutional overlays on public lands, management must vary from place to place, and in wilderness, questions about restoration as an act of trammeling are raised (McCool and Freimund 2000). Finally, it is not at all clear how aspen management (outside of commodity production), particularly restoration, may have consequences of significance for humans.

Decisions about aspen, including the decision to do nothing, reflect fundamental values and ethics of land managers charged with the responsibility for the stewardship of natural resources. The statement that aspen is in decline is only a *descriptive* statement; the suggestion that something ought to be done about it is a *prescriptive* statement. To sustain aspen in the Western landscape, both decisions—one based in science, the other in ethics—must be made. In this section, I review the different challenges to decisionmakers and scientists that derive from the decision to restore, including the ethical framework itself. There are a variety of challenges that may be briefly termed decisional, definitional, contextual, epistimological, and ethical.

Decisional Challenges

While it is clear that restoration of aspen will be driven by societal concerns about the condition of the natural environment (in general and public lands more specifically) and shifting demands for goods and services from ecosystems, actual restoration decisions are influenced by specific legal mandates and institutional directives. This institutional context is increasingly complex and confusing, as experience in the Pacific Northwest with northern spotted owls, marbled murrelets, and anadromous fisheries demonstrates. The resulting bureaucratic environment is a complex and frequently confusing web of regulatory agencies, federal land management agencies (e.g., Forest Service), court jurisdictions, unwieldy processes, funding sources, and oversight responsibilities (Congress). While it is difficult to foresee that such a similar bureaucracy will develop with respect to aspen itself, such questions may eventually involve aspen management as an important habitat for other endangered species.

Such a heterogeneous decision setting, with agencies operating under differing objectives (at best) or conflicting ones (at worst), agendas, and cultures, tend to be puzzling, confusing, and unresponsive to rapidly changing and spatially differentiated social preferences and environmental conditions. Institutional structures and processes for decisions differ among agencies. Mythologies and perceptions about what decisions, mandates, and strategies must be followed abound. Social and biophysical processes operating at different scales are not particularly well understood.

Managers of aspen and the landscapes embedding it will be making several decisions such as: What goods and services should this landscape be managed for? What actions are needed to produce, maintain, restore, or enhance those values? If restoration is needed, what should be restored? How should restoration occur? Where should restoration occur and when? These are important decision points that involve ecology but affect the meanings that people assign to landscapes.

Both regulatory and management agencies have chosen prescriptive techniques for dealing with habitat restoration when endangered species are involved. Yet, there are often perceptions among agency personnel and publics that these prescriptions do not take into account local conditions and situations. Such rigid approaches to restoration serve as an overwhelming barrier to the practice of adaptive management advocated by many contemporary scientists (see for example, Holling 1978; Gunderson and others 1995). For the learning to occur that is required for policy formulation, the system must be adaptable. Rigid institutional overlays remove the adaptability from the system simply because there is not opportunity to learn from and further experiment with policy (Gunderson 1999). And as Lee (1999, page 1) argues, experimentation and the consequent accrual of knowledge "is likely to be of strategic importance in governing ecosystems as humanity searches for a sustainable economy."

Definitional Challenges

Restoration is usually cast as a technical, scientific-based activity dealing solely with ecological function, process, and structure. While there are many definitions of restoration, they tend to center on reestablishment of predisturbance conditions and processes. While there is some dispute about restoration leading to healthy ecosystems or systems with high integrity, such definitions usually focus only on biophysical components of ecosystems.

The Western landscape provides a wide range of human benefits, including their capacity to maintain desired populations of wildlife. These human benefits are impacted when systems are degraded, and impacted as well when restoration practices are implemented. In a sense then, restoration can be defined as management processes that lead to protection or enhancement of the human meanings assigned to landscapes.

As Bardwell (1991) argues, defining the problem appropriately is a crucial precursor of the problem-solving process. Understanding what the problem is and specifying it explicitly is important to development of appropriate solutions. Clearly, restoration can only be defined in relation to the types of values and benefits to be preserved, renovated, or managed. The range of values is broad, and at some point, all must be addressed or accounted for in planning analyses. Additionally, there may be questions about the generalization of aspen decline, particularly at a regional level (see papers by Kay and Renkins, this proceedings). Thus, there may be a tendency to solve the wrong problem, solve a solution, address a symptom, or attempt to obtain agreement on a solution before the problem is defined as Bardwell argues. Clearly, we need agreement on what should be restored before action occurs. And it is just as clear that what should be restored is as much human meanings as ecological structure and function.

Relationships that exist between humans and their environment, that may have lead to a combined cultural-environmental system, or conditions that may have resulted from pre-EuroAmerican perturbations, are usually neglected in defining the purpose of restoration. Restoration is often defined as repair of systems damaged by human activity. However, as Geist and Galatowitsch (1999) argue, restoration provides a set of benefits distinctly human in nature.

This biotechnical focus of restoration, however, significantly miscasts restoration processes and practices. Human elements permeate restoration, from decisions that the environment needs restoration, through definitions of specific restoration goals, to organizing and scheduling people and materials for the restoration activity, to lobbying and appropriating funds for restoration activity.

Contextual Challenges

A variety of forces and changes are driving the need for restoration. Briefly, these forces involve a shift in expectations of what goods and services ecosystems are expected to provide, more rigorous standards concerning the acceptability of human-induced changes, and growing scientific-based knowledge about the consequences of human activity. Restoration occurs, moreover, within the dynamic, even chaotic, political and social context alluded to above. In particular, the goals and objectives needed to specify outcomes of restoration are ambiguous or in conflict with other resource management goals. The lack of specific, measurable goals for which a consensus exists hampers evaluation of progress and represents ongoing conflict within the public about both means and ends of restoration. In addition, the science necessary to restore riparian ecosystems is often insufficient to support management decisions, or leads to conflicting conclusions about projected consequences and effectiveness.

Epistemological Challenges

Action in society requires a variety of actors in different roles with varying capabilities and knowledge (Friedmann 1973). Each actor brings into a problematic situation different forms of knowledge—not only in content (e.g., fisheries, terrestrial ecology)—but different sources as well: science, managerial experience, personal experience, and so on. Each individual also has varying capacity to process different forms of knowledge; some can absorb and process scientific-based knowledge, for example, easier than others. For action to proceed, the different forms of knowledge must be respected by the various actors, even if its content is not completely understood.

The practice of restoration is dominated by calls for it to be "scientifically based." This bidding is probably rooted in past land management practices that did not exploit existing technical knowledge or were based on political expediency. The underlying and often implicit assumption that scientific knowledge provides answers to restoration questions is often accompanied by explicit statements that riparian systems are so complex that our current knowledge base is inadequate to the task.

Unfortunately, relying solely on scientific-based information leads to two negative consequences. First, science measures only tangible items of the world, which are not necessarily the most important values of ecosystems (Forest Ecosystem Management Assessment Team 1993). The development of a technocratic administrative service and the dominant rational-comprehensive or synoptic planning processes has exacerbated this problem as noted earlier. Because science measures only a few aspects of ecosystems, those aspects assume an importance, because they can be articulated, beyond what they really may be. Second, the ability of science to measure and describe things in technical language has led to scientific information being privileged in decisionmaking processes. As Friedmann argues, there are significant questions about this privilege (Friedmann 1987). Given these limitations of scientific methodologies and how they are applied in field situations over long-time scales and large spatial scales, this privilege may be unwarranted at best. Thus, biologists, when practicing restoration, must recognize the legitimacy of emotional forms of knowledge, for it communicates the importance of different values and thus provides information about priorities and the impacts of restoration practices.

The net effect of these contextual factors is that restoration decisions are made under the illusion that causes, effects, and consequences are known with certainty, when in fact, restoration decisions are more likely characterized as being made under conditions of risk or even uncertainty. To some extent, the lack of recognition of disagreement on goals may also lead policy makers to make decisions for which there is little broad support, thus endangering restoration and hampering future efforts to organize societal action.

Ethical Challenges

Restoration practices represent an ethical decision that humans have a responsibility to leave the earth in a "better" condition than what they found, the essence of the concept of sustainability. Yet, there is considerable debate about whether restoring nature is a credible activity: some authors suggest that restoration leads to "fake nature," restoration encourages more degradation (because of the technological capability to quickly repair damaged systems), restoration represents continued human domination of nature, and ecosystems are simply too complex to be completely restored. The debate on these points is quite serious, with the language at times outright acrimonious. The extreme language is sometimes cited as a good reason why ethicists have nothing to contribute to discussions about restoration.

Yet, restoration ecologists cannot escape the ethical foundation for their activities. Manipulation of nature, for commodity production or restoration, involves application of some kind of ethical framework to the landscape. It reflects how we perceive nature, the relative importance of various human benefits derived from nature, and responsibility toward future generations, all of which are based on a view of nature culturally derived.

Conclusions

Aspen is an important component of the Western landscape, although it has in many places a spotty distribution. Its importance derives not only from its role in the biophysical aspects of an ecosystem, serving critical habitat and forage functions for some species, but also as a source of fiber for human use, and equally important, in the meanings and attachments people place on landscapes. Quaking aspen also provides aesthetic values critical for the humans that expect to view it every fall. Our knowledge about aspen and how people interact with it is limited, as evidenced by the lack of literature and manuscripts submitted at this conference. The major challenge to aspen management appears to be finding the causes of its decline and correcting them so it retains its appearance in the landscape.

Yet, decisions to restore aspen to its pre-Euro-American abundance and distribution occur under conditions of uncertainty precisely because many socially important meanings of aspen have yet to be documented, researched, or archived. We know neither the distribution of these meanings functionally or spatially, nor do we understand how management and restoration might impact those meanings. To conduct restoration and active management without such knowledge risks losing the values associated with those meanings without understanding what is being lost. This is a paradox, because it appears to be clear that without restoration, we will lose aspen and the values associated with it as well.

It seems important, therefore, to complement the active research program on aspen ecology with one that addresses the recreational, aesthetic, cultural, and individual meanings associated with aspen. Such research would play valuable roles in establishing the basis for potential conflicts, ranking the priority of management actions, and suggesting ways in which landscape meanings and place attachments can be enhanced—such as when aspen stands are carefully managed for their instrumental value as a source of pulp. Research on these meanings can help managers understand what values and meanings are at stake, whose definitions are being impacted, and how and what planning processes may be useful in ensuring that such meanings are not inadvertently marginalized.

Only then can we fully understand what needs to be restored and why. Only then will managers be able to comprehensively document the effects of aspen management. And only then can management proceed with full knowledge of consequences.

The campers on the North Fork of the Sun River raised significant questions around the campfire that evening a few years ago. Scientists, managers, and citizens have important roles in addressing those questions. The human experience of Western landscapes includes the presence of aspen, but that experience is multidimensional, an assertion recognized by those campers. Will the scientific community broaden its scope of interest similarly when dealing with aspen?

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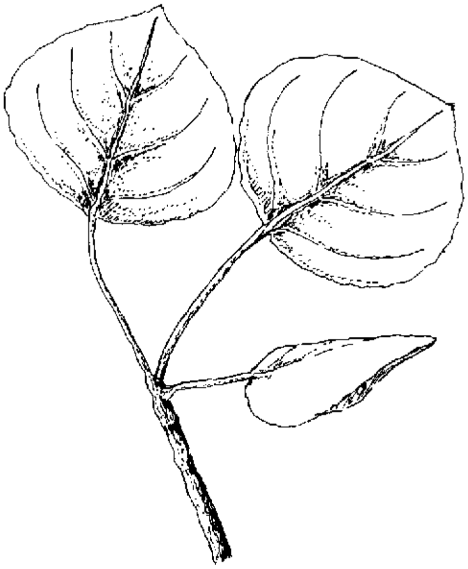

Animal/Aspen Interactions

Effects of Ungulate Browsing on Aspen Regeneration in Northwestern Wyoming[1]

Bruce L. Smith[2], J. Scott Dieni[3], Roxane L. Rogers[4], and Stanley H. Anderson[5]

***Abstract**—Although clearcutting has been demonstrated to be an effective means to regenerate aspen, stand replacement may be retarded under conditions of intense browsing of regeneration, such as that experienced near elk feedgrounds in northwestern Wyoming. We studied the effects of ungulate browsing on regenerating aspen following clearcutting on the National Elk Refuge. Nine deteriorating, aspen-dominated stands were clearcut in the spring of 1988, and regeneration characteristics were subsequently measured periodically through 1996. Big game exclosures were placed in three stands immediately following treatment. Post-treatment sucker densities were relatively low but theoretically sufficient for stand replacement. The percentage of "suckers" that obtained heights >2 m was significantly greater inside the exclosures after 9 years than outside the exclosures. Average heights of browsed and unbrowsed suckers were markedly taller within the exclosures. Our findings suggest that repeated annual browsing substantially increased sucker mortality and limited the height achieved by aspen stems. Small-scale clearcutting to regenerate aspen may not be effective in areas of winter ungulate densities similar to those adjacent to elk feedgrounds.*

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[1] Authors chose to submit abstract in the place of full report. The recently published manuscript can be found in the Intermountain Journal of Sciences 6(1):49-55.

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Predicting Nest Success From Habitat Features in Aspen Forests of the Central Rocky Mountains

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***Abstract**—We collected nesting data on bird use of aspen stands in the Routt and Medicine Bow National Forests between 1987 and 1989. We found active nest sites of 28 species of small nongame birds on nine study plots in undisturbed aspen forests. We compared logistic regression models predicting nest success (at least one nestling) from nest-site or stand-level habitat predictors. Most common species used nest sites in aspen trees in forest interior locations (distance to edge >100 m), with dense trees (opening >100 m away) despite no apparent positive correlation with use of these habitat features and nest success rates. Further investigation may demonstrate that these forest interior sites do not experience lower predation and cowbird parasitism rates than nest sites near openings. We recommend adaptive management experimental treatments, including carefully planned cutting and controlled burns, that should benefit most birds in western aspen forests.*

Several studies have examined nesting habitat relationships by exploring patterns in nest success of forest birds. Predation was the major cause of failure in several studies of birds nesting in forests (Hartley and Hunter 1998; Hannon and Cotterill 1998; Donovan et al. 1997; Robison et al. 1995; Martin 1992, 1993; Ricklefs 1969). Finch (1989) studied nesting habitat of house wrens (*Troglodytes aedon*) using nest boxes in southeastern Wyoming and found that success was higher on relatively open habitats that were actively selected by the birds. Predation by foliage climbing bullsnakes (*Pituophis melanoleucus sayi*) was the major cause of nest failure in this study. Open habitats were thought to hinder predator access to nests and allow early detection and deterrence of predators by the wrens (Finch 1989). Yahner (1991) found an overall inverse relationship between nest height and nest success in aspen forests of central Pennsylvania; higher nests had a significantly higher predation rate. Conversely, Li (1989) found that cavity-nesting birds on the Mogollon Rim in Arizona preferred to nest in aspen trees, and failed nests had greater concealment, shorter distances to conifers, and lower nest height. Li also found that excavators had a significantly higher success rate than secondary cavity nesters. Schmidt and Whelan (1998) found that both predation and competition influenced avian community patterns.

In the current study, we predicted that nest success would relate strongly to nest-site characteristics that are associated with nest predation, as in Christman and Dhont (1997), Yahner (1991), Finch (1989), and Martin (1998), parasite loads (Moller 1989), or disease and thermoregulation costs (Walsberg 1985). In addition, nest success could be influenced by the availability and abundance of some invertebrates or plant foods selected by adults during nesting (Winternitz 1980; Ehrlich et al. 1988; Martin 1987). Because of their association with specific host plants, some invertebrate species may have a patchy distribution associated with certain habitat conditions (Jones et al. 1985; Bernays and

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Chapman 1994; Jolivet 1998). The presence of abundant food near the nest could reduce foraging costs for parents feeding young by reducing travel costs (Dobkin et al.1995). Reducing travel associated with foraging away from the nest could increase energy and time available for egg incubation or predator and cowbird deterrence.

Study Area

The study area was located in the Routt and Medicine Bow National Forests on both sides of the Colorado-Wyoming border in the Southern Rocky Mountain (SRM) vegetation zone (2,300 to 2,700 m elevation) (Mueggler 1985). The average annual precipitation within the study area was 42.4 cm (Jones and Debyle 1985a). Aspen trees were typically over 50 years old and many were over 100 years old. Tree sizes were highly variable (d.b.h. = 2–215 cm with mean approximately 28 cm), depending on the clone, and were not closely related to age across clones. The topography included flat to mild slopes in the Medicine Bow National Forest to hillsides with up to 35% slope on the Routt National Forest. Disturbances to the area at the time of data collection included sheep herding during the nonbreeding season for birds and some small-scale historical tree harvesting. Around the turn of the century and through the late 1800s, the sites in the Medicine Bow National Forest were used as cattle runs (grazed during summer months).

Nine study plots were chosen in aspen stands about 40 ha in size. Six plots were located in the Battle Mountain area about 15 miles from the Sandstone work station in the Medicine Bow National Forest, and three plots were located in the California Park area of the Routt National Forest. Aspen comprised about 90% of all trees in these study plots with mixed understories of shrubs, grasses, and forbs. Aspen stands were mature to late seral with decay in more than 50% of the stems. Three aspen plots had grass-forb understories dominated by *Calamogrostis rubescens*, *Carex* spp., *Thalictrum fendleri*, *Lupinus argenteus*, and *Geranium* spp. Three aspen plots had small shrub understories dominated by *Symphoricarpos oreophilus* and a variety of forbs. Three aspen plots had tall shrub understories composed of *Amelanchier alnifolia, Prunus virginiana*, and *S. oreophilus*.

Methods

General Data Collection

Grids were used for vegetation sampling and locating bird nest sites. Study stands selected as examples of unfragmented aspen forests were: (1) large-sized (>40 ha) and mature, with forest openings of <2 acres; (2) accessible by 4-wheel drive vehicle, snowmobile, or motorbike; and (3) relatively level (slope <40%). Within each stand, 30 stations were established along E-W grid lines with 100 m between stations. Study plots were variable in length and width, depending on the shape and size of the stand, but all plots were approximately 36 ha (90 acres) in size with a buffer zone between plots of >450 m. Grids were laid out from a random start. Stations were located using a staff compass and measuring tape, and distances were measured along the ground surface. Each station was flagged and staked, and each stake was painted orange for visibility, numbered, and lettered with grid coordinates (e.g., A1, A2, B1, B2, etc.) Habitat structure was estimated at the 30 sampling stations on each plot. At each sampling station, a variety of habitat variables were measured following recommendations of Noon (1981) for tree habitats.

Habitat Features

Several spatial scales of vegetation measures were recorded, including stand, tree, and cavity characteristics. Nesting habitat features measured included: distance to water, distance to edge, nest plant height, snag decay, nest height, tree d.b.h. or shrub cd, cavity diameter, tree diameter at nest site, distance of nest from tree trunk, nest substrate, nest plant position within the forest, forest opening size, compass direction of nest within tree, nest plant species, and cavity location within tree. Vertical foliage density (Noon 1981) was measured in the shrub-sapling vegetation layer by counting hits of vegetation against a vertical rod marked off in increments of 0–0.3 m, 0.3–1 m, 1–2 m, 2–5 m, >5 m.

Avifauna

We designed our avian nest sampling methods to enable location of many small nongame species' nests in an unbiased way with respect to survival, and then to record nest survival. Observers visited each of the 30 stations within a plot each morning to collect bird count data for a related study (Finch and Reynolds 1987). Each afternoon during the nesting period (May–July), observers searched for nests of all small nongame bird species during 2-hour walks through the plot and sampling effort was carefully recorded. Adults observed carrying nesting material or food were followed to locate some nests. Others were located where adults had been flushed or began calling excitedly. Bird species, grid locations, nest sites, and behavior of all birds at nests were recorded. Nest observation sheets were used to record nest status over time. Nest trees were flagged so new observers could record nesting progress. Each station was visited five times per season, and the time interval between visits to each nest to check progress was usually 3 days but varied from 1 to 43 days. In addition, nest-site characteristics were recorded at the time of nest discovery.

Preliminary Analyses

Our main objective when conducting analyses was to identify relationships between nest success and habitat features for small nongame birds in aspen forests of the central Rocky Mountains. The first step in this process was to group avian species into clusters based on ecology and life history. These guilds were used to examine nest success-habitat relationships because they provided a way to examine whether patterns existed within and between groups of similar species and increased sample size.

We grouped all the species found in our study other than raptors and species with extremely small sample sizes (less than five nests found during the entire study) into nest guilds (open cup on ground, open cup in tree, primary cavity, and secondary cavity) and seven life-history guilds. To group birds into life-history guilds, we used a cluster analysis and principal components analysis (SYSTAT 9 1999) based on life-history traits recorded in the literature for the species found in this study. Grouping bird species into guilds increased the sample size for analysis and allowed us to make inferences concerning species with similar niches that may be affected in similar ways by conifer encroachment and anthropogenic habitat alterations.

Data Preparation

Nesting outcome was directly recorded for 126 nests out of 614 nests observed throughout this 3-year study. No outcome was recorded for 488 nests because no direct observations of success or failure were made. For example, the nest contents may have been empty yet no fledglings or signs of mortality were observed in the area. Therefore, we created a macro in Minitab that assigned nesting outcomes based on logic. The developmental stage of the offspring at the second-to-last visit was determined either from a direct record or from the adult behavior that was recorded. If a time interval elapsed that was shorter than the normal amount of time required for the young to fledge (Brown et al. 1992; Calder and Calder 1992; Dobbs et al. 1997; Ingold and Galati 1997; Power and Lombardo 1996; Robertson et al. 1992; Smith 1993) between visits and the observers noted an empty nest on the last visit, the nest was classified as a failure. We used a relatively conservative rule set which tended to assign a class of failure more often than would occur under other rule sets. This decision was based on knowledge suggested in the literature that a majority of nests of most birds fail (Murphy et al. 1997; Paton 1994; Yahner 1991; Martin 1998; Finch 1990). We chose to assume that the young were close to the beginning of each nesting stage (incubation or nestling) at the second-to-last observation. This assumption increased the amount of time required to reach fledging compared to the assumption that the young were at the center of each stage at the second-to-last observation. Therefore, nests were coded as failures more frequently using this logic. If adult behavior indicated the young reached at least the nestling stage, the nest was recorded as a success.

Logistic Regression

We used logistic regression (SYSTAT 9, Systat Inc. 1999) to elucidate relationships between nest success and habitat features for common species and guilds. Models predicting nest success from habitat features were fit and evaluated according to the advice of Hosmer and Lemeshow (1989). The overall significance of each model predicting nest success from habitat was evaluated using the G statistic. We interpreted each significant model predicting nest success from habitat features using odds ratios. The predictive ability of each model was evaluated using the total correct rate and success index values. We used Akaike's Information Criterion to compare the predictive ability of nest-site habitat features to that of stand-level habitat components.

Data Screening

Species, guilds, and variables with small sample sizes (less than 10 nests and less than 50% of the maximum possible sample size for the data set, respectively) were excluded from logistic regression analyses. In addition, after running the Minitab macro described above, we did not further analyze data for species with only one failure observed, only one success observed, no failures observed, or no successes observed.

Nest Site Analyses

Prior to evaluating nesting success and nest-site habitat relationships using logistic regression, we created a rank correlation matrix (SYSTAT 9, Systat Inc. 1999) to enable us to eliminate correlated variables that measured similar biological parameters. Each of the continuous habitat variables left in the set was evaluated for its potential contribution in explaining nest success patterns using univariate logistic regression analysis. Habitat variables with an insignificant relationship to nesting success were excluded from the complete model as recommended by Hosmer and Lemeshow (1989). The reduced set of habitat factors produced by these techniques was then used to create a logistic regression model of nest success patterns for common species and guilds (years pooled). The most parsimonious logistic regression models that still explained nest success patterns were chosen for each species or guild.

To further explore potential nest success and nest-site habitat relationships, we summarized the data using frequency tables and compared median values of continuous habitat variables between successful and failed nests to allow tentative conclusions regarding nest-site use by each common species or guild. To create frequency tables, we calculated the percent of nests that were successful for each species within each habitat feature used. We considered a nesting attempt within a habitat feature successful if the birds had at least one egg survive. These values were compared tentatively without using statistics such as chi-square analyses because many cells had low sample sizes (many were zero). We used the nonparametric Mann-Whitney U statistic (where overall comparisons were significant, $p < 0.05$, using the Kruskal-Wallis statistic) to compare median successful values to median failed values for the continuous nest-site habitat features.

Stand-Level Analyses

Stand-level vegetation data were collected using the same grid points to locate each sampling station as the grid points used to relocate a nest. Stand-level data collection sites were <100 m from each nest associated with that site. We calculated the mean value for continuous stand-level parameters measured within 100 m of each grid point and assigned these values to nest sites within 100 m of the same grid point. We analyzed stand data for three abundant species: American robins (*Turdus migratorius*), house wrens, and tree swallows (*Tachycineta bicolor*).

The logistic regression analysis described for nest-site habitat and success patterns was conducted once using only nest-site habitat parameters and once using only stand-level habitat parameters for each of the most abundant species. Since the only stand-level models that converged were insignificant, they could not be compared using Akaike's Information Criterion as planned.

Results

We found active nests of 28 small avian species (table 1) and assigned them to seven life-history guilds (table 2). Possible sources of mortality included predators, inclement weather, ectoparasites, nest parasites, and nest desertion due to disturbance and/or death of adults. Potential nest predators included northern flickers (*Colaptes auratus*), black-billed magpies (*Pica pica*), Clark's nutcrackers (*Nucifraga columbiana*), martens (*Martes americana*), striped skunks (*Mephitis mephitis*), red squirrels (*Tamiasciurus hudsonicus*), raccoons (*Procyon lotor hirtus*), and bull snakes (*Pituophis melanoleucus sayi*).

Bird nests were observed on all study sites. The most common nesting species in order of descending abundance were house wrens, American robins, tree swallows, warbling vireos (*Vireo gilvis*), western wood-pewees (*Contopus sordidulus*), northern flickers, red-naped sapsuckers (*Sphyrapicus nuchalis*), and dark-eyed juncos (*Junco hyemalis*). In a related study, none of these common species were more common in one aspen understory type than another except

Table 1—Bird species and number of observations of nests from 1987 to 1989 in aspen stands of the Routt and Medicine Bow National Forests of Wyoming and Colorado.

spp code	Common name	Scientific name	Number of observations
AMRO	American robin	*Turdus migratorius*	61
TRSW	Tree swallow	*Tachycineta bicolor*	54
WAVI	Warbling vireo	*Vireo gilvus*	44
WWPE	Western wood-pewee	*Contopus sordidulus*	25
NOFL	Northern flicker	*Colaptes auratus*	23
RNSA	Red-naped sapsucker	*Sphyrapicus nuchalis*	20
DEJU	Dark-eyed junco	*Junco hyemalis*	18
YRWA	Yellow-rumped warbler	*Dendroica coronata*	14
DOWO	Downy woodpecker	*Picoides pubescens*	13
MOBL	Mountain bluebird	*Sialia currucoides*	13
MOCH	Mountain chickadee	*Parus gambeli*	13
BCCH	Black-capped chickadee	*Parus atricapillus*	10
HAWO	Hairy woodpecker	*Picoides villosus*	9
HAFL	Hammond’s flycatcher	*Empidonax hammondii*	6
BTHU	Broad-tailed hummingbird	*Selasphorus platycercus*	5
LISP	Lincoln’s sparrow	*Melospiza lincolnii*	5
WETA	Western tanager	*Piranga ludoviciana*	4
WCSP	White-crowned sparrow	*Zonotrichia leucophrys*	4
DUFL	Dusky flycatcher	*Empidonax oberholseri*	3
VGSW	Violet-green swallow	*Tachycineta Thalassina*	3
YBSA	Yellow-bellied sapsucker	*Sphyrapicus varius*	3
CAFI	Cassin’s finch	*Carpodacis cassinii*	2
EVGR	Evening grosbeak	*Coccothraustes vespertinus*	2
MGWA	MacGillivray’s warbler	*Oporornis tolmiei*	2
WISA	Williamson’s sapsucker	*Sphyrapicus thyroideus*	2
HETH	Hermit thrush	*Catharus guttatus*	1
PISI	Pine siskin	*Carduelis pinus*	1

Table 2—Bird species and guild assignments used to analyze data on nest success from 1987 to 1989 in aspen stands of the Routte and Medicine Bow National Forests of Wyoming and Colorado.

Common name	Nest guild	Life-history guild
Western wood-pewee	Open cup in tree	1 = Intermediate migrants and residents
Yellow-rumped warbler	Open cup in tree	1
Hammond’s flycatcher	Open cup in tree	1
Western tanager	Open cup in tree	1
Cassin’s finch	Open cup in tree	1
Dusky flycatcher	Open cup in tree	1
Pine siskin	Open cup in tree	1
Warbling vireo	Open cup in tree	1
Dark-eyed junco	Open cup on ground	1
Lincoln’s sparrow	Open cup on ground	1
White-crowned sparrow	Open cup on ground	1
Hermit thrush	Open cup on ground	1
MacGillivray’s warbler	Open cup on ground	1
Downy woodpecker	Primary cavity	1
Yellow-bellied sapsucker	Primary cavity	2 = intermediate migrants and occasionals
Williamson’s sapsucker	Primary cavity	2
Red-naped sapsucker	Primary cavity	2
Tree swallow	Secondary cavity	2
Mountain bluebird	Secondary cavity	2
Violet-green swallow	Secondary cavity	2
Mountain chickadee	Secondary cavity	3 = small migrants and residents
House wren	Secondary cavity	3
Black-capped chickadee	Secondary cavity	3
Evening grosbeak	Open cup in tree	4 = large residents
Hairy woodpecker	Primary cavity	4
American robin	Open cup in tree	5 = large migrant
Broad-tailed hummingbird	Open cup in tree	6 = smallest migrant
Northern flicker	Primary cavity	7 = largest resident

the dark-eyed junco that was more common in small shrubs than tall shrubs (Finch and Reynolds 1987). All of these species only used aspen overstories for nesting except the American robin and dark-eyed junco that also used mixed aspen-conifer overstories and all overstories present in the forest (Struempf 2000).

Nest Site as Success Predictor

Most nests of the common species and life-history guilds were in forest interior locations (distance to edge >100 m) and oriented northeast of the aspen tree center (tables 3 and 5). This pattern in nest-site use was not positively correlated with nest success rates; birds using forest interior nest sites were not more successful than those nesting near edges (tables 3 and 5). However, comparisons of nest success rates are tentative because estimates with greater sample sizes have narrower confidence intervals. Northern flicker successful nests occurred in smaller diameter trees than did failed nests (table 4). In contrast, house wren successful nest sites were found near (26–100 m) small forest openings (£25 m radius), large forest openings (>200 m radius), or over 100 m away from an opening. Another deviation was found for tree swallow and red-naped sapsucker successful nests that were located near large openings or over 100 m away from an opening. Successful nests of most life-history guilds were placed in decayed or live trees that were not broken (table 5). However, the largest resident had success in broken trees that were decayed more than the nest sites of other birds.

Some patterns can be discerned in nest-site use as it relates to nest success in tree swallows (tables 3 and 4–6). Successful nests were usually located northwest of the nest tree center and all nest trees were aspen (table 3). Tree swallows placed most of their relatively successful nests in forest interior locations with dense trees near edges (£50 m) where forest openings were over 200 m in radius. Cavity diameter and nest tree height influenced tree swallow nest success (tables 4 and 6). More specifically, for every 1 cm increase in hole diameter, the nest was 0.12 times less likely to succeed. For every 1 m increase in nest plant height, the nest was 1.35 times more likely to succeed.

Nest success for small migrants and residents slightly decreased with an increase in distance to water and hole diameter while the pattern for snag decay was more complex (table 6). If distance to water increased by 1 m, the chance of success decreased by 0.99 times. If hole diameter increased by 1cm, the chance of success decreased by 0.55 times. Nests were 0.15 times less likely to succeed if they were in trees that were decayed and falling apart, or dead but not yet falling apart, than when they were in living trees. Nests were 0.01 times less likely to succeed if they were in living trees with dead wood at the cavity than nests in living trees with living wood at the cavity. Relatively successful nests were located in forest interiors over 100 m from an edge, northeast of the nest tree center (table 5). If these successful nests were in cavities, they were located in the central tree stem of an intact aspen tree (table 5).

Secondary cavity nest success decreased with increasing distance to water and hole diameter (table 6). Conversely, success increased near edges. If distance to water increased by 1 m, the chance of success decreased by 0.99 times. If hole diameter increased by 1 cm, the probability of nest success decreased by 0.50 times. A secondary cavity nest was 13.6 times more likely to succeed if it was in a location £100 m away from an edge than a nest further away.

A logistic regression model predicting nest success from nest-site habitat features was not calculated for some species because the data did not meet all

Table 3—Percent of nests successful for each nesting habitat feature used by each of the eight most common species in aspen of the Medicine Bow and Routt National Forests, 1987–1989.

Species	American robin	n	Dark-eyed junco	n	House wren	n	Northern flicker	n	Red-naped sapsucker	n	Tree swallow	n	Warbling vireo	n	Western wood-pewee	n
Nest plant position																
Isolated	unused	0	unused	0	100.00	1	unused	0	unused	0	0.00	1	unused	0	unused	0
Open	50.00	2	unused	0	100.00	4	unused	0	100.00	2	100.00	2	unused	0	0.00	1
Marginal	50.00	2	100.00	1	100.00	16	100.00	1	100.00	4	100.00	5	unused	0	0.00	1
Interior	41.03	39	75.00	8	0.82	142	41.67	12	76.92	13	64.71	17	58.82	17	20.00	5
Distance to edge																
>100 m away	26.92	26	0.00	1	82.65	98	57.14	7	87.50	8	20.00	5	60.00	10	77.78	9
£25m	33.33	3	100.00	2	100.00	9	unused	0	100.00	2	75.00	4	100.00	1	0.00	1
26£ x £50 m	100.00	1	unused	0	80.00	15	unused	0	77.78	9	100.00	3	unused	0	unused	0
51£ x £100 m	25.00	4	100.00	1	82.35	17	0.00	4	unused	0	0.00	1	50.00	2	0.00	1
Opening size																
£25m radius	unused	0	100.00	2	80.95	21	unused	0	0.00	2	50.00	4	unused	0	0.00	1
26£ x £100 m	50.00	2	unused	0	66.67	9	100.00	2	unused	0	unused	0	0.00	2	100.00	1
101£ x £200 m	100.00	1	unused	0	62.50	8	0.00	2	100.00	1	unused	0	100.00	1	unused	0
>200m radius	40.00	5	unused	0	100.00	16	33.33	3	100.00	9	83.33	6	0.00	1	unused	0
Opening >100 m away	23.08	26	75.00	4	84.71	85	25.00	4	85.71	7	25.00	4	66.67	9	75.00	8
Compass direction																
ne	33.33	18	87.50	8	83.00	100	33.33	9	80.00	15	57.14	14	83.33	6	0.00	1
nw	42.86	7	100.00	1	94.12	17	100.00	1	100.00	2	75.00	4	66.67	3	50.00	2
se	25.00	4	unused	0	100.00	13	unused	0	unused	0	100.00	4	50.00	4	0.00	1
sw	40.00	5	unused	0	94.12	17	50.00	2	100.00	2	100.00	3	33.33	3	0.00	3
Nest plant species																
AMAL	0.00	1	unused	0	unused	0	unused	0	unused	0	unused	0	unused	0	100.00	1
POTR	52.94	34	66.67	3	84.94	166	50.00	14	84.21	19	72.00	25	58.82	17	0.00	6

model assumptions. These unmet assumptions included noncolinearity among explanatory variables (despite the use of data screening techniques including correlation matrices), few missing values for explanatory variables, or some other unmet assumptions that prevented convergence. Only three of the models that converged were significant overall ($p < 0.05$) and had significant coefficients ($p < 0.05$).

Nest Site Versus Stand-Level Habitat

Only a tentative qualitative comparison is possible between stand-level and nest-site level habitat parameters as predictors of nest success. This is because most of the models predicting nest success from stand-level habitat features did not converge and others were not significant.

Discussion

Nest Site and Success Relationships

Forest interior

Most birds in this study used nest sites in forest interior locations despite no apparent positive correlation with nest success rates (tables 3 and 5). Similarly, Yahner (1991) found that bird nest success in aspen stands of Pennsylvania was independent of distance from edge. Tewksbury et al. (1998) discovered that avian nest predation rates in western Montana were higher in forested landscapes than in fragmented landscapes dominated by agriculture, while brood parasitism by brown-headed cowbirds decreased with increasing forest cover. In their

Table 4—Comparisons of median values for each continuous nest site parameter between successful (first line) and failed nests (second line) within each of the most common bird species in aspen stands of the Routt and Medicine Bow National Forests 1987-1989. Values of successful medians and failed medians for the same variable and species with the same letter following them are not significantly different (Mann-Whitney U, P-value <0.05).

Variable	AMRO median	SD	n	DEJU median	SD	n	HOWR median	SD	n	NOFL median	SD	n	RNSA median	SD	n	TRSW median	SD	n	WAVI median	SD	n	WWPE median	SD	n
Nest plant height (m)	20.0A	11.9	18	0.0A	18.2	12	13.0A	6.7	141	10.0A	6.6	9	16.0A	4.8	15	14.8A	4.3	18	2.0A	7.9	10	3.5A	*	1
	17.0A	10.3	25	0.0A	*	1	11.0A	10.0	24	10.0A	7.1	7	18.0A	6.4	3	9.0B	6.4	7	9.0A	5.2	7	20.5A	10.2	6
Distance from trunk (cm)	0.0A	22.8	19	0.0A	6.2	8	0.0A	12.5	128	0.0A	0.0	9	0.0A	0.0	15	0.0A	10.0	16	65.0A	90.8	10	150.0A	*	1
	0.0A	26.0	25	0.0A	*	1	0.0A	0.0	21	0.0A	0.0	7	0.0A	0.0	3	0.0A	0.0	4	25.0A	39.9	5	0.0A	10.5	6
Nest height (m)	4.0A	7.5	19	0.0A	0.0	17	3.8A	4.3	140	6.5A	2.8	9	5.0A	3.1	15	6.8A	2.5	18	3.8A	6.5	10	2.5A	*	1
	2.0A	4.6	25	0.0A	0.0	2	3.0A	2.3	25	8.5A	3.8	7	31.0A	5.9	3	7.0A	2.1	7	5.5A	4.8	7	8.5A	3.3	6
Tree d.b.h. or shrub cd (cm)	29.5A	11.4	19	0.0A	61.5	9	26.0A	9.5	140	25.2A	10.3	9	30.0A	6.9	16	29.5A	22.6	18	7.0A	11.3	10	3.0A	*	1
	30.0A	34.1	25	3.0A	*	1	26.0A	5.3	25	29.3B	9.0	7	4.5A	3.3	3	30.5A	7.7	7	12.3A	3.8	6	24.0A	10.8	6
Hole diameter (cm)	n/a	n/a	n/a	n/a	n/a	n/a	4.0A	1.8	136	6.0A	1.7	9	4.3A	4.7	16	4.0A	0.9	18	n/a	n/a	n/a	n/a	n/a	n/a
	n/a	n/a	n/a	n/a	n/a	n/a	4.0A	2.2	21	6.0A	0.45	5	4.5A	1.9	3	6.0B	1.0	7	n/a	n/a	n/a	n/a	n/a	n/a
Site diameter (cm)	43.0A	619	3	n/a	n/a	n/a	23.0A	14.3	112	13.8A	6.2	4	25.0A	3.9	16	25.0A	28.6	9	n/a	n/a	n/a	n/a	n/a	n/a
	30.0A	*	1	n/a	n/a	n/a	23.0A	5.0	21	27.0B	6.7	7	27.0A	5.0	3	21.4A	8.0	6	n/a	n/a	n/a	n/a	n/a	n/a

Table 5—Percent of nests successful for each nesting habitat feature used by each of the life-history guilds in aspen of the Medicine Bow and Routt National Forests, 1987-1989.

Guild	Intermediate migrants and residents	n	Intermediate migrants and occasionals	n	Small migrants and residents	n	Large residents	n	Large migrant	n	Smallest migrant	n	Largest resident	n
Nest plant position														
Isolated	unused	0	66.67	3	100.00	1	unused	0	unused	0	unused	0	unused	0
Open	0.00	1	100.00	4	100.00	4	unused	0	50.00	2	unused	0	unused	0
Marginal	66.67	3	84.62	13	100.00	16	100.00	1	50.00	2	100.00	1	100.00	1
Interior	55.00	60	64.58	48	80.92	152	88.89	10	41.03	39	75.00	4	41.67	12
Distance to edge														
£25 m	80.00	5	66.67	9	100.00	9	100.00	1	33.33	3	unused	0	unused	0
26£ x £50 m	100.00	1	84.62	13	80.00	15	unused	0	100.00	1	unused	0	unused	0
51£ x £100 m	42.86	7	60.00	5	82.35	17	100.00	1	25.00	4	unused	0	0.00	4
> 100m	58.33	24	55.56	27	80.37	107	100.00	7	26.92	26	100.00	2	57.14	7
Opening size														
Opening >100 m away	42.86	35	59.26	27	81.91	94	100.00	8	23.08	26	100.00	2	25.00	4
£25 m radius	75.00	4	37.50	8	80.95	21	100.00	1	unused	0	unused	0	unused	0
26£ x £100 m	50.00	4	0.00	1	66.67	9	unused	0	50.00	2	unused	0	100.00	2
101£ x £200 m	unused	0	100.00	1	62.50	8	unused	0	100.00	1	unused	0	0.00	2
>200 m radius	100.00	3	88.24	17	100.00	16	unused	0	40.00	5	unused	0	33.33	1
Compass direction														
ne	70.00	30	60.47	43	80.73	109	87.50	8	33.33	18	0.00	1	33.33	9
nw	61.54	13	87.50	8	94.12	17	100.00	1	42.86	7	unused	0	100.00	1
se	57.14	7	85.71	7	100.00	13	100.00	2	25.00	4	100.00	1	unused	0
sw	22.22	9	90.91	11	94.12	17	unused	0	60.00	5	100.00	1	50.00	2
Cavity location														
Trunk	28.57	7	64.81	54	84.13	126	100.00	8	100.00	2	unused	0	36.36	11
Branch	unused	0	unused	0	66.67	9	unused	0	unused	0	unused	0	unused	0
Other	0.00	1	100.00	1	100.00	3	unused	0	0.00	1	unused	0	unused	0
Nest plant species														
ABLA	unused	0	unused	0	unused	0	unused	0	0.00	8	unused	0	unused	0
AMAL	100.00	3	unused	0	unused	0	unused	0	0.00	1	unused	0	unused	0
POTR	48.08	52	71.01	69	83.52	176	90.91	11	52.94	34	80.00	5	50.00	14
SYOR	75.00	4	unused	0	unused	0	unused	0	unused	0	unused	0	unused	0
Tree type														
Intact	12.50	8	77.50	40	83.33	96	100.00	8	66.67	3	100.00	5	33.33	3
Broken	100.00	1	16.67	12	81.25	48	unused	0	unused	0	unused	0	37.50	8
Snag decay														
Decayed snag	100.00	1	37.50	8	85.71	28	unused	0	100.00	1	unused	0	50.00	4
Dead tree and dead at cavity	40.00	10	64.00	25	81.03	58	100.00	4	100.00	1	unused	0	37.50	8
Live tree and dead at cavity	0.00	2	100.00	2	63.64	22	unused	0	75.00	4	unused	0	unused	0
Live tree and live at cavity	80.00	10	82.35	34	93.33	60	83.33	6	80.00	5	66.67	3	100.00	2

Table 6—Logistic regression models for predicting nest success from habitat variables collected at bird nests in the Medicine Bow and Routt National Forests, 1987–1989.

Logistic regression model variables	G[a](p–value)	Total correct rate[b]	Success index[c]
Tree swallow 8.15constant – 2.13hole diameter + 0.30nest plant height	13.85(0.0010)	0.7929	0.1362
Small migrants and residents 9.61constant – 1.84snag_ DC – 1.90snag_ DD – 4.23snag_ LD – 0.01distance to water – 0.61hole diameter	28.75(0.00001)	0.8830	0.0531
Secondary cavity nesters 7.43constant – 0.007distance to water – 0.69hole diameter + 2.61distance to edge	21.12(0.0001)	0.8325	0.0367

[a] Tests the null hypothesis that all the coefficients associated with the predictors equal zero versus these coefficients not all being zero (SYSTAT9 1999).

[b] The ratio of the sum of correctly predicted observations divided by the total number of observations (SYSTAT9 1999).

[c] The gain that this model shows over a purely random model that assigned the same probability of success to every observation in the data (SYSTAT9 1999).

study, forest cover was not the best predictor of cowbird parasitism; the abundance of human development on the landscape and the density of cowbird host species were the best predictors of parasitism. Cowbirds were present in the current study but sample sizes were too low to analyze. In contrast, Donovan et al. (1997) found that landscape fragmentation patterns interacted with edge effects to create nest predation and cowbird parasitism patterns.

Orientation within a tree

Most bird nests in this study were oriented northeast of the center of the nest tree or shrub (tables 3 and 5). Finch (1985) also found that Abert's towhees (*Pipilo aberti*) in Colorado oriented their nests in different directions, depending on whether it was early or late in the nesting season. In the current study, the dominant slope direction in the study area could have been such that a northeast nest plant location decreased thermoregulatory costs or allowed early detection and repulsion of nest predators.

Nest plant species

The use of aspen as the nest plant (tables 3 and 5) was probably in proportion to availability and related to susceptibility to heart rot and thus ease of cavity excavation for the cavity nesters as in Daily (1993). Another possible reason for a bird to use aspen as its nest plant is the abundance and diversity of associated plants it could use as cover from weather and predators.

Snag decay

Most successful nests were located in intact and living trees in this study (tables 3 and 5). This could be due to an increase in cover from weather and predators over that surrounding broken snags. It could also be due to a greater diversity and abundance of insect or plant food sources over that found near broken snags. However, this result should be interpreted with caution because over 50% of aspen stems (including living stems) in the study area were infested with heart rot that probably increased ease of cavity excavation as in Winternitz (1980). In contrast to the overall nest-site use pattern, northern flicker successful nests were on broken snags (table 5). Similarly, Daily (1993) found a correlation between the placement of red-naped sapsucker nests and the spread of heart rot through a tree.

Tree diameter at cavity

Northern flicker successful nest trees were smaller in diameter than those of failed nests in aspen-dominated stands (tables 4 and 6). This is contrary to the results of Loose and Anderson (1995) who found that woodpeckers nested in aspen trees of south-central Wyoming with an average d.b.h. of 26.7 cm, and this diameter was larger than the mean d.b.h. of available aspen (11.8 cm or snags, 9.0 cm). Dobkin et al. (1995) found that living trees and snags with d.b.h. >4 cm were favored as nest sites by all bird species in aspen of southeastern Oregon. In the current study, perhaps trees with a larger diameter were more likely to have been excavated in previous years and thus provided search cues to predators that could remember nest locations from year to year as in Sonerud (1985, 1989).

Cavity diameter

Secondary cavity nesting birds' nest success decreased as hole diameter increased (table 6). These results correspond with the conclusion by Roberston and Rendell (1990) that greater cavity entrance area (mean = 32.4 +/– 0.3) at natural cavities (than in nest boxes) resulted in increased interspecific competition for tree swallow nest sites in Ontario. Nest sites with smaller entrance diameters probably gave birds an advantage by reducing the risk of nest depredation.

Proximity to standing water

Distance to water influenced nest success of small migrants and residents and secondary cavity nesters. Nest success decreased as distance to water increased (tables 5 and 6). It makes sense that birds at an intermediate distance from water would have the greatest nest success relative to birds over 300 m from water because predation (Wilcove 1985; Donovan et al. 1997) may be greater closer to water (an edge), yet the presence of water may increase forage availability (insect abundance).

Another possible explanation for increased success near water could be increased food availability. Insects are commonly more abundant (Schimpf and MacMahon 1970) and aspen usually have a faster growth rate closer to water within suitable habitats. Loose and Anderson (1995) observed that woodpeckers in Wyoming used larger than average trees for foraging. They concluded this foraging pattern could be due to an increase in foraging efficiency as larger trees and snags contain higher concentrations of insects.

Nest plant height

Tree swallow nest success increased with nest plant height (table 6). Similarly, Li (1989) found that failed nests of cavity-nesting birds on the Mogollon Rim in Arizona were closer to the ground than successful nests. Conversely, Yahner (1991) found an overall inverse relationship between nest height and nest success in aspen forest of central Pennsylvania. These differences may be explained by differences in the most common predator search strategies. Avian predators may be more likely to find taller nests while terrestrial mammalian predators may be more likely to find shorter nests.

Nest Site Versus Stand-Level Habitat

Nest success may be more strongly correlated with nest-site characteristics than it is with stand characteristics since none of the stand-level logistic regression models that converged were significant and contained more than one explanatory variable (table 6). Similarly, Martin (1998) found that microhabitat parameters of nesting birds in aspen forests of Arizona are under selection and adaptive. However, other studies such as Tewksbury (1998) and Donovan (1997) have found large-scale habitat features good predictors of forest bird nesting success.

Importance of Aspen Nesting Habitat

When the results of the current study are considered along with those of a related study (Struempf 2000), one can see that the value of aspen forests as a major landscape component should not be underestimated. We reached this conclusion because Struempf (2000) found that most birds and guilds had lower mortality rates in aspen forests than they had in nearby mixed or conifer forests. Therefore, a decline in aspen on the landscape could lead to significant declines in nest success for birds that experienced greater nest success in aspen than they did in mixed or conifer forests. The next logical step toward elucidating relationships between habitat and avian survival rates in aspen forests and wintering grounds would be to investigate overall population trends for residents and migrants and create models to determine the most important life-history transition to population persistence.

Management Implications

Avian habitat and nest success relationships in aspen forests of the Western United States are still poorly understood. Therefore, an adaptive management approach to maintain nesting bird diversity in aspen forests would probably be best until more is known. In all of the significant logistic regression models for cavity nesters, smaller hole diameters experienced greater nest success. This suggests that management actions should provide and maintain suitable habitat for a variety of primary cavity excavators who build several sizes of nest holes to allow the secondary cavity nesters to thrive. We hypothesize that birds more susceptible to predation (primary cavity nesters in Struempf 2000 and Martin 1993) should exhibit greater nesting survival rates as the area of contiguous habitat increases than birds less susceptible to predation (ground nesters in Struempf 2000 and Martin 1993). Furthermore, a greater diversity of primary cavity excavators should exhibit increased nest success in forested landscapes with more variation in aspen seral stage, stem size, clone age, and degree of heart rot infestation than more homogenous landscapes.

A few studies investigating disturbance and area effects on bird assemblages in western conifer and aspen forests have produced preliminary results that need further investigation (Johns 1993; Scott et al. 1982; and Scott and Crouch 1988). Scott et al. (1982) and Scott and Crouch (1988) found that clearcuts in subalpine forests of Colorado had little to no effect on breeding bird densities. Johns (1993) found that avian species richness in aspen parklands of Saskatchewan was positively correlated with aspen grove area, and densities of some species were positively or negatively correlated with aspen grove isolation. However, further investigation is required because presence and density data do not adequately indicate the quality of a habitat. Survival data are needed because birds may be forced to use substandard habitat at high densities due to low availability of quality habitat.

Possible treatments that could be used in adaptive management experiments include carefully planned cutting and controlled burns, and monitoring of natural disturbances such as fungal infestations, fires, and avalanches. These treatments should benefit most birds by maintaining aspen on the landscape and increasing overstory complexity and understory diversity (Bartos et al. 1991; Shepperd and Smith 1993; Turchi et al.1995). Further support for this conclusion was found in a related study (Struempf 2000) where most birds had greater nest success in aspen forests than they experienced in adjacent mixed or conifer forests. Pilot studies using these treatments should be conducted and the effects of habitat manipulations on nesting success and adult survival closely monitored.

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Model-Based Assessment of Aspen Responses to Elk Herbivory in Rocky Mountain National Park[1]

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Abstract—*In Rocky Mountain National Park, aspen has been observed to decline on elk winter range for many decades. The SAVANNA ecosystem model was adapted to explore interactions between elk herbivory and aspen dynamics on the elk winter range. Several scenarios were explored that considered different levels of overall elk population; different levels of elk utilization of aspen, reflected by the length of time during which elk utilized the aspen stand; and different fencing treatments where fences were removed following a specified, variable number of years.*

Simulated aspen regeneration success was much greater when elk use was less prolonged over the course of the year. Under the Heavy Use scenario (8 months of elk use), there was a threshold between four and five elk per km^2 *where regeneration success became dramatically less. Under the Light Use scenario (3 months of elk use), aspen regeneration success was high at elk densities up to 10 elk per km*^{2}*, moderate at 11 elk per km*^{2}*, and nil at 12 elk per km*^{2}*. Aspen regeneration success was significantly improved by fencing aspen stands, even without stimulating additional aspen suckering through burning or mechanical disturbance. At the landscape level, the Heavy Use scenario yielded the interesting result that aspen regeneration success, represented in terms of proportion of aspen stands on the winter range to re-establish successfully over a 60-year period, was little affected by elk population level. This was because elk distribution was highly aggregated.*

The results of this modeling exercise suggest that managing the overall elk population level may not be as effective for stimulating successful aspen establishment as managing local elk distributions and access to aspen stands. However, aspen may be serving as an indicator species for a system that is outside its range of historic variability due to anomalously high elk numbers. It is recommended that Rocky Mountain National Park take action to control the overall elk herd size, while simultaneously conducting intensive, site-level management activities to propagate aspen within the heavily utilized portion of the winter range.

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Do Pine Trees in Aspen Stands Increase Bird Diversity?

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***Abstract**—In the Black Hills of South Dakota, quaking aspen (*Populus tremuloides*) is being replaced by conifers through fire suppression and successional processes. Although the Black Hills National Forest is removing conifers (primarily ponderosa pine [*Pinus ponderosa*]) to increase the aspen communities in some mixed stands, Forest Plan guidelines allow four conifers per hectare to remain to increase diversity in the remaining aspen stand. We compared bird species richness in pure ponderosa pine, mixed stands dominated by ponderosa pine with quaking aspen, mixed stands dominated by aspen with ponderosa pine, and pure aspen stands. Stands dominated by ponderosa pine had lower ($P < 0.01$) bird species richness than stands dominated by aspen. Aspen in ponderosa pine stands or pine in aspen stands did not increase bird species richness ($P \geq 0.68$) over the respective pure stands. Thus, leaving ponderosa pine in aspen stands will not have the desired effect of increasing bird diversity but may have the negative effect of speeding successional processes that replace aspen with conifers.*

Introduction

Quaking aspen (*Populus tremuloides*) is an important vegetation community for wildlife in the West (Buttery and Gillam 1983). The importance of this vegetation community is demonstrated by the numerous symposia and publications addressing its importance to wildlife, livestock, and recreation. In the Black Hills, aspen frequently occurs with paper birch (*Betula papyrifera,* Hoffman and Alexander 1987). Aspen comprised about 5% of the Black Hills landscape about 25 years ago (Severson and Thilenius 1976). Currently, aspen comprises 4% of the Black Hills National Forest and is being replaced by ponderosa pine (*Pinus ponderosa*) through successional processes (Revised Land and Resource Management Plan, Black Hills National Forest, Custer, SD, 1996).

Many aspen stands are old or have been invaded by conifers (Revised Land and Resource Management Plan, Black Hills National Forest, Custer, SD, 1996). To reverse this trend, the current management direction is to increase the extent of aspen and birch communities by 10% during the 10-year period applicable to the Revised Land and Resource Management Plan. Aspen in the Black Hills regenerates mostly by vegetative regeneration (Schier et al. 1985). Yet to preserve diversity, stands treated to convert mixed conifer/aspen to aspen may include up to four conifer trees per hectare (10 per acre; Revised Land and Resource Management Plan, Black Hills National Forest, Custer, SD, 1996).

Aspen stands provide habitat to some species that would not occur without it (Finch and Reynolds 1987; Mills et al. 2000; Scott and Crouch 1988). Presumably, stands of mixed conifer with aspen support the greatest diversity of wildlife (DeByle 1985b). We tested the hypothesis that including conifers in aspen stands increases bird species diversity (e.g., species richness) in the Black Hills.

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Study Area and Methods

The Black Hills encompasses approximately 15,540 km^2 in west-central South Dakota and east-central Wyoming. Elevation ranges from 1,450 to 1,770 m. The climate is continental with cold winters and warm summers; temperatures range from –11to 2 °C in winter and 15 to 29 °C in summer (Orr 1959) and annual precipitation averages approximately 50 cm (South Dakota Climatological Summary, U.S. Department of Commerce, Asheville, NC).

The Black Hills National Forest is primarily a conifer forest, with approximately 84% of the forest in ponderosa pine (Hoffman and Alexander 1987). The Forest is managed in 4 to 32 ha land units (hereafter referred to as stands) in which the vegetation is relatively homogeneous. The vegetation in stands is described using the dominant vegetation type; for units forested, descriptions include average diameter at breast height (d.b.h.) categories and overstory canopy cover categories. These vegetation structural stages are described by Buttery and Gillam (1983). We used the same criteria, as did the Black Hills National Forest, for describing vegetation in stands.

The data for bird species richness come from two studies of breeding nongame birds in the Black Hills (Mills et al. 2000; Dykstra et al. 1999). Both studies used variable radius plots for counting birds (Reynolds et al. 1980). Mills et al. counted birds during 1992 and 1993 in 48 stands of ponderosa pine and 28 stands of aspen. Ponderosa pine stands included seven vegetation structural stages ranging from sapling/pole to old growth, and included all d.b.h. categories. Aspen stands included four vegetation structural stages, the shrub/seedling stage, and all overstory canopy cover (OCC) categories of sapling/poles. These stands were selected from the forest inventory database and represent the range of vegetation structural stages in ponderosa pine and aspen in the Black Hills. Mills et al. (2000) counted birds at each of three sites on 2 consecutive days, twice each year.

Dykstra et al. (1999) counted birds in 40 ponderosa pine stands in 1993 and 1994. These stands included 20 sapling/pole to mature stands of ponderosa pine with 40 to 70% OCC and 20 mature to old growth pine stands with >70% OCC. These stands were representative of the managed and unmanaged ponderosa pine forest in the Black Hills. Birds were counted at two to five sites in two sample sessions in 1993 and three sample sessions in 1994.

Bird species richness represents the number of species of passerines and woodpeckers (*Picidae)* observed ≤50 m of the count point (Hutto et al. 1986) in each stand. Birds flying overhead or birds that flew by and did not land were excluded from tallies of species richness. In the Black Hills, species accumulation curves reached an asymptote for species richness in stands at between two and three bird count sites per stand (Rumble et al., in press).

We measured the vegetation at each of the bird count sites once during each study to characterize the habitat. Mills et al. measured vegetation in five 0.04 ha circular plots—one at the bird count point and four others in the cardinal directions 30 m away. In some aspen stands that occurred in drainages, only three plots could be measured within the drainage. Dykstra et al. (1999) measured vegetation in five variable-radius (using a 20 basal area factor prism [BAF]) over 0.04 ha circular plots at each site—one at the bird count point and four in the cardinal directions 40 m away. Trees ≥15 cm d.b.h. were measured in the variable radius plots and trees <15 cm d.b.h. were measured in the 0.04 ha circular plots. Estimates of tree basal area were averaged among plots at sites and then sites in stands.

We plotted the frequency of stands in incremental basal area (BA) categories of ponderosa pine and aspen/birch. Based on the frequency plots, we evaluated four treatments that described the tree composition of stands: pure ponderosa pine stands (≤0.02 m^2/ha of aspen, $n = 72$), ponderosa pine stands with aspen (>0.02 m^2/ha aspen/birch, $n = 16$), pure aspen stands (≤0.1 m^2/ha ponderosa pine, $n = 12$), and aspen stands with ponderosa pine (>0.1 m^2/ha pine, $n = 16$). Most of the pure ponderosa pine stands had no aspen and most pure aspen stands had no ponderosa pine. When we evaluated the bird species richness for homogeneity of variances among these treatments using Levene's test, we found that variances did not differ ($P = 0.48$). We compared species richness among treatments using one way analysis of variance followed by Tukey's multiple range test. Because stands with more bird count sites could have more species (Hutto et al. 1986), we repeated these tests using species richness per count site. These variances also were homogeneous ($P = 0.31$). We selected $\alpha \leq 0.10$ as significant for all tests.

Results

Overstory canopy cover in these stands was similar among all stands except the pure aspen, in which it was lower ($P \leq 0.01$; table 1). Basal area of ponderosa pine differed among all treatments ($P < 0.01$). The increased ponderosa pine basal area in stands of pine with aspen reflected the increased aspen component in unmanaged pine stands in the northern portions of the Black Hills. Aspen basal area increased ($P < 0.01$) consistently among treatments from pine to aspen. Percent canopy cover of grasses and forbs also generally increased among treatments from pure ponderosa pine to pure aspen. Shrub cover varied little among treatments with one exception: percent shrub cover was higher in the pine with aspen treatment ($P < 0.02$) than the pure pine or aspen with pine treatments. Abundance of snags did not differ among treatments ($P \geq 0.24$).

Bird species richness was lowest in ponderosa pine stands (table 2). Ponderosa pine stands with aspen did not have more ($P \leq 0.10$) bird species than pure pine stands. Stands of pure aspen and aspen with ponderosa pine had more ($P \leq 0.10$) bird species than either pure ponderosa pine or ponderosa pine with aspen. Among stands dominated by aspen, those with ponderosa pine in them did not have greater bird species richness ($P \leq 0.10$). Bird species richness showed negative correlations to overstory cover (Adj. $R^2 = 0.14, P < 0.01$) and ponderosa pine basal area (Adj. $R^2 = 0.21, P < 0.01$). Bird species richness was positively correlated with aspen basal area (Adj. $R^2 = 0.10$, $P < 0.01$),

Table 1—Vegetation measurements from stands of pure ponderosa pine, ponderosa pine with aspen, aspen with ponderosa pine, and pure aspen in the Black Hills, South Dakota.[a]

Variable	Ponderosa pine (n = 72)		Pine with aspen (n = 16)		Aspen with pine (n = 16)		Aspen (n = 12)	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
Overstory cover	53.4	2.4A	58.7	3.6A	53.7	4.7A	21.0	5.2B
Ponderosa pine basal area	15.3	1.1A	22.3	1.8B	2.4	0.6C	0.1	<0.1D
Aspen basal area	<.1	<.1A	0.4	0.2B	6.7	0.9C	2.3	1.1D
Percent cover grasses	10.3	1.0A	8.1	1.2A	28.8	3.8B	30.2	2.7B
Percent cover forbs	8.9	0.7A	18.1	2.3B	27.6	2.6C	32.1	2.6C
Percent cover shrubs	20.5	1.2AC	31.0	2.0B	23.5	1.9AC	24.1	2.0AB
Number of snags/ha	11.2	1.1	6.8	1.0	9.1	1.8	7.6	4.2

[a] Averages (± SE) followed by different letters are significantly different ($\alpha \leq 0.10$, MRPP test.

Table 2—Average species richness and species richness per bird count site in stands of pure ponderosa pine, ponderosa pine with aspen, aspen with ponderosa pine, and pure aspen in the Black Hills, South Dakota.[a]

Stand type	*n*	Species richness	± SE	Species richness/site	± SE
Pure ponderosa pine	72	14.6	0.4A	5.2	0.1A
Ponderosa pine with aspen	16	15.5	0.7A	4.4	0.2A
Aspen with ponderosa pine	16	18.9	0.7B	6.3	0.2B
Pure aspen	12	18.3	0.7B	6.1	0.2B

[a] Averages ± SE followed by the same letter do not differ ($\alpha \leq 0.10$, Tukey's multiple range test).

percent cover of grasses (Adj. $R^2 = 0.16, P < 0.01$), and percent cover of forbs (Adj. $R^2 = 0.20, P < 0.01$).

The same patterns of bird species richness were evident when data were evaluated using species richness per bird count site. Stands of ponderosa pine and ponderosa pine with aspen had similar but fewer ($P \leq 0.10$) bird species per count site than stands of pure aspen or aspen with ponderosa pine.

Despite the habitat affinities of species, very few birds were restricted to a particular vegetation community in our study and most bird species were observed a few times in habitats considered unsuitable (table 3). Nonetheless, some species demonstrated affinities for pure aspen stands: Swainson's thrush (*Cartharus ustulatus*), common yellowthroat (*Geothlypis trichas*), and mountain bluebird (*Sialia currucoides*). Others occurred mostly in pure aspen or aspen with ponderosa pine: northern flicker (*Colaptes auratus*), flycatchers (*Empidonax* spp.), MacGillvray's warbler (*Oporornis tolmiei*), ovenbird (*Seiurus aurocapillus*), red-napped sapsucker (*Sphrapicus nuchalis*), chipping sparrow (*Spizella passerina*), American robin (*Turdus migratorius*), and warbling vireo (*Vireo gilvus*).

Discussion

Aspen communities are important habitats for wildlife in the Rocky Mountains (DeByle 1985b). Young birds require protein from invertebrates for proper growth and development (Johnson and Boyce 1990). Invertebrate abundance in both the aspen canopy and aspen understory are greater than invertebrate abundance in conifers (Schimpf and MacMahon 1985; Rumble and Anderson 1996). Thus, the positive correlation between cover of grasses and forbs and species richness likely reflects the increased food resources for birds.

Several bird species would be absent or occur in low abundance without aspen in the Rocky Mountains (Finch and Reynolds 1987; Scott and Crouch 1988). Mills et al. (2000) reported that red-naped sapsuckers, dusky flycatchers, warbling vireo, MacGillvray's warblers, and ovenbirds would likely be absent from the central Black Hills without aspen. In addition to these, our study also suggests that common yellowthroats, mountain bluebirds, other flycatchers, chipping sparrows, and American robins preferred habitats dominated by aspen within the forested landscapes of the Black Hills.

The origin of the idea for including conifers in aspen stands to increase diversity and niches for wildlife (e.g., DeByle 1985b) is unknown. In Canada, bird species richness and the abundance of some birds was greater in "old" aspen stands that also had conifers (Schieck and Nietfeld 1995). However, age of aspen was confounded by presence of conifers in the aspen in their study design in that stands of large old aspen trees also had conifers. The increased species richness

Table 3—Percent of bird counts that bird species occurred in that were conducted in ponderosa pine, ponderosa pine with aspen, aspen with ponderosa pine, and pure aspen in the Black Hills, South Dakota.

Species[a]	**Ponderosa pine**	**Pine with aspen**	**Aspen with pine**	**Aspen**
Ammodramus savannarum	<1	0	0	0
Carduelis pinus	11	23	4	5
Carduelis tristis	<1	3	0	0
Cartharus ustulatus	<1	4	3	17
Certhia americana	2	3	0	0
Chordeiles minor	<1	0	0	0
Colaptes auratus	4	5	14	14
Contopus sordidulus	3	0	<1	3
Dendroica coronata	68	68	51	30
Dendroica petechia	<1	0	0	0
Empidonax difficilis	<1	2	1	4
Empidonax minimus	0	0	4	3
Empidonax oberholseri	<1	2	52	57
Empidonax trailii	0	0	1	0
Empidonax spp[a]	0	<1	17	19
Euphagus cyanocephalus	<1	1	0	0
Geothlypis trichas	<1	0	4	18
Icteria virens	<1	0	0	0
Junco hyemalis	63	60	81	88
Loxia curvirostra	55	42	52	61
Molothrus ater	11	13	13	20
Myadestes townsendii	34	17	11	14
Oporornis tolmiei	<1	<1	10	17
Passerina amoena	0	0	3	0
Perisoreus canadensis	14	12	1	0
Pheucticus melanocephalus	<1	1	0	1
Picoides arcticus	2	0	<1	0
Picoides pubescens	5	1	9	3
Picoides villosus	19	15	27	15
Pipilo erythrophthalmus	<1	0	0	0
Piranga ludoviciana	26	20	19	9
Poecile atricapillus	47	37	64	53
Pooecetes gramineus	<1	0	1	1
Regulus calendula	1	1	13	2
Regulus satrapa	0	0	2	1
Seiurus aurocapillus	17	22	54	28
Setophaga ruticilla	0	0	2	0
Sialia currucoides	5	1	6	20
Sialia sialis	<1	0	0	0
Sitta canadensis	57	57	49	28
Sitta carolinensis	21	7	23	6
Sphyrapicus nuchalis	3	1	29	22
Sphyrapicus varius	1	7	0	1
Spizella passerina	24	17	38	41
Spizella pusilla	<1	0	0	0
Troglodytes aedon	0	0	2	1
Turdus migratorius	20	17	50	35
Tyrannus tyrannus	<1	0	0	0
Vireo gilvus	10	21	84	88
Vireo olivaceus	<1	0	0	1
Vireo solitarius	7	1	3	5
Zenaida macroura	2	0	2	1
Zonotrichia leucophrys	0	0	<1	0

[a] Several *Empidonax* flycatchers were not identified to species during the counts.

in aspen/conifer stands in Canada resulted from adding species common in conifer habitats to those common in the aspen. Increasing within-stand diversity (alpha diversity) by adding conifer species to aspen habitats in a landscape dominated by conifers does not contribute to diversity at scales for which diversity should be managed (Knopf and Samson 1994). We did not observe an increase in alpha diversity when ponderosa pine occurred in aspen stands. Finch and Reynolds (1987) also did not observe increased bird species richness in stands of mixed aspen/conifer compared to spruce-fir stands in Colorado.

The decline of aspen in the Black Hills can be attributed to the control of fires since European settlement. Fire was once common in the Black Hills landscape (Brown and Sieg 1996). Historically, occasional intense fires would regenerate aspen stands through sprouting (Jones and DeByle 1985). Aspen in the Black Hills is currently regenerated by clearcutting. But grazing by livestock and wild ungulates reduces the number of sprouts (DeByle 1985a; Rumble et al. 1996), allowing conifer regeneration to increase growth (Shepperd and Jones 1985). Ponderosa pine within aspen sites indicates that aspen is seral on these sites (Mueggler 1985). Seeds of ponderosa pine typically disperse within 40 m of trees (Fowells 1965).

Conclusions

Leaving ponderosa pine in stands treated to increase aspen does not increase bird species diversity. It may, in fact, speed the seral processes of converting the site to conifers. In some areas, succession of aspen to conifers occurs within a single generation of the aspen (Mueggler 1985). If successional processes lead to dominance of ponderosa pine in aspen, then bird diversity, as measured by bird species richness, will decline to that typical of the surrounding ponderosa pine forest. Managers will need to suppress conifer succession in aspen to maintain high bird species diversity.

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Aspen Fencing in Northern Arizona: A 15-Year Perspective

James M. Rolf[1]

Abstract—*Aspen clearcuts in the 1960s and 1970s on the Peaks Ranger District of the Coconino National Forest in northern Arizona failed to regenerate successfully because of browsing primarily by elk. Since 1985, over 400 acres have been successfully regenerated using fencing of various designs to exclude elk. The expense and visual impact of establishing and maintaining over 20 miles of fence along with continued damage to aspen greater than 3.0 inches d.b.h. outside the fenced areas have resulted in the Arizona Game and Fish Department increasing the elk hunting permits by 400% in an effort to reduce the elk herd in the area of the San Francisco Peaks.*

The Coconino National Forest, located in northern Arizona, encompasses 1.5 million acres of forested land consisting mostly of ponderosa pine (*Pinus ponderosa*) and pinyon pine-juniper (*Pinus edulis-Juniperus* spp.) woodland. Aspen (*Populus tremuloides*) comprises 10,500 acres (less than 1%) of the forest. The forest around the San Francisco Peaks contains 98% of the aspen on the Coconino. In most cases aspen is a minor component of extensive ponderosa pine and mixed conifer forests. Pure aspen stands are usually small and surrounded by encroaching conifers, especially on warmer, drier sites. Many of these isolated stands consist of a single genotype (clone) that is critical to the forest ecosystem. Often, these isolated clones occur in environments where competition for moisture and light, or pressure from browsing animals, severely stress aspen's ability to persist in the landscape. These forests are heavily used during the summer and winter by recreationists and highly valued during the fall leaf change by the public from around the state. Public interest in the scenic beauty of aspen and the limited quantity of aspen on the forest have focused management objectives on perpetuating these aspen stands while maintaining mature aspen in our landscapes.

While the Forest Service manages the vegetation, the Arizona Department of Game and Fish manages the wildlife populations. The original population of Merriam elk (*Cervus elaphus merriami*) went extinct during the period of market hunting and agriculture at the end of the 19th century. Elk numbered only 90,000 across North America in 1922, and of these, 40,000 were in Yellowstone Park. The Park's herds became a reservoir for breeding elk. Between 1912 and 1967, more than 13,500 elk were transplanted from the Park. In February 1913, 83 elk were released in Cabin Draw near Chevelon Creek in east-central Arizona. From these transplants, the Arizona elk population has grown to nearly 35,000 animals. This population is very important to the economy of northern Arizona through revenue generated from hunting and tourism.

In the 1960s, the Peaks Ranger District began regenerating aspen using public fuelwood clearcuts. A total of 254 acres were treated with cattle fencing as the only protection. Nearly all of these areas failed as repeated browsing prevented the successful regeneration of the aspen (figure 1).

In 1985, a one-half acre portion of one of the earlier clearcuts was fenced with salvaged material to exclude deer and elk. The fencing was stapled to live

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Figure 1—Failed aspen fuelwood treatment.

trees surrounding a clearcut that had been cut several years earlier. The suckers were heavily browsed, but existing root reserves were sufficient to regenerate the area once the fence had removed the browsing pressure.

Since 1986, approximately 400 acres have been treated and protected with fencing. This required construction of over 20 miles of fence. Over the years, several different designs have been tried in an effort to find the best balance between durability and cost. The majority of the fences consist of two 39 inch panels of 14-gauge field fence overlapped and joined with hog-rings to create a 6½-foot fence. The fence is stretched between existing trees, especially at the corners, to avoid building braces. Where trees are used to support the fence, the fencing is stapled to 8-foot wooden 2 x 2s wired to the tree to avoid stapling directly to the trees. Eight-foot steel T-posts are placed at 22-foot intervals between trees to provide additional support. These fences were constructed at a cost of $6,000/mile evenly split between labor and materials. The current fence design utilizes a single 47 inch panel of 14-gauge field fence together with three strands of high-tensile wire instead of two 39-inch panels. The first strand of high-tensile wire is positioned 6 inches off the ground with another 6 inches to the bottom of the field fence panel. The second and third high-tensile strands are positioned above the top of the field fence panel at 6–12 inch intervals (figure 2).

The high-tensile wire is stretched with wire strainers between the same trees that are used to stretch the field fence. Steel posts and wooden 2 x 2s are placed the same as the previous design. Eliminating the second field fence panel reduces the cost of materials by $1,200/mile and saves an additional $1,000/mile in labor. We also built several solar powered electric fences using ½-inch polytape and 9-strand polywire in a double fence design. Two areas of 35 acres were fenced using this design. This promised a 60% savings in material and labor costs, but the design was ultimately rejected because of extremely high maintenance cost and low durability.

Funds for the fencing projects came from three sources. The fuelwood clearcuts generated sufficient revenue from the sale of aspen fuelwood and pine sawtimber greater than 12 inches d.b.h. to pay for the material and labor costs

Figure 2—Current fence design.

of the fences. The areas were between 16 and 40 acres. These were handled under our small sales program and involved quantities less than 50,000 board feet. Numerous small clones less than 5 acres in size were treated as part of a larger timber sale that removed the competing pine and provided Knutson-Vandenberg (K-V) funds to pay for the fences. Several individual small clones were fenced with material donated by partners (i.e., Coconino Sportsman, Rocky Mountain Elk Foundation, and Arizona Game and Fish Department) and constructed with volunteer labor (Elderhostel International, Coconino County Probation Crew, Americorps, and Youth Conservation Corps).

The original prescription required that the fences be removed after 70% of the aspen stems were over 12 feet tall and beyond the reach of the elk. It was anticipated that 3 to 5 years would be needed to reach these conditions. A 22-acre aspen stand clearcut in 1986 had the fence removed in October 1991 with 20,000 stems per acre and dominant stems 12–15 feet tall after five growing seasons. By October 1992, most of the stems in one clone had been severely damaged by elk. Damage was caused by biting and breaking the stems at a height of 5 feet, stripping the terminal foliage, and infecting the residual stem. This clone was almost completely gone by October 1994 (figure 3).

Although other clones also suffered extensive browsing, stems larger than 1.5 inches d.b.h. were too large for animals to break. Unfortunately, elk are stripping the bark from the larger stems, resulting in infection and/or girdling. Current estimates are 10 to 15 years before fence removal.

Figure 3—Severe elk damage.

With fences between 5 and 50 acres in size, some amount of damage can be expected during the first couple of months as elk and deer crash into the fence until they learn to travel around it. On fences under 5 acres, little or no damage occurs as animals can easily move around the fences. The one fence greater than 50 acres is 130 acres and 2 miles in length. With the exception of the solar powered electric fences, this fence has experienced the highest amount of damage from elk, tree tops falling on the fence, runoff washing out sections of the fence, and woodcutters breaking the fence to access the fuelwood. The fence bisects several travel corridors and the animals have persisted in going over or through the fence. A different design consisting of two smaller fences with room to travel in-between would be a better solution. The addition, 1 year ago, of two strands of high tensile wire at the top of the fence has greatly reduced the impacts from elk.

In the summer of 1996, about 16,000 acres burned north of the San Francisco Peaks. About 1,200 of these acres contained aspen. In spite of a reduction of the elk herd in the Unit by about 30% (2,500 to 1,870) over the last 4 years, elk made heavy use of most aspen suckers that grew after the burns of 1996. These aspen stands have a 3- to 5-year period to become established before exhausting the root reserves. The fire that produced the new aspen suckers burned in the San Francisco Peaks area, Game Management Unit 7 East. The Arizona Game and Fish Department proposed to significantly reduce the elk herds in Unit 7 for a period of 10 to 15 years. This effort should enable aspen suckers resulting from the wildfire of 1996 to survive and grow sufficiently to withstand the browsing of elk. It is also expected that there will be a decline in the barking and browsing damage to the larger established aspen trees.

Interaction Among Cervids, Fungi, and Aspen in Northwest Wyoming

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Abstract*—Eighty-five 0.02-ha plots in the Gros Ventre River drainage of northwestern Wyoming with high elk usage had 39% fewer aspen stems in 1985 than in 1970. Sixty-five of these plots were remeasured in 1989 and 53 additional plots established in 1986 on the Hoback River drainage (lower winter elk usage) were remeasured in 1990. Overall mortality (average/year) of aspen stems >2.5 cm d.b.h. was 2.6% (1970–1985), 2.4% (1985–1989), and 2.3% (1989–1999) for the Gros Ventre plots, and 1.9% (1986–1990) for the Hoback plots. Larger stems (>15 cm) had lower mortality rates than smaller stems. Additional studies conducted near elk feedgrounds also showed that mortality caused by pathogenic fungi was correlated with the amount of prior cervid injury to stem boles. Aspen sprouts exposed to cervids rarely exceeded 1 m in height. These observations indicate that herbivory and disease may be reducing aspen distribution in these ecosystems.*

Introduction

The direct impact that elk browsing and barking have on aspen stands has been reviewed (DeByle 1985). Through the early sapling state, browsing reduces aspen growth, vigor, and numbers. Aspen (*Populus tremuloides*) is especially susceptible to gnawing or stripping of its bark by elk (*Cervus elaphus*) and moose (*Alces alces*) (Miquelle and Van Ballenberghe 1989). Deer (*Odocoileus* spp.) browsing prevented aspen regeneration in Utah (Mueggler and Bartos 1977) and Michigan (Westell 1954). A single, heavy late summer grazing by cattle (*Bos* spp.) after overstory removal practically eliminated aspen regeneration (Fitzgerald and Bailey 1984). Smith et al. (1972) reported that deer alone had little effect on the development of aspen reproduction, but when deer were present with cattle, aspen regeneration was virtually eliminated.

Severe browsing by elk in Michigan on aspen prevented the development of new stands following harvest (Spiegel et al. 1963), and in Montana 50% of the aspen sprouts were killed by elk during a single winter (Gaffrey 1941). Olmstead (1979) found that if more than 30% of the current year's production of twigs was eaten by elk, stand density decreased. He reported twig volume losses ranged from 43% to 79% on aspen stands in Rocky Mountain National Park. In the same area from 1968 to 1978, twig use averaged 69% and the number of mature stems declined in most aspen stands surveyed (Stevens 1980). During a five-year period in Yellowstone National Park, twig loss averaged 66%, and 76% of the stems under study died (Kittams 1959). Even much lower levels of defoliation may decrease plant fitness (Crawley 1985).

The nation's expanding elk, moose, and deer herds appear to be having a negative impact on aspen regeneration, especially in locations where the herds are protected from hunting (e.g., national parks). Most of the damage is restricted to winter ranges where elk are concentrated near feedgrounds. Aspen sprouts exposed to elk rarely exceeded 1 m in height on the Gros Ventre watershed in Wyoming (Krebill 1972; Hart 1986) or along Pacific Creek in

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Grand Teton National Park (Weinstein 1979). If unable to reproduce, these seral aspen stands deteriorate rapidly (Schier 1975) and may be replaced by communities with lower multiple-use values.

Relationships between cervids, aspen, and pathogenic fungi have been studied previously (Packard 1942; Graham et al. 1963; Hart 1986; Hart et al. 1986; Kittams 1959; Krebill 1972; Mielke 1943; Walters et al. 1982). The barking of aspen by elk or moose often has provided a point of entry for canker fungi that hasten the death of the stems. Sludge application to aspen stands in Michigan increased elk damage that altered growth form and created wounds, predisposing clones to pathogenic fungi (Hart et al. 1986). In areas of moderate to light herbivore pressure, the direct damage caused by the animals may not be severe enough to cause stand deterioration except for the secondary action of pathogens and insects. In some areas in Colorado where elk barking was light, no elk wounds became visibly infected with a pathogen (Walters et al. 1982). The reason for the disparity between the studies of Packard (1942), Krebill (1972) and Hart (1986), and those of Walters et al. (1982) is unknown.

The objective of this study was to conduct a long-term survey of aspen stands in northwest Wyoming to determine the relationships between aspen demographics and elk, moose, and disease.

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Gros Ventre/Hoback Studies

Methods

In 1970 Krebill (1972) sampled one hundred 0.02 ha plots on the Gros Ventre River drainage (cervid injury common and severe) to determine the rate of overstory aspen mortality and its causes. Browsing and pests severely limited the replacement of dying trees. His data predicted a 44% reduction in aspen overstory by 1985.

To test Krebill's prediction, ninety-seven 0.02 ha circular plots were established on the Gros Ventre watershed in 1985. Using Krebill's original map, 85 of the plots were established in the same locale as his 1970 plots. Condition of aspen stems was recorded by diameter breast height (d.b.h.) in three size classes (2.5–15 cm, 15–30 cm, >30 cm). Occurrence of potentially lethal pathogens and insects and the amount of cervid injury to the bark 0.5–2.5 m above ground were recorded. The number of suckers, average height, and amount of browse on suckers were determined for each plot. Pathogens and insects were identified by field symptoms and signs.

In 1986, 55 similar plots were established in a drainage (Hoback River watershed) adjacent to the Gros Ventre in aspen stands with little or no cervid damage. In 1989, 65 plots were resurveyed and in 1999 32 plots on the Gros Ventre were resurveyed. Plots (53) on the Hoback drainage were resurveyed in

1990, thus the time between the initial and final samplings was the same (four years) for both areas.

Results

The 85 plots sampled in 1985 on the Gros Ventre drainage had 39% fewer stems >2.5 cm d.b.h. than in 1970, similar to the 44% decrease predicted by Krebill (1972). Mortality rates during 1985–1989 and during 1989–1999 based on the 32 plots sampled in 1999 were not significantly different ($p = 0.659$) (table 1). Smaller diameter trees died faster than larger diameter trees ($p = 0.001$) (table 1). Mortality was caused mainly by pathogenic fungi (primarily *Valsa sordida* [*Cytospora chrysosperma*], and *Encoelia pruinosa* [*Cenangium singulare*]) following prior cervid injury to stem boles.

Mortality during the 4-year period (1985–1989, Gros Ventre, or 1986–1999, Hoback) was significantly ($p = 0.0001$) greater for stems between 2.5 cm and 30 cm d.b.h. on the Gros Ventre watershed (high cervid numbers) compared to the Hoback watershed (low cervid numbers) (table 2). Most of the aspen in plots on the Gros Ventre drainage had more than 40% of the bark between 0.5 m and 2.5 m above groundline removed or damaged when the plots were sampled in 1985 (table 3). The aspen on only one of 55 plots on the Hoback drainage had damage above 40%. There was a significant difference ($p < 0.001$) in the amount of barking between locations. The number of dead aspen stems on the ground per plot correlated with the amount of prior cervid damage to the bark. Plots with stems having less than 40% of the bark damage averaged 4.5 dead stems per plot, while plots with stems with 40–70% and >70% damage averaged 15.1 and 17.7 dead stems per plot, respectively.

Number of suckers remained constant (table 4) as did their height ($p = 0.2064$) (table 5). On the Gros Ventre watershed, only 3–8% of the plots had suckers >1 m in height, while on the Hoback watershed over a third of the plots had suckers >1 m in height ($p < 0.0001$ for location) (table 5). Amount of browse on the current year's growth on suckers was lower ($p = 0.0331$) for plots sampled on the Hoback drainage compared to the Gros Ventre drainage (table 6). In 1999 the amount of browse was lower ($p = 0.0174$) in plots on the Gros Ventre

Table 1—Average annual mortality rates for aspen stems on the Gros Ventre drainage in northwestern Wyoming between 1985–1989 and 1989–1999. Number of live stems at the beginning of each interval is in parentheses.

	2.5–15 cm d.b.h.	15–30 cm d.b.h.	>30 cm d.b.h.
		percent	
1985–1989	4.2 (96)	2.0 (402)	0.1 (32)
1989–1999	4.6 (80)	1.8 (370)	1.9 (31)

Table 2—Average annual mortality rates during a 4-year period for aspen stems in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids.

	2.5–15 cm d.b.h.	15–30 cm d.b.h.	>30 cm d.b.h.
		percent	
Gros Ventre[a]	5.0 (164)	2.0 (770)	0.4 (64)
Hoback[b]	2.7 (621)	1.1 (715)	1.3 (19)

[a] Number of live stems in 1985 is in parentheses.
[b] Number of live stems in 1986 is in parentheses.

Table 3—Amount of aspen bark that cervids have removed 0.5–2.5 m above groundline in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids.

% bark removed	Gros Ventre (1985) # of plots	Hoback (1986) # of plots
<10	0	31
10–40	9	23
40–70	53	1
>70	33	0

Table 4—Number of aspen suckers per 0.02 ha plot in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids. Number of 0.02-ha plots is in parentheses.

	1985/1986	1989/1990	1999
Gros Ventre	26 (97)	32 (65)	20 (31)
Hoback	18 (55)	20 (53)	

Table 5—Percent of 0.02 ha plots with aspen suckers >1 m in height in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids. Number of 0.02-ha plots is in parentheses.

	1970	1985/1986	1989/1990	1999
	percent			
Gros Ventre	3 (100)[a]	6 (85)	8 (65)	3 (31)
Hoback		33 (55)	40 (53)	

[a] 1970 data from Krebill (1972).

Table 6—Percent of current year's growth of aspen suckers browsed by late August in northwestern Wyoming in areas with high (Gros Ventre) and low (Hoback) densities of cervids. Number of 0.02-ha plots is in parentheses.

	1985/1986	1989/1990	1999
	percent		
Gros Ventre	72% (75)	66% (52)	30% (28)
Hoback	39% (36)	50% (36)	

than on the same plots in 1985 or 1989 (table 6). This reduction appears to be correlated with fewer cattle in 1999 compared to the 1980s.

Heart Six Studies

Methods—Study I

The winter of 1983–1984 was especially severe in western Wyoming, and elk were fed in 1984 near the Heart 6 Ranch, Moran, Wyoming, an area where elk had not previously wintered. Hence the aspen stems in this area were free of stem scars prior to the feeding program. The stems in the immediate area of feeding were severely damaged in early 1984, but nearby (300 m) clones were not attacked. No significant reinjury occurred during 1985, 1986, or 1987.

Although moose winter commonly in the willow flats below the feedground, they were not reported in the area where the elk were being fed.

Seven 0.02-ha plots were established in July 1985 in the injured (feedground) and in the nearby uninjured clones. The condition of stems 2.5 to 15 cm d.b.h. was recorded. The diameter, amount of injury, and presence of any pathogens were recorded for each stem >15 cm d.b.h. Stems were permanently marked and were examined again in July 1986 and August 1987, and their condition was recorded.

Results—Study I

From the data collected in 1985, it was estimated there were 428 stems 2.5–15 cm d.b.h. alive in the seven feedground plots in 1984 and 357 live stems in the seven control plots. In 1984, 82% (347/428) and 1.7% (6/357) of the stems received elk injury in the feedground and control plots, respectively. By 1985, 28% (97/347) of the injured stems had died in the feedground plots; the mortality dropped to 11% in 1986 and 1987. Mortality rates varied from 1.4% to 8.5% per year for the uninjured stems in the feedground area and from 5% to 14% per year in the control area. Cumulative mortality (1984 to 1987) was 43% for injured stems compared to 14% and 21% for uninjured stems in the feedground and control areas, respectively.

The bulk (72%) of the first-year mortality of injured stems 2.5–15 cm d.b.h. was the result of elk completely girdling the stem; the remaining mortality in 1985 and nearly all of the mortality in 1986 and 1987 was the result of elk wounds being colonized by canker fungi. *Valsa sordida* (*Cytospora chrysosperma*) was the pathogen present except for one case in 1986 when *Encoelia pruinosa* (*Cenangium singulare*) was identified. In addition, 61 of the 198 wounded stems still alive in 1987 in the feedground plots had active *Cytospora* cankers in 1987.

There were 141 and 136 live stems >15 cm d.b.h. on the feedground and control plots, respectively. Ten injured stems over 15 cm d.b.h. died between 1985 and 1986, but only one death resulted from colonization of an elk wound by a pathogenic fungus (*Cenangium*). Five more stems died in 1987, but none died from cankers associated with elk damage. Cumulative mortalities (1985–1987) of elk-damaged and healthy stems were 2.7% and 1.5%, respectively.

Methods—Study II

During 1988, elk and moose were again fed near the Heart Six Ranch, Moran, Wyoming, in areas free of stem scars prior to the feeding program. During August 1989, 14 plots of 0.02 ha were established in areas where some barking had occurred; seven of these plots were the “control” plots for Study I. The condition of 529 stems 2.5 to 10 cm d.b.h. was recorded; 54% of the stems had damage caused by elk or moose. The diameter, the number of cervid wounds, the percent of the circumference girdled, the presence of canker fungi, and the presence of the heartrot fungus *Phellinus tremulae* were recorded for each stem >10 cm d.b.h. There were 163 stems that received some damage and 99 undamaged stems. Plots were sampled annually in late summer from 1989 to 1995, with the year of death recorded for each stem that died. There was little new damage after 1988, but a few stems had to be eliminated because of üubsequent damage.

Results—Study II

From 1989 to 1995, 55% of the damaged and 46% of the undamaged stems 2.5–10 cm d.b.h. died. Seventy-two percent of the mortality of the damaged

Table 7—Annual mortality rate of aspen stems in northwestern Wyoming with and without *Phellinus tremulae* and with or without cervid damage to the bark, 1988–1995. Number of stems is in parentheses.

	percent
Healthy	2.4 (76)
Cervid wounds only	2.9 (129)
P. tremulae, no wounds	1.9 (23)
P. tremulae, cervid wounds	5.9 (34)

stems occurred by 1991. As in Study I, most of the mortality was from mechanical injury followed by infection of wounds by *V. sordida*.

The annual mortality of stems >10 cm d.b.h. was 3.5% for damaged stems and 2.3% for stems not injured by cervids. Stems that had fruiting bodies of *P. tremulae* and cervid damage were three times more likely to die than unwounded stems with *P. tremulae* fruiting bodies and twice as likely to die as wounded stems without *P. tremulae* or healthy stems (table 7). Wounded stems that died by 1995 had an average of 69% of the circumference of the trunk girdled in 1988 compared to 37% girdled for wounded stems that did not die by 1995 ($p = 0.0001$). Wounded stems that became infected with canker-causing fungi had an average of 53% of the circumference girdled in 1988 compared to 40% girdled for wounded stems that did not become infected by 1995. Reduction in the percent of the trunk girdled between 1988 and 1995 was 41% and 23% for stems that did not and stems that did become infected with canker fungi, respectively. The 56 stems that died between 1988–1995 had an average d.b.h. of 17.3 cm, while the average d.b.h. of the 206 stems that did not die was 18.7 cm ($p = 0.849$).

Goosewing Exclosure

Methods

Near the Goosewing ranger station (Gros Ventre watershed) there was an exclosure that contained a considerable number of aspen. During 1985 and 1986, moose broke a hole in the fence and scarred a number of stems, most injury apparently being the result of a single feeding episode.

In 1985, the d.b.h. (average 9.1 cm, 4.3–26.1 cm) and percent of circumference girdled were recorded for 80 recently scarred stems. The d.b.h. (average 8.8 cm, 3.4–22.9 cm) was also determined for 75 uninjured stems, and all 155 stems were permanently numbered. Similar data were recorded for 25 stems injured in 1986. All stems were observed annually until 1995 except for 1988.

Results

Annual mortality of stems was 3.5% and 1.3% for stems injured by moose and uninjured stems, respectively, results very similar to those obtained from the Heart Six, study II. Annual mortality for the 25 stems injured in 1986 was 1.8%. Wounded stems that died by 1995 and wounded stems that remained alive had nearly identical amounts of girdling in 1985: 37.3% and 36.0% ($p = 0.633$), respectively, which differs from the data collected from the Heart Six, study II. As reported in the previous studies, smaller d.b.h. stems were more likely ($p = 0.0648$) to die than stems with a larger d.b.h. Average d.b.h. of uninjured stems that died was 7.7 cm versus 9.0 cm for stems remaining alive. For injured stems, those that died had an average d.b.h. of 7.8 cm versus 9.7 cm for stems that lived.

Discussion

These results support previous research which has demonstrated that aspen has a difficult time maintaining itself when subjected to intense herbivory from cervids (Kay 1997; Romme et al. 1995; Bartos and Mueggler 1981; Krebill 1972). Mortality increased as the amount of bark injured increased (Miquelle and Van Ballenberghe 1989). Death of overstory stems coupled with heavy browsing of suckers, especially when fire was excluded from the environment, resulted in the reduction of the aspen type over time.

Increased grazing pressure resulted in increased pathological stress. Injured stems usually succumbed to invasions by pathogenic fungi rather than from mechanical injury alone. These fungi are secondary in time (not in importance) because changes in host condition are required for their successful attack. The canker fungi are part of the natural biota that occur on the trees. Aspen are highly resistant to these secondary pathogens until wounds enable them to succeed. Yet most injured trees were not attacked by canker fungi or were able to recover over time. The combination of *P. tremulae*, ungulate barking, and canker fungi was a deadly combination for most stems.

The effect of herbivory or disease on a clonal plant may differ significantly from the effect on a non-clonal plant, especially in evolutionary terms. Predation or disease on a clonal plant may have no influence on fitness if the predator removes only what would have died later from density-dependent processes. The birth and death rate for stems may represent a population behavior distinct from but interacting with the birth and death rates of clones. Perhaps by reducing the amount of energy-requiring stem tissue, dieback of part of the clone (usually the smaller diameter stems) adjusts the clone's energy balance to its environment without significantly reducing clonal fitness.

The major role of most mammalian herbivores is related to their indirect effects rather than those related directly to energy consumption. These herbivores, while minor participants in ecosystem energy flow, can have important effects out of proportion to the quantity of energy consumed. Damage by animals to the cambium of trees or to the apical meristem may have effects far greater than the fraction of the plant body eaten, particularly when the effect is to change the morphology of the plant. Thus by altering growth form or by creating wounds for pathogens, herbivores may cause significant successional consequences.

Kay (1997) has reviewed the literature which strongly suggests that cervid populations in much of the West are higher now than in the past. Feedgrounds (three of which are on the Gros Ventre watershed) further concentrate these animals during the winter. To persist, aspen must not only be resistant to disease and competition by conifers, but also be inaccessible to cervids or be resistant to herbivory. Historically, periodic winter die-offs reduced cervid populations (at least before winter feeding) and allowed aspen to grow above browse levels before cervid populations recovered. Under current conditions (reduced fire frequency; high, constant cervid populations), the future of aspen in this area is limited by the intensity of herbivory in the winter and competition with conifers. Hence, more fires and/or fewer cervids would favor the growth of aspen.

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Heartrot Fungi's Role in Creating Picid Nesting Sites in Living Aspen

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Abstract—*To determine the number of cavity-containing aspens in old-growth (>80 years), we counted the number of stems containing cavities in 132 0.02-ha plots in Wyoming. There were 8.7 cavities/ha of aspen type. At least 84% of the cavity stems were alive when the initial cavity was constructed; 60% were alive when examined. Fruiting bodies and* Phellinus tremulae *(a heartrot fungus) were present on 71% of all cavity-bearing stems but on only 9.6% of all stems >15 cm d.b.h. Cavities were present in 7.7% and 0.2% of living stems with and without fruiting bodies, respectively. Average d.b.h. of cavity stems was 27.4 cm. During a 4-year interval, 74 of 226 snags >15 cm d.b.h. fell, giving an average instantaneous rate of snag loss of* r *= –0.099. Ninety-six new snags >15 cm d.b.h. were created during the 4-year study period. Our results indicate that some primary cavity-nesting birds in northwest Wyoming preferentially selected living aspens with heartrot as nest sites and that the average longevity of aspen snags >15 cm d.b.h. is about 10.7 years.*

Introduction

Cavity-nesting birds are a major component of many avian communities, and the value of snags (standing dead trees) for nesting, feeding, and perching has been well documented (Davis 1983). The importance of living trees as nest sites has been studied less, but the importance of living pine with heartrot as a necessary component of red-cockaded woodpecker habitat is well documented (Ligon 1970; Jackson 1977; Conner and Locke 1984; Hooper et al. 1991; Conner et al. 1994). These woodpeckers select pines over 80 years old that are infected with the heartrot fungus *Phellinus pini* in which to excavate their cavities.

The aspen type in the mountainous west contains an abundant and diverse avian population. Approximately 34 species nest in cavities in aspen, *Populus tremuloides*; some species, e.g., the red-naped sapsucker (*Sphyrapicus nuchalis*), may be obligate aspen-nesters (Crocket and Hadow 1975). The importance of the aspen community to forest birds has been summarized by DeByle (1985).

Aspen is especially prone to attack by heartrot fungi, primarily *Phellinus tremulae* (*Fomes ignarius* var. *populinus*). This organism attacks aspen throughout its range, and the incidence of infection increases with tree age (Hiratsuka and Loman 1984). Previous studies support the conclusion that several species of sapsuckers select aspen that have fruiting bodies of *P. tremulae* (Kilham 1971; Erskine and McLaren 1972; Crockett and Hadow 1975; Winternitz and Cahn 1983). This fungus causes extensive decay of the heartwood while the sapwood remains intact, protecting the nest cavity. Over 55% of sapsucker nests in Colorado were in trees on which *P. tremulae* was fruiting (Crockett and Hadow 1974; Winternitz and Cahn 1983). Nest cavities were evenly distributed between live and dead aspen in trees with an average age of 170 years (Winternitz and Cahn 1983).

The rate at which conifer snags fall has received some attention (Bull 1983) but the longevity of aspen snags is unknown. DeByle (1985) predicted that, once

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dead, aspen snags are unlikely to stand for more than a few years, while Krebill (1972) assumed that most aspen remain standing for about 10 years after death. Others (Buttery and Gillam 1984; Wills 1984) predicted that aspen snags cannot be expected to remain standing for more than five years.

Our objectives were to determine: (1) the density of aspen cavity trees, (2) whether or not the trees were alive when the first cavity was constructed, (3) the presence or absence of *Phellinus tremulae* conks on cavity trees, and (4) the longevity and density of aspen snags.

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Study Area and Methods

The study was conducted on the Bridger-Teton National Forest, northwest Wyoming. Aspen stands examined were located in three areas: north of the Buffalo Fork River, about 10 km east of Moran; within 10 km of the Goosewing ranger station on the Gros Ventre River; and between Cliff Creek and the Hoback River, approximately 10 km south of Bondurant. Stands studied occurred between 2,100 and 2,700 m elevation, with an interspersion of Engelmann spruce (*Picea engelmannii*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*). A more detailed description of the vegetation has been published (Mueggler 1988). The average age (as determined by counting annual rings in increment borer cores) of the aspen was 115 years (Gros Ventre) and 80 years (Hoback and Buffalo Fork).

During 1985, 65 0.02-ha circular plots in the aspen type were established on the Gros Ventre watershed and 14 similar plots were established near Moran. During 1986, 53 similar plots were established on the Hoback watershed. The condition and size of each aspen stem over 2.5 cm d.b.h. were recorded. There were 1,001 aspen snags >2.5 cm d.b.h. in the 118 Hoback and Gros Ventre plots at the time of establishment. Plots were originally established to determine the effect of elk (*Cervus elaphus*) on aspen demographics (Krebill 1972; Hart 1986).

Four years after plot establishment the plots were re-surveyed to determine the number of new aspen snags and the number of original snags still standing. At that time the d.b.h., whether the tree was alive or dead, the number of cavities and their height, the presence or absence of callus tissue at the cavity entrance (to determine if the tree was alive when the cavity was first constructed), and the presence or absence of *P. tremulae* conks were recorded for each cavity tree within a plot and for other cavity trees that were encountered between plots.

Results

Data were collected on 23 cavity trees in the research plots and on an additional 22 cavity trees located outside the plots. These 45 trees contained 73 cavities. There were 9.2 cavity trees per hectare of aspen type in the Gros Ventre plots and 8.2 cavity trees per hectare in the Moran-Hoback plots, or an overall average of 8.7 cavity trees per hectare. The average d.b.h. of stems with cavities was 27.4 cm (range 14 to 41 cm), very similar to previously reported values (Crockett and Hadow 1975; Winternitz and Cahn 1983). Based on the development of callus tissue at the cavity entrance, we determined that at least 84% of the stems with cavities were alive at the time the cavities were constructed; 60% were alive when the data were collected. Average height of cavities was 2.7 m (1.4 to 6.1 m); a similar value was reported by Crockett and Hadow (1975). Our value was much lower than the minimum nesting height (4.6 m) listed by Thomas et al. (1979:382) or the mean value (4.0 m) reported by Winternitz and Cahn (1983). Seventy-four percent of the cavities were not associated with knots, and 33% of the cavity trees contained more than one cavity (maximum of five).

P. tremulae conks were present on 71% of all cavity trees but on only 9.6% of all trees. As stem d.b.h. increased, the presence of *P. tremulae* conks increased from 6% for stems 2-15 cm d.b.h. to 13.5% for stems >30 cm d.b.h. All but one cavity entrance associated with the presence of *P. tremulae* conks (figure 1) were less than 6.5 cm in diameter and typical of the size cavity made by sapsuckers, downy woodpeckers (*Picoides pubescens*), or hairy woodpeckers (*P. villosus*). Only five cavity entrances were over 7 cm in diameter (northern flicker, *Colaptus auratus*); three were in dead trees without conks. The cavity in figure 1 was used by red-naped sapsuckers in 1985 and by house wrens (*Troglodytes aedon*) in 1990. In 1989 there were four cavities in this tree and a fifth was constructed in 1990. Newer cavities were constructed above older cavities. The tree failed to produce leaves in the spring of 1991 and no new cavities were constructed during 1991. The construction of new cavities by red-naped sapsuckers in the same aspen in successive years has been reported previously (Weydemeyer and Weydemeyer 1928; Kilham 1971; Erskine and McLaren 1972; Daily 1993).

Figure 1—Red-naped sapsucker under a *Phellinus tremulae* fruiting body on an aspen in northwest Wyoming.

The instantaneous rate of snag loss may be calculated from the equation for exponential population growth rate (Sedgwick and Knof 1992):

$$r = [\log_e N(t) - \log_e N(o)]/t$$

where r is the rate of loss, $N(t)$ is population size at time t (1989 or 1990), $N(o)$ is the population size at the beginning of the period (1985 or 1986), and t is the time period (four years). For all snags >2.5 cm d.b.h., $r = -0.087$, and for snags >15 cm d.b.h., $r = -0.099$. During the four-year interval, 293 of 1,001 snags >2.5 cm d.b.h. fell, while 191 new snags developed. While total snags decreased, those >15 cm d.b.h. increased from 226 to 248.

The year of death is known for 104 aspen trees >10 cm d.b.h. in the 14 0.02-ha plots near Moran that were monitored annually from 1985 to 1995. Snag fall appears to be minimal for the first four years following tree death (figure 2). Ten years after death, one-half of the snags had fallen. The approximate density of aspen snags >15 cm d.b.h. was 100/ha of aspen type and remained fairly constant during the four-year study period (table 1) and is similar to the 114 snags/ha reported for the Gros Ventre watershed in 1970 (Krebill 1972). The number of snags between 2.5 and 15 cm d.b.h. decreased from 328 to 276 snags/ha.

Discussion

These results, in combination with previously published papers (Kilham 1971; Crockett and Hadow 1975; Winternitz and Cahn 1983), strongly suggest that living aspen with heartrot caused primarily by *P. tremulae* may be a significant component of the breeding requirements of sapsuckers and possibly of other similar-sized picids (Hardin and Evans 1977). Our data suggest the

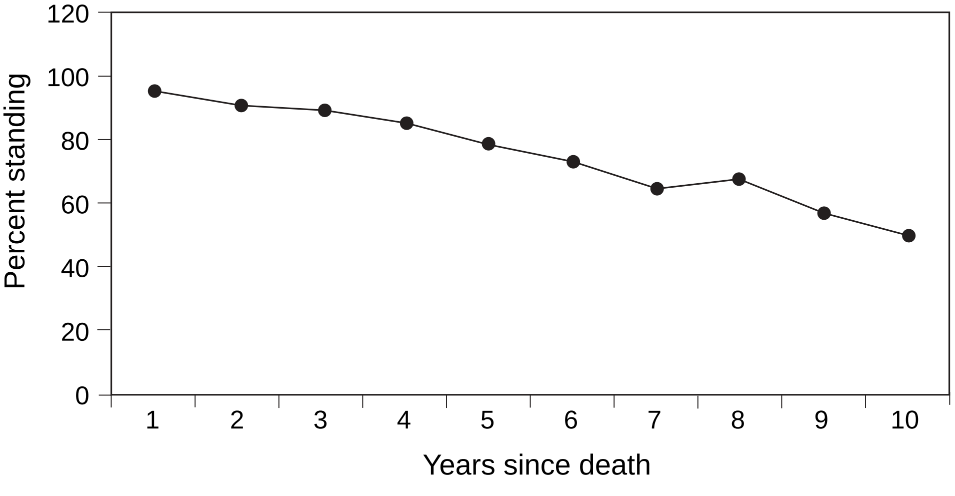

Figure 2—Percentage of aspen snags 10 cm d.b.h. standing, by number of years since death, Bridger-Teton National Forest, Wyoming, 1985–1995.

Table 1—Density of aspen snags in the aspen type in northwest Wyoming, 1985–1990 (no./ha).

Area	All snags >2.5cm d.b.h.		Snags >15cm d.b.h.	
	1985–1986	1989–1990	1985–1986	1989–1990
Hoback	415	398	47	62
Gros Ventre	432	367	135	140
Both areas	424	381	96	105

Phellinus infection was related in some way to nest site selection. The presence of the fungal conks may provide sapsuckers with a visual cue that such trees have a soft core and hence make optimal nest locations (Kilham 1971; Crockett and Hadow 1975). Conner et al. (1976) hypothesized that woodpeckers detect the presence of heartrot by pecking the tree and listening for a particular resonance.

Cavities made by primary cavity makers are subsequently used by numerous secondary cavity nesters (Winternitz and Cahn 1983). In Minnesota, 22 of 23 cavities used by boreal owls (*Aegolius funereus*), classified as a sensitive species by the U.S. Forest Service, were located in old aspen (Lane 1990). Buffleheads (*Bucephala albeola*) have been discovered breeding in Colorado in large aspen infected with *P. tremulae* following cavity excavation by northern flickers (Ringelman 1990). Both flying (*Glaucomys* spp.) and red squirrels (*Tamiasciurus hudsonicus*) (Kilham 1971), as well as other mammals (Thomas et al. 1979), frequently use cavities in aspen.

While the minimum d.b.h. needed by sapsuckers and many other cavity nesters before they will utilize a snag has been reported as 25 cm (Thomas et al. 1979), 36% of the cavity trees in this study had a d.b.h. <25 cm. The d.b.h. of the tree in figure 1, used repeatedly as a nest site by red-naped sapsuckers, was 23 cm. A red-breasted nuthatch (*Sitta canadensis*) nested in an aspen snag with a d.b.h. of 18 cm, considerably smaller than the minimum d.b.h. of 30 cm reported for this species (Thomas et al. 1979). Red squirrels also used trees with a smaller d.b.h. (21 cm) than is normally associated with this species (Thomas et al. 1979).

Species such as the boreal owl and bufflehead would require trees with at least a d.b.h. of 30 and 38 cm, respectively (Thomas et al. 1979). In this study, only 25% of the stems with cavities exceeded 30 cm d.b.h., and only two of 44 stems with cavities had a d.b.h. >38 cm despite the fact that many of the aspen in this area were over 120 years old. The combination of 2.2 living cavity trees/ha of aspen type over 30 cm d.b.h. and the 3.8 snags/ha greater than 30 cm d.b.h. may or may not have limited the density of intermediate-sized-cavity users (e.g., northern flickers or small owls) (Thomas et al. 1979:390). The 100 snags >15 cm d.b.h./ha of aspen type, in combination with living trees with heartrot, should have provided ample nesting habitat for the smaller cavity users (Thomas et al. 1979:390).

Although maintaining an abundance of snags (dead standing trees) has been emphasized in the management of cavity users (Thomas et al. 1979; Hoover and Wills 1984), living trees with heartrot may be more critical than snags to the maintenance of certain species. Sapsuckers (Crockett and Hadow 1975, this proceedings) and hairy woodpeckers (Lawrence 1967; Kilham 1968) nest almost exclusively in living trees with rotten centers. Decay increases as stand age increases (Hiratsuka and Loman 1984). The percentage of trees with decay is usually less than 10% before age 80, increasing to over 20% by age 100. Stands >100 years old begin to deteriorate (Schier 1975), although many stands reach an age of 120 years or older (Mueggler 1989). It may be possible to regenerate declining stands by cutting or burning at approximately 120-year intervals.

Mature or old-growth aspen (>80 years old) appears to represent valuable wildlife habitat that cannot be duplicated in other forest communities. Species such as red-naped sapsuckers, and perhaps boreal owls in some areas, apparently require mature aspen forests. Land managers should strive to maintain a mixture of successional stages and ages in different-sized stands. We recommend at least part of each management unit should be scheduled for a long rotation period in excess of 100 years. The best way to manage for old growth aspen is to protect an adequate supply of what is now available and leave it alone even if it begins to deteriorate. Shorter rotations, or cutting large portions of an aspen forest, may cause a serious decline in avian species that depend on older forests. Trees with heartrots may have little or no commercial value but have significant value in maintaining biodiversity in our aspen ecosystems.

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Evaluation of Burned Aspen Communities in Jackson Hole, Wyoming

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Abstract—*Aspen has been declining in Jackson Hole for many years, a condition generally attributed to the fact that lightning fires have been aggressively suppressed since the early 1900s. It is also believed that burning will successfully regenerate aspen stands despite high elk numbers. To test this hypothesis, I evaluated 467 burned and 495 adjacent, unburned aspen stands at eight different locations within Jackson Hole. Aspen suckering was stimulated by burning, but most aspen stands still failed to produce new stems greater than 2 m tall where ungulate use was moderate or high. Only when elk use was low were burned aspen stands able to successfully regenerate. At those locations, however, unburned aspen stands also successfully regenerated. Evidence suggests that a combination of fire and continued elk use may eliminate many aspen clones.*

Introduction

The relationship between vegetation and ungulates in Jackson Hole, Wyoming, has long been a subject of conflicting opinions and intense debate (Anderson 1958; Boyce 1989). Until the 1960s, it was thought that (1) Jackson Hole was not historic elk (*Cervus elaphus*) winter range; (2) European settlement forced elk to winter in the valley; and (3) supplemental feeding permitted the growth of an abnormally large elk herd; which (4) caused substantial damage to the winter range and a marked decline of aspen (*Populus tremuloides*) (Preble 1911; Murie 1951; Anderson 1958; Krebill 1972; Beetle 1974, 1979; Basile 1979; DeByle 1979; Weinstein 1979). However, federal and state biologists now believe that (1) large numbers of elk have wintered in Jackson Hole for the last several thousand years; (2) feedlots have only replaced winter range lost to human developments; (3) therefore, today's elk population is not unnaturally high, although the distribution of wintering animals may have changed; (4) serious elk-induced range damage has not occurred (Cole 1969; Gruell 1979; Gruell 1980a,b; Boyce 1989); and (5) the elk herd would "naturally regulate" if sport hunting were terminated (Boyce 1989). Under this interpretation, aspen is thought to be a seral species maintained by fire, and human suppression of lightning fires is believed to be primarily responsible for the observed decline in aspen, not ungulate browsing (Loope and Gruell 1973; Gruell and Loope 1974).

Gruell and Loope (1974:19–20) and Gruell (1980a:2) indicated that aspen stands burned in Jackson Hole were able to successfully regenerate, defined as producing new stems >2 m tall, despite heavy browsing—a claim similar to that made by the Park Service in Yellowstone (Kay 1990). According to Houston (1982:127), "data from [Yellowstone's] northern range and adjacent areas showed that aspen often reproduced successfully when burned in the presence of ungulate populations." While Despain et al. (1986:107) stated that "data from some locations on the northern range have proven that aspen, when

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burned, has actually regenerated despite heavy elk use." However, Basile (1979) and Bartos and Mueggler (1979, 1981) reported that even though an experimental burn in Jackson Hole greatly increased the number of aspen suckers, elk browsing eliminated all incremental height growth after the first summer. The authors cautioned that fire-induced suckering was probably not sufficient to regenerate aspen under current browsing pressures in Jackson Hole.

To determine which of these competing views is correct, and whether burning can, in fact, regenerate aspen despite heavy utilization by elk and other ungulates, I measured burned aspen stands at eight different locations in Jackson Hole (table 1). These sites were prescribe-burned by the Forest Service or U.S. Fish and Wildlife Service to regenerate aspen and to improve range conditions. In addition, the burns have different histories of elk use, making them ideal subjects for this study (Kay 1990).

Methods

I first searched agency files to obtain all existing information for each burn; data on the location, timing, and size of each burn are presented in table 1. Within each burn, I visually evaluated every aspen stand to determine whether it had regenerated. A burned stand was recorded as regenerating if at least one aspen stem had grown taller than 2 m after the fire. Even if only a small portion of the original stand had regenerating stems >2 m tall, those stands were still considered to have regenerated successfully for this study. Thus, visual evaluation of the proportion of aspen stands that regenerated following fire is biased in favor of successful regeneration. I also visually evaluated unburned aspen

Table 1—Location and description of aspen burns in Jackson Hole, Wyoming.

Burn	Area[a]	Location T	R	S	Date burned	Approx. area burned	Aspect	Elevation
						ha[b]		*(m)*
Burro Hill	BTNF	45N 45N	113W 112W	25 19,30	8/27/1974	178	NE-S-SW	2,100-2,200
Russold Hill	BTNF	42N 43N	114W 114W	1,2 35	5/15/1975	188	NE-S-NW	2,150-2,255
Coal Mine Draw	BTNF	44N	113W	3,4,9	5/18/1976	121	N-E-S-W	2,200-2,270
Lightning Creek[c]	BTNF	42N 42N 42N	112W 113W 113W	7,18,19 10,11,14 15	4/21-23/1977 Spring 1978 Spring 1980	466 26 24	NE-S-NW	2,286-2,560
Breakneck Ridge	BTNF	42N	112W	25,26,35	8/29/1974	366	NE-S-NW	2,377-2,590
Dry Cottonwood[d]	BTNF	42N 42N	112W 111W	23,24,27,30 30	Spring 1978, 1979, 1980	226	NE-S-NW	2,377-2,652
Dry Dallas[e]	BTNF	42N	112W	15,16,17,20, 21,22,23	Spring 1978, 1979, 1980	340	NE-S-NW	2,317-2,621
Elk Refuge	NER	42N	115W	20	8/1973	16	W-N	2,134-2,164

[a] BTNF = Bridger Teton National Forest and NER = National Elk Refuge.
[b] Total area burned including sagebrush-grasslands.
[c] Includes the area between Lightning and Dry Dallas Creeks.
[d] Includes the area between Dry Cottonwood and Cottonwood Creeks.
[e] Includes the area between Dry Dallas and Dry Cottonwood Creeks.

stands immediately adjacent to each burn to determine if they had regenerated. An unburned stand was recorded as having regeneration if and only if the number of aspen stems >2 m tall but ≤5 cm d.b.h. (diameter at breast height) were equal to or greater than the number of trees in the largest d.b.h. size class (Kay 1985).

Next, 20% of the aspen stands within each burn were randomly selected for more detailed measurement, except at Russold Hill and the Elk Refuge where all burned aspen stands were measured (Kay 1990). At Burro Hill, Russold Hill, Coal Mine Draw, and the Elk Refuge, 20% of adjacent, unburned aspen stands were also randomly selected for measurement. At each randomly selected stand, a 2 x 30 m belt transect was used to record aspen stem numbers by various size classes: <2 m tall, >2 m but <5 cm d.b.h., 6-10 cm d.b.h., 11-20 cm d.b.h., and >20 cm d.b.h. Data were also collected on aspect, elevation, slope, and burn intensity. Based on aerial counts and other data, the Wyoming Game and Fish Department provided estimates of long-term winter and summer elk use for all burn areas. Elk use was ranked as none, low, moderate, or high (Kay 1990).

Results

At each burn site in Jackson Hole (table 1), I first visually scanned each aspen stand to estimate whether the stands had successfully regenerated. Visual regeneration estimates were then checked by measuring 111 burned and 28 unburned stands. In all instances, the 139 stands were correctly classified by the visual estimation technique. On Yellowstone's northern range, 268 out of 268 unburned stands (a 20% random sample of 1,342 stands) were correctly classified by the same method (Kay 1990:124). Thus, this technique appears to be accurate for the purposes of this study.

In Jackson Hole, I visually evaluated 467 burned aspen stands and 495 adjacent unburned stands for the presence of regeneration >2 m tall (table 2). The proportion of burned aspen stands with regeneration >2 m tall varied from 0 to 100%, while the rate in unburned stands ranged from 8 to 98% (table 2). In general, the areas with the highest regeneration rates had the lowest levels of elk use, especially winter use. Some burned areas had higher regeneration rates than their unburned counterparts while the reverse was true

Table 2—Proportion of aspen stands with regeneration >2 m tall in burned and adjacent unburned areas, Jackson Hole, Wyoming.

	Stands visually evaluated				Measured stands					
	Number		Percent of stands with regeneration >2 m tall		Number		Percent of stands with regeneration >2 m tall		Level of elk use[a]	
Area	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Winter	Summer
Burro Hill	71	50	100	98	14	10	100	100	Low	Low
Russold Hill	19	26	68	38	19	5	68	40	Low-high	None
Coal Mine Draw	51	58	27	38	10	11	40	45	Low-moderate	Moderate
Lightning Creek	98	62	48	16	20	—	50	—	Moderate-high	None
Breakneck	80	48[b]	5	19	16	—	0	—	High	None
Dry Cottonwood	54	48[b]	13	19	10	—	10	—	High	None
Dry Dallas	90	186	17	19	18	—	22	—	High	None
Elk Refuge	4	65	0	8	4	2	0	0	High	Moderate
Totals	467	495			111	28				

[a] Unpublished data in Wyoming Department of Game and Fish files, Jackson, WY, and personal communication, Garvice Roby, Wyoming Game and Fish. A few moose also utilize these areas in winter and summer. Mule deer are rare.

[b] The unburned stands in these two areas are the same because Breakneck Ridge is located between Dry Cottonwood and Cottonwood Creeks.

in other areas (table 2). Only where elk use was low at Burro Hill did all burned aspen stands successfully regenerate, but then, all the adjacent undisturbed stands had also successfully regenerated (table 2).

Variation in regeneration rates was related to aspect. In both burned and unburned areas, aspen stands with a northeast aspect were more likely to have regeneration >2 m tall than stands with other aspects (table 3). The prevailing southwest winds drift snow onto northeast aspects, which apparently limits ungulate use on those sites (Kay 1990). When aspect is taken into consideration, there was no significant difference between burned and unburned stands in their ability to produce regeneration >2 m tall (table 3).

The aspen burns in Jackson Hole with the lowest levels of elk use also had the highest densities of regenerated stems >2 m tall (table 4). All stands apparently had sufficient initial sucker growth after burning (Bartos and Mueggler 1979, 1981), and many still had large numbers of stems <2 m tall (table 4). Repeated elk browsing, however, prevents those stems from growing >1 m tall. One stand in Coal Mine Draw had initial post-fire sucker densities >100,000 per ha (Bartos and Mueggler 1979, 1981), while 11 years later it still had stem densities >50,000 per ha, but they were all <1 m tall. On Breakneck Ridge, none of the burned aspen stands had been able to produce any stems >2 m tall (table 4). Aspen stands in the Breakneck Ridge burn also had low densities of stems <1 m tall. I was unable to locate live aspen stems in several of those stands. Apparently, burning plus repeated elk use has led to the elimination of some clones.

The Russold Hill burn extends from the Gros Ventre road (USFS 015) upslope to the north. Thus, burned and unburned aspen stands are located at varying distances from the road. This road is not plowed during winter but is open to snow machine use, which in recent years has increased 300-400% (Kay 1990:130). For unburned stands near the road, 90% produced regeneration >2 m tall, while at distances >800 m from the road, no stands successfully regenerated (table 5). This same pattern occurred in burned aspen stands. Those nearest the road had over 11,000 stems per ha >2 m tall, but that dropped to only 595 stems per ha at distances >800 m from the road (table 5). This pattern cannot be attributed to site or climatic differences since the stands

Table 3—The effect of aspect on the ability of burned and unburned aspen stands to produce regeneration >2 m tall in the Gros Ventre Valley, Jackson Hole, Wyoming.

	Percent of stands with regeneration >2 m[a]	
Aspect	**Burned**	**Unburned**
	(n = 323)	*(n = 302)*
N	5	0
NE	56	59
E	7	11
SE	14	15
S	4	2
SW	5	2
W	0	0
NW	8	11

$\chi^2 = 4.95$, $df = 4$, $p > 0.25$

[a] Based on visual evaluations of each stand (table 1).

Table 4—Aspen regeneration in burned and adjacent unburned areas in Jackson Hole, Wyoming.

Area	Number of stands	Number of stems <2 m per ha		Number of stems >2 m but <5 cm d.b.h. per ha		Level of elk use	
		Mean	SEM	Mean	SEM	Winter	Summer
Burro Hill							
Burned	14	1,512	228	13,727	1,115	Low	Low
Unburned	10	2,584	584	4,917	816		
Russold Hill							
Burned	19	4,571	959	5,089	1,822	Low-High	None
Unburned	5	4,101	1,440	3,234	2,142		
Coal Mine Draw							
Burned	10	7,085	2,677	5,201	2,617	Low-moderate	Moderate
Unburned	11	1,515	434	3,758	1,556		
Lightning Creek							
Burned	20	8,335	1,572	3,051	1,030	Moderate-high	None
Breakneck Ridge							
Burned	16	1,125	424	0	0	High	None
Dry Cottonwood							
Burned	10	6,601	2,167	1,317	1,317	High	None
Dry Dallas							
Burned	18	5,066	1,718	2,917	1,587	High	None
Elk Refuge							
Burned	4	3,209	1,667	0	0	High	Moderate
Unburned	2	3,334	2,000	0	0		

farthest from the road are at increasing elevation and if anything, receive more precipitation. Apparently, human disturbance limited elk use close to the road, which allowed nearby aspen stands to produce more stems >2 m tall. This is not unexpected since other studies have shown that elk avoid roads and other areas of human disturbance (Lyon 1979, 1983; Gruell 1980a:7; Edge and Marcum 1985). Gruell and Loope (1974:21) reported a similar pattern of aspen regeneration near roads in Jackson Hole.

Table 5—Aspen regeneration at various distances from the road in the Russold Hill burn, Gros Ventre Valley, Jackson Hole, Wyoming.

Stand condition	Percent of stands regenerating at three distances from road: Stands <400 m	Stands >400 m but <800 m	Stands >800 m
Unburned[a]	90% (n = 10)	25% (n = 25)	0% (n = 11)
Burned	100% (n = 7)	40% (n = 5)	57% (n = 7)
	Mean number of stems >2 m but <5 cm d.b.h. per ha		
Burned[b]	11,086	767	595

[a] Based on visual evaluation of each stand.
[b] All burned stands were measured.

Discussion

Bartos et al. (1991, 1994) reported on several of the aspen burns used in this study and concluded that "the demise of aspen was attributed to heavy ungulate use, primarily elk" (Bartos et al. 1994:79). "Suppression of [aspen] suckers is attributed mainly to heavy elk use. We question the continued use of fire to regenerate aspen stands that are subjected to heavy ungulate use. Such action could speed the elimination of aspen stands under these conditions" (Bartos et al. 1994:83).

Kay et al. (1999:6–18 to 6–22) evaluated Parks Canada's prescribed burn program in Banff National Park. As in Jackson Hole (Bartos and Mueggler 1979, 1981; Bartos et al. 1981, 1994), burning did stimulate aspen suckering, but most aspen stands still failed to produce new stems >2 m tall due to repeated ungulate browsing, again primarily by elk. "Evidence also suggests that combination of fire and continued heavy elk use may actually hasten the demise of the park's aspen communities" (Kay et al. 1999:6-21). White et al. (1998a,b) concluded that because aspen was a key indicator of ecological integrity in the Canadian Rockies, managers should not burn aspen stands if ungulate herbivory was high, unless elk populations were first returned to more natural levels (Kay 1997a,b,c,d, 1998).

It has been suggested, however, that prescribed burns have generally been too small to successfully regenerate aspen. Thus, Gruell (1980b) surmised that it may be necessary to burn large areas in a single event to keep elk and other ungulates from consuming all the fire-stimulated aspen suckers. This experiment, though, was tried in 1988 when wildfires burned approximately one-third of the aspen in Yellowstone National Park, as well as a significant portion of the entire ecosystem (Romme et al. 1995; Kay and Wagner 1996). Despite initial post-fire aspen sucker densities averaging over 120,000 per ha and first-year height growth of 2 m or more, each and every sucker in Yellowstone was repeatedly eaten to within centimeters of the ground by elk and other ungulates (Kay and Wagner 1996). In no instances were burned aspen stands in Yellowstone able to successfully regenerate due to repeated ungulate browsing (Romme et al. 1995). In fact, many burned aspen clones have been eliminated in Yellowstone National Park due to that park's unnatural concentration of wild ungulates (Kay 1998; White et al. 1998b). My other paper in this proceedings ("Long-Term Aspen Exclosures in the Yellowstone Ecosystem," Aboriginal Overkill section) explains how aspen was able to flourish in Yellowstone and throughout the Intermountain West for the last 10,000± years.

Management Implications

When this research (Kay 1990) was initially presented to the Wyoming Fish and Game Department, the agency said, "We are not even going to consider your data because if you are even close to being correct, then everything we are doing is wrong, and we are not ever going to consider that possibility" (Garvice Roby, personal communication 1989). This is similar to what Wright (1984; Kay 1992:316) experienced when he presented his archaeological work in Jackson Hole to the agencies:

> Keep in mind that I have [been] battling wildlife biologists from Grand Teton and Yellowstone Parks for some years. One told me, after a seminar I gave at the Jackson Hole Biological Research Station on the faunal resources of the regions, "Even if you demonstrate that no elk were here, we would still continue to argue for them because our management policies require a herd of at least 10,000 elk by the end of the Pinedale ice (the last deglaciation)."

The U.S. Forest Service has been no more responsive to these data than have the other agencies in Jackson Hole, despite independent confirmation of these findings by Forest Service ecologists from the Intermountain Research Station (Dale Bartos, personal communication 1995). Instead, Wyoming Game and Fish, the Forest Service, the Rocky Mountain Elk Foundation, and others continue to burn aspen in Jackson Hole and aspen repeatedly fails to regenerate (personal observation), which is unfortunate because aspen has the highest biodiversity of any forest type in the West (Kay 1997a). Unless new management philosophies are implemented, aspen will continue to decline in Jackson Hole, and eventually aspen will be eliminated from much of its historic range.

Conclusions

1. Aspen suckering is stimulated by burning.
2. Even when burned, though, most aspen stands in Jackson Hole failed to produce stems >2 m tall when ungulate use was moderate or high. There is no evidence that burned aspen stands in Jackson Hole, or elsewhere, will regenerate successfully despite intense browsing as claimed by some.
3. Evidence also suggests that a combination of fire and continued heavy elk use will eventually eliminate most aspen clones.
4. Fire cannot be used to restore aspen communities unless ungulate herbivory is low.
5. As explained elsewhere (Kay, this proceedings), disturbance is not necessary to regenerate aspen stands. Instead, most aspen stands will regenerate without disturbance if ungulate use is low.
6. Thus, controlling ungulate use is paramount if burned or unburned aspen stands are to successfully regenerate and maintain their presence on the landscape, as aspen clones have done for thousands of years (Kay 1997a).

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Long-Term Aspen Exclosures in the Yellowstone Ecosystem

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Abstract—*Aspen has been declining in the Yellowstone Ecosystem for more than 80 years. Some authors have suggested that aspen is a marginal plant community in Yellowstone and that recent climatic variation has adversely affected aspen, while others contend that excessive browsing by native ungulates is primarily responsible for aspen's widespread decline. To test these hypotheses, I measured all the long-term aspen exclosures (n = 14) in the Yellowstone Ecosystem. Aspen stands inside all exclosures successfully produced new stems greater than 2 m tall without fire or other disturbance, while few outside stands successfully regenerated due to repeated browsing. Understory species composition was also significantly different inside and outside exclosures. Protected aspen understories were dominated by tall, palatable shrubs and forbs, while grazed understories were dominated by exotic grasses and unpalatable, low-growing forbs. None of the enclosed aspen exhibited any signs of physiological stress, even on dry south-facing hillsides, an indication that climatic variation has not adversely impacted aspen. Instead, exclosure data suggest that aspen has declined throughout the Yellowstone Ecosystem due to repeated browsing by native ungulates, primarily elk.*

Introduction

After Yellowstone was designated as the world's first national park in 1872, a succession of civilian (1872–1886), military (1886–1916), and National Park Service (1916–present) administrators concluded that there were not enough game animals; so they fed wintering elk (*Cervus elaphus*) and other ungulates, and they killed predatory animals such as wolves (*Canis lupus*) and mountain lions (*Felis concolor*). During the 1920s, however, concerns grew that too many elk were overgrazing the park's northern winter range, so the agency began trapping and transplanting elk to areas outside the park. Because trapping alone did not reduce the herd to the range's estimated carrying capacity, rangers began shooting elk in the park to prevent resource damage. This program was called direct reduction, and by 1967 the Park Service had killed over 13,500 elk from Yellowstone's northern herd (Houston 1982).

This upset many people who exerted political pressure to stop the Park Service from shooting elk in the park. After a U.S. Senate (1967) Subcommittee hearing at which the chairman threatened to terminate park funding, the Park Service agreed to abandon its direct reduction program—although the agency still contended that Yellowstone was seriously overgrazed. By 1968, the Park Service had switched to a management program called "natural control" which was changed to "natural regulation" during the early 1970s. These changes occurred without public review or comment (Chase 1986; Wagner et al. 1995). The Park Service originally based "natural regulation" on a presumed "balance-of-nature," but more recently the agency has cited Caughley's (1976) plant-herbivore model to support its "natural regulation" paradigm (Kay 1990).

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Under "natural regulation," the Park Service completely revised its interpretation of the history and ecology of elk in Yellowstone.

Until 1968, Park Service officials contended that an unnaturally large elk population, which had built up in Yellowstone during the late 1800s and early 1900s, had severely damaged the park's northern winter range, including aspen (*Populus tremuloides*) communities. However, agency biologists now hypothesize that elk and other ungulates in Yellowstone are "naturally regulated," being resource (food) limited, and that the condition of the ecosystem today is much like it was at park formation (Houston 1982; Despain et al. 1986). Elk influences on Yellowstone's vegetation are now thought to be "natural" and to represent the "pristine" condition of the park. According to the Park Service, Yellowstone is not now nor has it ever been overgrazed, and all previous studies to that effect are wrong (Houston 1982).

There are several tenets to the "natural regulation" paradigm (Wagner et al. 1995). First, under "natural regulation," predation is an assisting but nonessential adjunct to the regulation of ungulate populations. If wolves are present, they take only the ungulates slated to die from other causes, such as starvation, and hence predation will not lower ungulate numbers. In the ongoing reintroduction of wolves to Yellowstone, the Park Service has denied that wolves are needed to control the park's elk herds or that wolves will have any significant impact on elk numbers (Boyce 1992). Second, if ungulates and vegetation have coevolved for a long period of time and if they occupy an ecologically complete habitat, the ungulates cannot cause retrogressive plant succession or range damage. The ungulates and vegetation will reach an equilibrium, termed ecological carrying capacity, where continued grazing will not change plant species composition or the physical appearance of plant communities. According to the Park Service, thousands of elk starving to death during winter is natural. Third, at equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means that competition by elk has not reduced the numbers of other ungulates or beaver (*Castor canadensis*) since park formation.

The Park Service's "natural regulation experiment" (cf. Despain et al. 1986) is predicated on the assumption that large numbers of elk (12,000–15,000) wintered on Yellowstone's northern range for the last several thousand years. Park Service biologists hypothesize that elk, vegetation, and other herbivores have been in equilibrium for that period of time (Houston 1982; Despain et al. 1986). The agency now believes that any changes in plant communities since the park was established are due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. Park Service biologists contend that (1) aspen is a seral species in Yellowstone, which in the course of plant succession is replaced by conifers or other vegetation, (2) burned aspen stands will regenerate despite heavy utilization by elk and other ungulates, (3) Yellowstone is marginal habitat for aspen and that recent climatic variation has adversely effected aspen, and (4) elk have not been primarily responsible for the changes that have occurred in the park's aspen communities (Houston 1982; Despain et al. 1986).

The Gallatin is located in the northwest corner of Yellowstone Park and historically has had an elk problem and reinterpretation similar to that on the northern range (Lovaas 1970; Kay 1990). Jackson Hole is situated to the south of Yellowstone Park, and it too has had a long-standing elk situation (Anderson 1958; Beetle 1974, 1979; Boyce 1989). At first, it was thought that (1) Jackson Hole was not a historic elk winter range, (2) European settlement forced elk to winter in the valley, and (3) supplemental feeding permitted the growth of an abnormally large elk herd, which (4) caused substantial damage to the winter range and a marked decline of aspen (Preble 1911; Murie 1951; Anderson 1958; Krebill 1972; Beetle 1974, 1979). However, federal and state biologists now believe that (1) large numbers of elk have wintered in Jackson Hole for the last several thousand years; (2) feedlots have only replaced winter range lost to modern development; (3) therefore, today's elk population is not unnaturally high, though the distribution of wintering animals may have changed; (4) serious elk-induced range damage has not occurred (Cole 1969; Gruell 1979; Boyce 1989); and (5) the elk herd would "naturally regulate" if sport hunting were terminated (Boyce 1989). Under this interpretation, aspen is thought to be a seral species maintained by fire, and human suppression of lightning fires is believed to be primarily responsible for the observed declined in aspen, not ungulate browsing (Loope and Gruell 1973; Gruell and Loope 1974). Based on repeat photographs, aspen has declined by as much as 95% throughout the Yellowstone Ecosystem since the late 1800s (Gruell 1980a,b; Houston 1982; Kay 1990; Kay and Wagner 1994).

As part of a larger project to test these competing hypotheses and to determine why aspen has declined in Yellowstone (Kay 1990), I measured all the long-term aspen exclosures throughout that ecosystem, because exclosures can be used to study the successional status and trend of plant communities, as well as to evaluate the impact of grazing (Laycock 1975). Exclosures can also be used to evaluate climatic effects since the general climate is the same within the exclosures and on adjacent outside plots. I then analyzed those data to determine whether the aspen stands were seral or climax, whether climatic variation was important in aspen ecology, and what impact ungulate grazing has had on aspen communities. Livestock use does not occur, or is minimal, around the aspen exclosures in the Yellowstone Ecosystem, and all exclosures are situated on big-game winter ranges where elk are the most abundant ungulate.

In addition, to measuring all the aspen-containing exclosures in the Yellowstone Ecosystem, I randomly sampled aspen stands over large areas both inside and outside Yellowstone Park. I also compiled 101 repeat photosets of aspen communities dating to the 1870s, and I evaluated 467 burned and 495 adjacent unburned aspen stands in Jackson Hole. After Yellowstone's 1988 wildfires, I established 865 permanent plots in burned aspen stands. Since those data have been reported elsewhere (Kay 1990, this proceedings), they are here incorporated by reference.

Methods

I first searched agency files to obtain all existing information on each exclosure. Care was taken to locate all prior vegetation data, any written description of permanent vegetation sampling schemes, and any old photographs (Kay 1990). The locations, dates of establishment, and sizes of the aspen exclosures found in the Yellowstone Ecosystem are presented in table 1. At most exclosures, I used multiple 2- x 30-m belt transects to measure aspen stem dynamics on inside and outside plots. To facilitate data collection, I subdivided each 30-m transect into 3-m segments and recorded the number of aspen stems by five size classes within each 3-m segment: (1) <2 m tall, (2) >2 m tall but <5 cm d.b.h. (diameter at breast height), (3) 6–10 cm d.b.h., (4) 11–20 cm d.b.h., and (5) >20 cm d.b.h. I also recorded the number, size, and species of all conifers in each transect. In addition, I visually estimated the percent conifer canopy cover in each stand according to procedures established by Mueggler

Table 1—Location and description of aspen exclosures in the Yellowstone Ecosystem.

Winter range exclosure	Area[a]	Location[b] T	R	S	Date established	Size	Elevation	Aspect
						ha	*m*	
Northern Yellowstone								
1. Mammoth	YNP	—	—	—	1957	2.116	1,902	N
2. Junction Butte	YNP	—	—	—	1962	2.116	1,890	NW
3. Lamar-East	YNP	—	—	—	1957	2.116	2,027	S
4. Lamar-West	YNP	—	—	—	1962	2.116	2,027	S
5. Range Plot 10	YNP	—	—	—	1934	0.004	1,881	E
6. Range Plot 25	YNP	—	—	—	1936	0.004	1,951	NW
Jackson Hole								
7. East Elk Refuge	BTNF	41N	114W	3	1952	0.110	2,057	SW
8. Upper Slide Lake	BTNF	42N	112W	20	1960	152.376	2,317	S
9. Goosewing	BTNF	41N	112W	3	1942	0.819	2,271	N
10. Uhl Hill	GTNP	44N	114W	1	1963	0.364	2,112	S
Gallatin								
11. Porcupine	GNF	7S	4E	16	1945	1.866	1,920	SE
12. Crown Butte	GNF	9S	5E	7/8	1945	2.066	2,210	S
13. Range Plot 16	YNP	—	—	—	1935	0.004	2,195	W
Pinedale								
14. Soda Lake[c]	BTNF	34N	109W	23	1964	0.431	2,332	S

[a] YNP—Yellowstone Naitonal Park, GNF—Gallatin National Forest, BTNF—Bridger-Teton National Forest, and GTNP—Grand Teton National Park.

[b] Yellowstone Park has not been surveyed.

[c] Located in the Green River drainage to the east of Jackson Hole but within the Yellowstone Ecosystem. Exclosure is behind the Soda Lake elk feedground and was included to maximize sample size.

(1988). Inside the smaller exclosures—Range Plots 10, 16, and 25; East Elk Refuge; and Elk Ranch Reservoir—I made complete counts of all aspen and conifers, as well as on comparable outside areas. Following Mueggler (1988), I estimated understory species composition of shrubs, grasses, and forbs on all inside and outside plots. Finally, I rephotographed all previously established photo sites.

Results

Repeat Photographs

Based on the photosets that were examined (figures 1–3), all enclosed aspen successfully regenerated into multisize-class stands. Aspen did not produce new stems >2 m tall in any of the unprotected stands except at Goosewing and Soda Lake. Aspen outside the exclosures experienced continued mortality and all of the mature trees outside several exclosures had died, including Range Plot 10, Junction Butte, and Lamar-East. Based on the presence of dead, standing trees, all mature aspen outside the Uhl Hill exclosure had also recently died. Aspen clones within all exclosures increased in area, and many expanded into and replaced sagebrush-grasslands within the exclosures (figure 3). Within most exclosures, there was a substantial increase in understory shrubs, but conifers had not encroached upon most of the inside or outside aspen communities.

Aspen Stem Dynamics

Aspen stands inside Yellowstone exclosures (table 2) had a significantly different size-class stem distribution than aspen outside the exclosures ($p < 0.001$, Hotelling's T^2 test) (Kendall 1980). At all but one, East Elk Refuge, there were

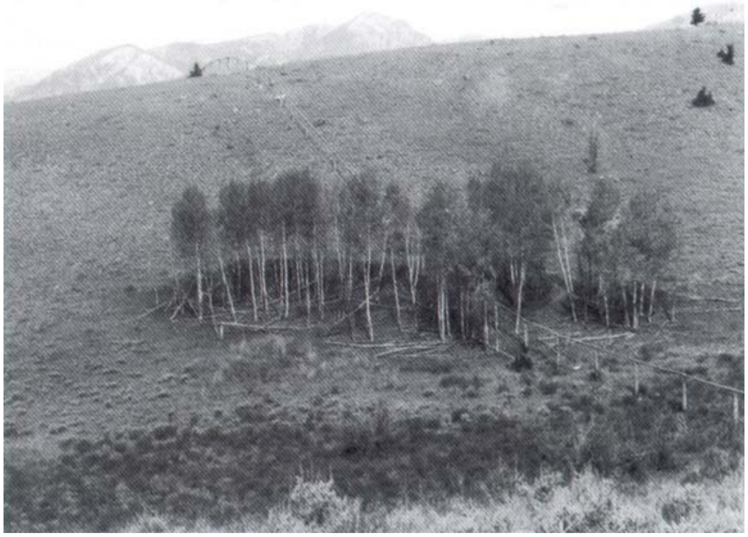
Figure 1—Aspen belt transect outside Yellowstone Park's Junction Butte exclosure in 1962 (top) and 1986 (bottom). The two steel posts mark the north end of the belt transect. Exclosure fence is on the right. Four mature aspen were alive outside the exclosure in 1962, the year this exclosure was built, but all had died by 1986. NPS photo 62-548, 9/18/62. Charles Kay photo 58, 9/82-12, 7/25/86.

more stems <2 m tall per unit area outside than inside. This was not unexpected since larger aspen often suppress new suckers (Schier et al. 1985). All stands protected from ungulate browsing successfully regenerated and produced stems >2 m tall without fire or other disturbance, and most developed multiple size-classed stems characteristic of stable or climax aspen (Mueggler 1988). In only two instances, Goosewing and Soda Lake, did aspen outside exclosures produce ramets >2 m tall. In those cases, however, there were significantly greater stem densities (>2 m tall but <20 cm d.b.h.) inside the exclosures (table 2).

Figure 2—Aspen belt transect inside Yellowstone Park's Junction Butte exclosure in 1962 (top) and 1986 (bottom). Exclosure fence is to the top of the 1962 photo, and the two steel posts mark the west end of the belt transect. NPS photo 62-547, 9/20/62. Charles Kay photo 58, 982-17, 7/25/86.

Conifer Invasion

There were few conifers inside or outside Yellowstone aspen exclosures (table 2). This may be because most exclosures were built on winter range sites where conifers are less common than at higher elevations. A significant proportion of aspen communities throughout the Yellowstone Ecosystem, though, have not been invaded by conifers, including aspen stands immediately adjacent to coniferous forests (Kay 1990).



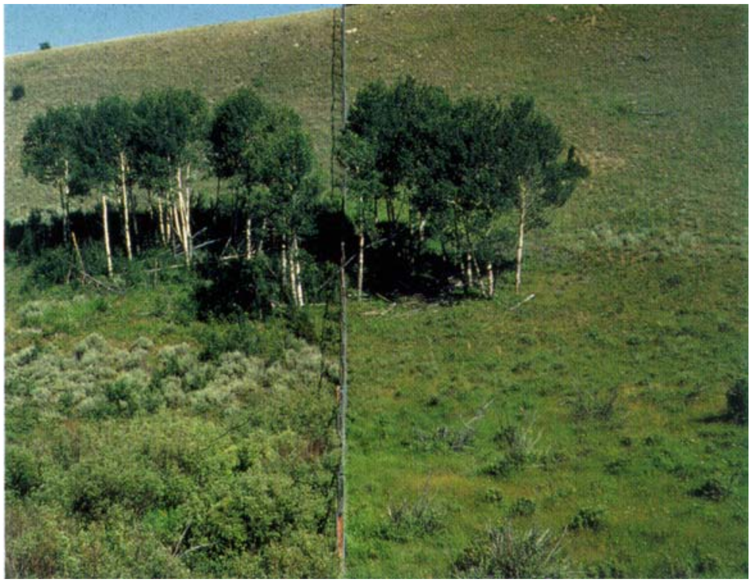


Figure 3—Porcupine Creek exclosure on the Gallatin National Forest. Top: The exclosure was built in 1945, and this photograph was taken 1 year later in 1946. Note that the exclosure fence bisects a single aspen clone. U.S. Forest Service photo. Middle: By 1963, willows in the foreground had increased dramatically in height and canopy cover, but the enclosed aspen showed little apparent change. Photo taken in July by James Peek. Bottom: By 1987, however, aspen inside the exclosure had increased markedly and replaced sagebrush and grasslands on this dry, southeast-facing hillside. Photo taken on August 26 by Charles E. Kay.

Table 2—Aspen stem densities and estimated conifer canopy cover inside and outside 14 Yellowstone exclosures.

Exclosure[a]	Area sampled	Mean number of live stems per m^2 by size classes					Estimate conifer canopy cover
		<2 m	>2 m – ≤5 cm	6–10 cm	11–20 cm	>20 cm	
	m^2	*number per m^2*					*percent*
1. Mammoth							
Inside	106	0.15	0.16	0.35	0.02	0.00	<5
Outside	106	3.40	0.00	0.00	0.00	0.07	>5
2. Junction Butte							
Inside	95	0.11	0.26	0.49	0.15	0.00	None
Outside	95	0.49	0.00	0.00	0.00	0.00	None
3. Lamar-East							
Inside	106	0.63	0.37	0.27	0.06	0.00	<1
Outside	106	1.91	0.00	0.00	0.01	0.04	None
4. Lamar-West							
Inside	106	0.12	0.29	0.09	0.00	0.00	None
Outside	60	1.63	0.00	0.00	0.00	0.03	None
5. Range Plot 10							
Inside	41	0.00	0.51	0.12	0.34	0.00	None
Outside	41	1.90	0.00	0.00	0.00	0.00	None
6. Range Plot 25							
Inside	45	0.70	0.36	0.36	0.34	0.38	None
Outside	22	3.00	0.00	0.00	0.13	0.00	None
7. East Elk Refuge							
Inside	1,100	2.30	0.05	0.03	0.03	0.01	None
Outside	60	1.28	0.00	0.00	0.10	0.00	None
8. Upper Slide Lake							
Inside	93	0.40	0.20	0.09	0.00	0.01	>50
Outside	93	1.45	0.00	0.00	0.00	0.00	None
9. Goosewing							
Inside	360	0.66	0.94	0.37	0.10	0.05	<2
Outside	360	1.51	0.44	0.00	0.02	0.04	<2
10. Uhl Hill							
Inside	218	0.06	0.09	0.09	0.00	0.00	<1
Outside	180	0.09	0.00	0.00	0.00	0.00	None
11. Porcupine							
Inside	180	0.44	1.12	0.58	0.07	0.03	<1
Outside	180	1.80	0.00	0.00	0.00	0.02	None
12. Crown Butte							
Inside	180	0.07	0.47	0.19	0.13	0.03	<1
Outside	300	0.93	0.00	0.00	0.00	0.03	<5
13. Range Plot 16							
Inside	37	0.16	0.35	0.30	0.05	0.00	>15
Outside	37	1.05	0.00	0.00	0.00	0.00	None
14. Soda Lake							
Inside	180	0.09	0.52	0.27	0.05	0.02	None
Outside	300	0.89	0.03	0.03	0.04	0.01	None
Total (n = 14)							
Inside		0.48	0.41	0.26	0.10	0.04	
Outside		1.52	0.03	0.002	0.02	0.02	
t		4.52	4.22	6.45	2.45	0.70	
p		<0.01	<0.01	<0.01	<0.05	NS	
Total (n = 12)[b]							
Inside		0.43	0.35	0.25	0.10	0.04	
Outside		1.58	0.00	0.00	0.02	0.02	
t		3.37	4.17	4.63	2.10	0.59	
p		<0.01	<0.01	<0.01	<0.10	NS	

[a] Exclosure numbers correspond to those given in table 1.
[b] Not including Goosewing and Soda Lake.

Understory Species Composition

At all exclosures, there were major differences in understory species composition between inside and outside plots (table 3). These differences were especially pronounced at exclosures where the inside and outside plots were located within the same aspen clone. This included Range Plots 10, 16, and 25, Junction Butte, Porcupine, Uhl Hill, Soda Lake, and Goosewing. The vegetation inside and outside these exclosures often keyed as entirely different aspen community types (Kay 1990) according to the classification developed by Youngblood and Mueggler (1981).

On average, shrubs predominated inside exclosures, although forbs and a few grasses were present. In areas exposed to elk and other ungulates, though, there were substantially fewer shrubs and the sites were dominated by grasses (table 3). A large proportion of those grasses were nonnative species, such as timothy (*Phleum pratense*) or Kentucky bluegrass (*Poa pratensis*), which increase under grazing pressure (Mueggler 1988). In Yellowstone Park, timothy and Kentucky bluegrass had an average canopy coverage of 56% outside exclosures and 19% inside ($t = 3.47$, $p < 0.01$, arcsine transformed data).

While the difference between average percentage of forbs inside and outside Yellowstone exclosures was not statistically significant (table 3), there were major differences in species composition. Forbs that tend to decrease under grazing or trampling such as *Epilobium augustifolium*, *Thalictrum fendleri*, and *Smilacina stellata* averaged 14.9% canopy coverage inside exclosures and 3.0% outside ($t = 2.70$, $p < 0.02$, arcsine transformed data). Forbs more immune to grazing like Geranium spp. and *Fragaria virginiana* averaged 8.2% canopy coverage inside exclosures and 17.2% outside ($t = 2.50$, $p < 0.02$, arcsine transformed data). Thus, aspen understories inside exclosures were dominated by species associated with climax communities, while on adjacent outside plots, understories were dominated by species characteristic of grazing disclimaxes (Mueggler 1988).

Discussion

Other Aspen Exclosure Studies

Mueggler and Bartos (1977) reported that shrubs increased inside two, three-part aspen exclosures in southern Utah where mule deer (*Odocoileus hemionus*) and cattle were the primary ungulate herbivores. They (p. 13) concluded that "the most striking difference in understory attributable to animal use was the great reduction in total shrubs.... After 41 years, the ungrazed area at Grindstone Flat produced almost 10 times more shrubs than the area grazed by both cattle and deer and over three times more than that grazed just by deer.

Table 3—Mean canopy coverage of understory plants inside and outside 14 aspen exclosures in the Yellowstone Ecosystem.

Vegetation class	Mean percent canopy coverage Inside	Mean percent canopy coverage Outside	t[a]	p
Shrubs	68	22	3.78	<0.01
Forbs	25	29	0.50	NS
Grasses	15	48	4.06	<0.01

[a] Arcsine transformed data.

The graminoids increased under grazing at Grindstone Flat.” Aspen protected from all grazing developed multisize-class stands while those outside did not.

Coles (1965:38–41) measured the age structure of aspen communities inside and outside a three-part exclosure in central Utah. Where all ungulates were excluded, aspen were multiaged. Where cattle were excluded but mule deer were not, few new stems had grown taller than 2 m. While in South Dakota’s Custer State Park, aspen expanded into and replaced grassland inside an exclosure within 2 years following exclusion of grazing (Hoffman and Alexander 1987:15). At South Dakota’s Wind Cave National Park, aspen inside an exclosure developed into a multisize-class stand while those subject to ungulate grazing did not (Kay 1990:115). Similarly, Hurlburt and Bedunah (1996:23) measured three-part aspen-containing exclosures in north-central Montana and reported that “grazing solely by wild ungulates dramatically influenced…aspen communities” as elk and deer use tended to eliminate aspen and understory shrubs.

Trottier and Fehr (1982:28–33) reported on an aspen exclosure in Canada’s Banff National Park where elk are the most abundant ungulate. They (p. 28) noted that “browsing by elk in this area has a tremendous influence on shrub and tree regeneration in the aspen forest.” The protected plot had greater shrub density and a more diverse height class distribution than the browsed plot. “About 97% of the shrubs in the browsed plots were less than 100 cm high and there were no plants taller than 150 cm” (p. 30). Trottier and Fehr (1982:30) concluded that aspen regeneration was limited by ungulate browsing: “Under protection there were plants [aspen] in all height classes indicating that growth to tree stage was proceeding. On the browsed plot all plants were less than 100 cm.”

When Banff’s aspen exclosure was erected in 1944, two photopoints were established, one inside the protected area and another immediately outside. Retakes 50 years later showed that a dense multiaged aspen stand had grown up inside the exclosure, while no aspen stems had successfully regenerated on outside plots (Kay et al. 1999). Kay et al. (1999) also reported on aspen that had been protected for approximately 10 years within the game-proof fenced Trans Canada Highway right-of-way through Banff’s lower Bow Valley. Where elk were excluded, aspen had successfully regenerated, while there was no response on grazed plots.

Milner (1977) measured aspen communities inside and outside four exclosures in Canada’s Elk Island National Park where elk and moose (*Alces alces*) are the primary ungulates. Inside each exclosure, aspen “attained a greater basal area, height and d.b.h. class” than on outside plots (p. 52). Moreover, “regeneration of the tree structure was restricted in unprotected areas…[and] shrub height and diameter class were greater in the exclosures” (p. 52–53). Highly palatable shrubs increased significantly inside the exclosures. That is to say, ungulate browsing prevented aspen regeneration and favored grasses over shrubs.

Gysel (1960), Olmsted (1977), Stevens (1980), and Baker et al. (1997) reported on aspen exclosures in Colorado’s Rocky Mountain National Park where elk and mule deer are the most common ungulates. Inside three out of four exclosures, aspen developed into multisize-class stands while those outside did not. In the fourth, aspen was completely replaced by conifers, but conifers did not establish in the other exclosures (Olmsted 1977:27). Inside the three exclosures, aspen spread into and replaced grasslands while outside, grazing changed aspen communities into grasslands (Gysel 1960; Stevens 1980; Baker et al. 1997). Shrubs were more common inside the exclosures than out (Stevens 1980). A temporary reduction of elk numbers in that park allowed some aspen stems to escape browsing and to grow into larger size classes (Olmsted 1977, 1979; White et al. 1998).

Harniss and Bartos (1990) and Bartos and Harniss (1990) reported on an exclosure in eastern Utah where the mature aspen trees had been killed by herbicide to stimulate resprouting. "Where livestock were excluded, aspen were essentially eliminated from the site by deer and elk" (Harniss and Bartos 1990:37). While in Arizona, treated aspen had to be protected by game-proof fencing, and when the fencing was removed from a 6.5-ha aspen stand that had produced 50,000 stems per ha more than 3 m tall, the regenerated aspen were severely damaged by elk (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999).

More recently, Kay and Bartos (2000) measured all known aspen exclosures on the Dixie and Fishlake National Forests in south-central Utah. Five of the exclosures were of a three-part design with a total-exclusion portion, a livestock-exclusion portion, and combined-use portion that permitted the effects of mule deer and elk herbivory to be measured separately from those of livestock. Aspen within all total-exclusion plots successfully regenerated and developed multiaged stems without the influence of fire or other disturbance. Aspen subjected to browsing by wildlife, primarily mule deer, either failed to regenerate successfully or regenerated at stem densities significantly lower than that on total-exclusion plots. On combined wildlife-livestock-use plots, most aspen failed to regenerate successfully, or did so at low stem densities. Aspen successfully regenerated on ungulate-use plots only when deer numbers were low. Similarly, ungulate herbivory had significant effects on understory species composition. In general, utilization by deer tended to reduce shrubs and tall palatable forbs while favoring the growth of various grasses. There was no evidence that climate variation affected aspen regeneration. Instead, observed differences were attributed to varied histories of ungulate herbivory.

Thus, aspen exclosure studies throughout the Western United States and Canada support the results reported here—namely, that native ungulate use can have a significant effect on aspen regeneration and understory species composition. Moreover, aspen stands dominated by old-age or single-age aspen, which are common in the Yellowstone Ecosystem and across the West (Mueggler 1989, 1994), are not a biological attribute of aspen, but an artifact of excessive ungulate browsing.

Climate Change

The decline of aspen on Yellowstone's northern range has been attributed by some to climatic change and especially the drought during the 1930s (Houston 1982). That supposition, though, is not sustained because newly enclosed aspen in Range Plots 10, 16, and 25 grew vigorously during and after the 1930s drought, while aspen outside did not (Kay 1990). Similarly, if as Despain et al. (1986:109) claimed, "Yellowstone is not the center of good aspen habitat and even a slight change in climate could have significant effects on aspen here," then aspen inside exclosures should show signs of physiological stress such as stunted growth or twisted trunks. But, none of the aspen inside any exclosure in the Yellowstone Ecosystem show signs of physiological stress. Aspen 60 years old inside Range Plot 25 were approximately 20 m tall, over 20 cm d.b.h., and had straight trunks (Kay 1990:108). Furthermore, aspen stands on south-facing hillsides inside several exclosures (Lamar-East, Crown Butte, Porcupine; figure 3) had expanded and replaced grass-sagebrush, which would not have been possible if those aspen had been in physiological stress or if the climate had been limiting or marginal for aspen. It is also clear that it is not climate that prevents aspen from reaching its biological potential outside Yellowstone exclosures. Instead, repeated browsing by elk and other ungulates has kept aspen from successfully regenerating, and it is ungulate browsing that is primarily responsible for the decline of aspen throughout the Yellowstone Ecosystem.

The more profuse vegetation inside the exclosures does, itself, alter the microclimate, but that is an incorporated variable caused by the plants' response to the elimination of ungulate browsing, not the cause of the vegetation's response. Such microclimatic conditions would prevail in any aspen stand not subject to heavy ungulate use, whether in an exclosure or not. Moreover, Baker et al. (1997) and White et al. (1998) reported no correlation between climatic variation and aspen regeneration anywhere in western North America.

Aboriginal Overkill

How then was aspen able to flourish in Yellowstone and throughout the Intermountain West for the last 10,000± years? Simple: The large elk and other ungulate populations assumed under "natural regulation" (Houston 1982; Despain et al. 1986, Romme et al. 1995) did not exist until after Yellowstone was designated a national park. Historical journals, old photographs, and archaeological data all indicate that there are now more elk in Yellowstone than at any point prior to 1872 (Kay 1990, 1994, 1995a,b, 1996, 1997a,b,c,d,e, 1998; Kay and Walker 1997). Archaeologically, elk are rare to nonexistent from sites in the Yellowstone Ecosystem and throughout the Intermountain West (Kay et al. 1999). Historically, elk and other ungulates were also rare there. Between 1835 and 1876, for instance, 20 different expeditions spent 765 days in the Yellowstone Ecosystem on foot or horseback, yet reported seeing elk only once every 18 days. Today there are over 100,000 elk in that system. Similarly, bison (*Bison bison*) were only seen three times by early explorers, none of which were in the present confines of Yellowstone Park, while recently there have been as many as 4,000 bison in the park. Moreover, if elk and other ungulates were as abundant in the past as they are today, then late 1800s photographs of preferred forage species such as aspen and willows (*Salix* spp.) should show that those plants were as heavily browsed historically as they are today. But early photos of aspen and other species in Yellowstone show no evidence of ungulate browsing, unlike present conditions (Kay and Wagner 1994). Thus, there is no evidence to support the view that large numbers of elk were ever common in Yellowstone until after 1900.

Before park establishment, Yellowstone's elk population was limited at low densities by predation, primarily by Native Americans. Contrary to prevailing beliefs, Native Americans were not conservationists (Kay 1994, 1998). Because native peoples could prey-switch to small mammals, plant foods, and fish, they could take their preferred ungulate prey to low levels or extinction with little adverse effect on human populations. In fact, once Native Americans killed off most ungulates, human populations actually rose. As explained elsewhere, Native Americans were the ultimate keystone species, and their removal has completely altered ecosystems, not only in Yellowstone, but throughout North America (Kay 1994, 1995a, 1997a,b,e, 1998).

It must also be remembered that large numbers of native peoples inhabited the Yellowstone Ecosystem for the last 10,000± years (Hultkrantz 1974; Wright 1984). The claim that Native Americans seldom visited Yellowstone because they feared the park's geysers and hot springs is false—that myth was invented by early park administrators to promote tourism (Hultkrantz 1979).

Yellowstone's original inhabitants were forcefully removed ca. 1878 to reservations in Idaho and Wyoming for the same reason (Haines 1974, 1977).

Conclusions

1. Aspen stands inside all Yellowstone exclosures successfully regenerated without fire or other disturbance.
2. Aspen inside all exclosures developed multisize-classed stands characteristic of stable or climax aspen communities.
3. Few aspen stands, inside or outside exclosures, had been heavily invaded by conifers—another characteristic of stable or climax aspen.
4. Inside exclosures, aspen understories were dominated by shrubs and tall forbs characteristic of stable or climax aspen, while outside plots were dominated by nonnative grasses and unpalatable forbs representative of grazing disclimaxes.
5. Aspen stands dominated by old-age or single-age class trees are not a biological attribute of aspen, but an artifact of excessive ungulate browsing.
6. Yellowstone is not marginal habitat for aspen nor has climatic variation had any measurable effect on that ecosystem's aspen communities.
7. Instead, aspen has declined and is declining in Yellowstone Park and throughout the ecosystem due to repeated browsing by unnatural numbers of elk and other native ungulates.
8. As explained elsewhere (Kay, this proceedings), fire cannot be used to successfully regenerate aspen communities subject to high levels of ungulate herbivory. In fact, burning only hastens the demise of aspen subjected to even moderate levels of ungulate use (White et al. 1998; Kay et al 1999). Instead, the only way for aspen to maintain its historic presence in Yellowstone is to reduce ungulate herbivory to more natural levels (Kay 1998; White et al. 1998). One way to accomplish this objective would be to honor existing treaties and to allow Native Americans to hunt in Yellowstone, as they did for more than 10,000 years (Kay 1998).

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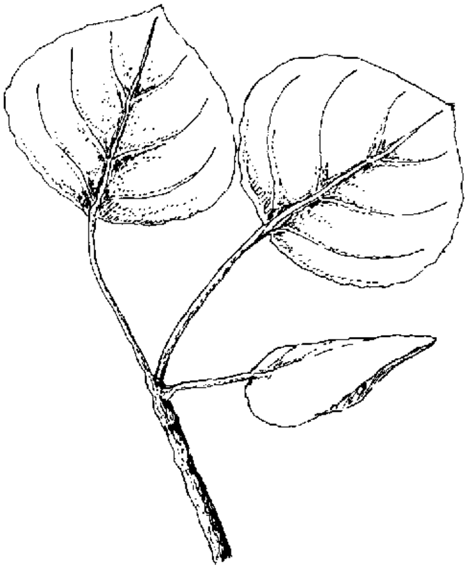

Aspen's Ecological Role in the West

Aspen's Ecological Role in the West

William H. Romme[1], Lisa Floyd-Hanna[2], David D. Hanna[2], and Elisabeth Bartlett[3]

Abstract*—Aspen exhibits a variety of ecological roles. In southern Colorado, the 1880 landscape mosaic contained a range of stand ages, of which half were >70 years old and half were younger. Pure aspen stands in southern Colorado are widespread and may result from previous short fire intervals that eliminated local conifer seed sources. Aspen regeneration in northern Yellowstone Park is controlled by ungulate browsing pressure and fire, so it has been limited since 1920. However, an episode of aspen seedling establishment occurred after the 1988 fires. We urgently need additional detailed, local case studies of aspen ecology to inform management decisions.*

Introduction

As the most widely distributed tree species in North America (Fowells 1985), quaking aspen (*Populus tremuloides*) exists within a great diversity of ecological settings and exhibits a similar diversity of ecological roles. Generalizations about aspen's ecological role are therefore difficult—and potentially dangerous. Nevertheless, several key questions about aspen ecology need to be answered to help guide our decisions about sustainable aspen management today and in the future.

In this paper we address three basic questions about the ecological role of aspen in the Rocky Mountain West. For each question, we offer more than one answer, based on several case studies that reflect the wide range of ecological settings in which aspen occurs. One important outcome of this comparative analysis is the recognition that we urgently need additional detailed, local case studies of aspen ecology. The questions are:

1. What was the range of variability that existed prior to EuroAmerican settlement in the late 1800s, with respect to aspen disturbance regimes and landscape patch dynamics?
2. What are the major factors, biotic and abiotic, that control aspen successional dynamics and responses to disturbance?
3. Do aspen's life history traits and reproductive mechanisms provide adequate resilience to impending climatic and environmental changes?

Question 1: Pre-1900 Aspen Disturbance Regimes and Landscape Patch Dynamics

Aspen disturbance regimes and landscape patch dynamics have been highly variable in both time and space. We illustrate this range of variability by examining two very different case studies. The first comes from the southern Rocky Mountains, in the western San Juan National Forest. Here aspen is the dominant cover type, creating the landscape matrix over thousands of hectares. In this area fire clearly was a major disturbance agent in the past, but ungulate

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browsing apparently was of minimal importance. The second case study is from the northern Rocky Mountains, specifically the winter ungulate range of Yellowstone National Park. Aspen stands in this area exist as relatively small patches within a matrix of other vegetation types, and both fire and ungulate browsing have been important components of the disturbance regime.

Aspen Fire History and Patch Dynamics in the San Juan National Forest

Aspen forest is a dominant cover type over extensive areas at middle elevations in the western San Juan National Forest, where individual patches of aspen forest may cover hundreds of hectares (Jones and Schier 1985; Romme et al. 1992). The most important agent of disturbance in aspen forests of the southern Rocky Mountains before 1900 was fire, although other natural disturbances were locally important including windthrow, fungal diseases, tent caterpillars and other insects, snow damage, hail, lightning, and sunscald (Jones and DeByle 1985a; Jones et al. 1985; Romme et al. 1999; Veblen 2000).

Jones and DeByle (1985b:77) observed that "... almost all even-aged aspen stands in the West appear to be the result of severe fire, whether or not the aspen type is climax on the site." Yet despite this widespread recognition of the importance of past fire in aspen forests, we have little specific information on aspen fire history in the southern Rockies. Baker (1925) studied fire scars in Ephraim Canyon in central Utah and concluded that light fires had occurred every seven to 10 years within the general region of his study area (actual extent of the study area not specified). Meineke (1929) determined that fires had occurred in every decade of the nineteenth century at the Great Basin Range Experiment Station in the Wasatch Range, Utah, but that the only severe fire was in 1867. Harniss and Harper (1982) found that the conifers were older in subalpine fir-aspen stands at higher elevations than in white fir-aspen stands at lower elevations. They suggested that this may reflect longer fire intervals at the higher elevations, but their study provided no estimates of actual fire intervals in the aspen zone. To obtain more detailed and quantitative estimates of past fire intervals and landscape dynamics within the aspen forest type, we studied fire history in an aspen-dominated landscape on the western flanks of the La Plata Mountains in the San Juan National Forest.

Methods

Reconstructing fire history is more difficult in aspen forests than in some other forest types, because aspen are easily killed by fire and few fire-scarred trees can be found with which to date past fires. Therefore, we used a less precise method of determining fire history that was based on the statistical distribution of current stand ages, i.e., the time since the last lethal fire (Johnson and Gutsell 1994). To develop this method, we began by sampling five aspen stands in 1995 within the Lime Creek burn, an area near Silverton, Colorado, where an extensive fire in 1879 was documented by written records. In two aspen stands, we removed an increment core from every stem within a circular plot at a height of about 1 meter. The cores were glued to slotted boards, air dried, sanded, and stained. The number of annual rings was counted under 20-power magnification using a dissecting microscope. Additional years were added to the estimate of stem age for cores that had missed the center of the tree, based on the radius of curvature of the innermost rings, and three years were added to the age of each stem as an estimate of the time required to grow to coring height.

The age structure of aspen stems in the 1879 Lime Creek burn was constructed from all readable cores in the two stands (about 20% of the sampled increment cores were rotten, lacking centers, or otherwise unreadable). The post-fire aspen that which resprouted after the documented 1879 burn was clearly detectable in the current age structure of the stands (figure 1). Nearly 60% of the aspen trees in our sample had established between 1880 and 1890, even though many individuals of younger age classes were present due to continued recruitment of stems into the canopy for several decades following the fire. The Lime Creek data also revealed that very few aspen trees had survived the fire in 1879, as would be expected in such a fire-sensitive species. Next, we collected increment cores only from 15–20 of the largest and oldest appearing stems in three additional stands within the Lime Creek burn area. The age structure of these stands similarly contained a prominent cohort of stems that had established within a decade after 1879, plus numerous younger stems from the 1890s–1910s (data not shown). From this preliminary analysis of current age structure in stands of known fire history, we determined that in subsequent analyses of stands with unknown fire history, we could assume that the oldest cohort of 2+ living aspen stems dating to a single decade in any stand today represents the initial postfire cohort.

Landscape-scale fire history

Once we had verified that postfire aspen cohorts could still be detected in aspen stands that burned >100 years ago, we determined fire history in a 76 km^2 area of unknown fire history at an elevation of 2,650–3,310 m in the western portion of the San Juan National Forest (Romme et al. 1999). A 1 km^2 grid was overlaid on the 7.5-minute topographic quadrangles for the study area based upon the UTM 1,000 m grid tics. A sample point was randomly chosen within each 1 km^2 grid cell such that each unit of the total study area had an equal probability of being sampled (Johnson and Gutsell 1994). The sampling sites identified on the map then were located in the field. If the sampling point appeared to have been logged, we randomly selected another point within the 1 km grid cell. At each point we collected an increment core at breast height from the 20 largest sound aspen trees. Cores were glued to boards, sanded, stained, and dated as described above.

We then summarized the ages of dominant aspen stems in each of the 76 sampled stands, and estimated the decade in which the most recent lethal fire

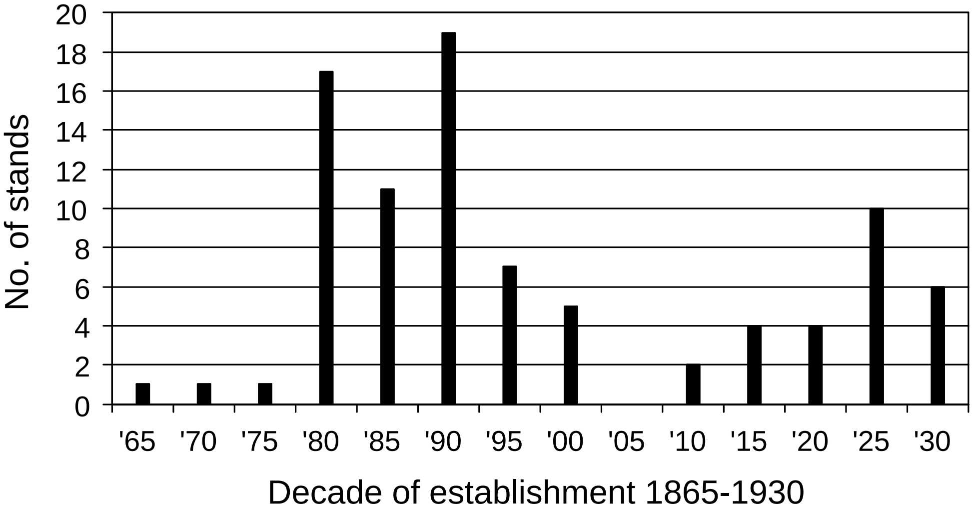

Figure 1—Age structure in 1995 of all aspen stems >5 cm d.b.h. within two aspen stands known to have originated after a lethal fire in 1879, Lime Creek burn, San Juan National Forest, Colorado.

had occurred. The oldest postfire cohort detected was from the 1760s, and we found cohorts in other stands representing fires in every decade from the 1810s through 1870s (figure 2). Twenty-seven stands did not contain any set of 2+ trees established within the same decade that was old enough to represent a postfire cohort, but these stands did contain individual old aspen trees (>150 yr). In these stands, we assumed that the stand had originated long ago and that most or all of the original postfire cohort had died through natural causes such as disease. We could not assign a precise age to these stands but called their date of origin "pre-1760s" since the oldest recognizable postfire cohort was from the 1760s. Some of these stands may have originated more recently than the 1760s and had simply lost their postfire cohort, but we think that most actually did date from before the early 1800s because of their all-aged, all-sized canopy structure. Another 19 stands contained no apparent postfire cohort but no old trees either; time since fire in these stands could not be determined and they were listed as "unknown" and deleted from the statistical analysis. See Romme et al. (1999) for additional details of sampling and determining stand ages.

Fire History and the Landscape Mosaic During the Reference Period

Table 1 summarizes the number of aspen stands that became established in each decade from the 1870s to the 1760s, as well as the number of old stands of uncertain origin date ("pre-1760s"). None of the stands that we sampled had originated later than 1880, apparently because no extensive fires occurred in our study area after this time. However, small fires have occurred elsewhere in the San Juan Mountains during the 20th century, and small patches of younger aspen stands can be found in those areas. Extensive fires occurred in our study area in the 1870s and 1860s. Fewer stands date from the early to mid 1800s, either because there were fewer or less extensive fires during that time, or because evidence of these early fires has been destroyed by the fires of the later 1800s. Approximately 45% of the sampled stands appeared to have last burned at some time prior to the early 1800s ("pre-1760s" in table 1).

What kind of a landscape mosaic existed in the aspen zone prior to the grazing, logging, and fire control efforts of the 20th century? Figure 2 summarizes the distribution of stand ages as they must have existed in the mid-1880s. These ages were determined by subtracting the decade of stand origin (table 1) from 1880. For example, the 10 stands that originated in the 1870s (table 1) would have been about 10 years old in the mid-1880s (figure 2). We determined in this way

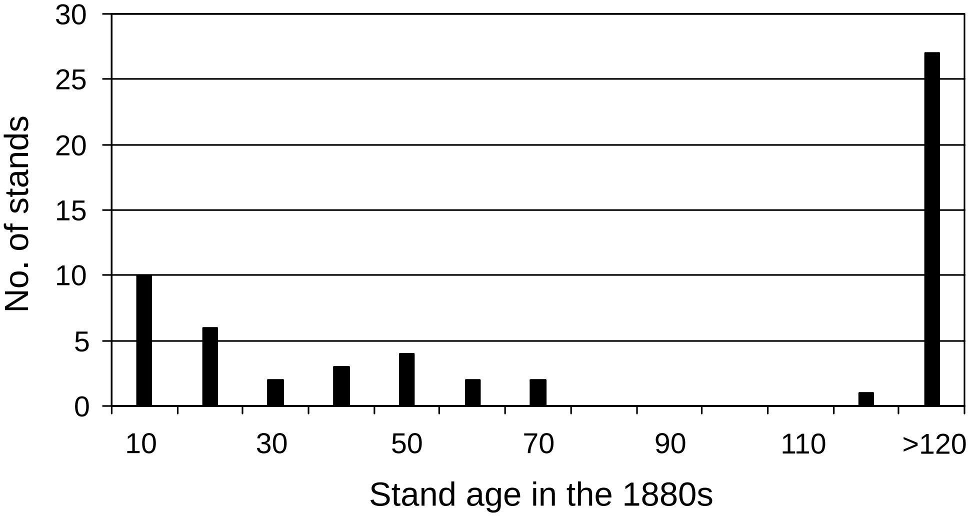

Figure 2—Distribution of stand ages in the 1880s within a 77-km^2 study area within the San Juan National Forest, Colorado, estimated by subtracting the decade of stand origin (table 1) from 1880.

Table 1—Number of stands within a 77-km^2 study area in the western San Juan National Forest, Colorado, that established after lethal fires in each decade since the 1760s.

Decade of last fire	Number of sampled aspen stands
1870s	10
1860s	6
1850s	2
1840s	3
1830s	4
1820s	2
1810s	2
1800s	0
1790s	0
1780s	0
1770s	0
1760s	1
Pre-1760s	27
Unknown	19
Total	76
Total, exc. unknown	57

that the median stand age in the 1880s was about 70 years. This means that about half of the stands in the landscape were >70 years old and half were <70 years old. If half of the landscape had burned within the previous 70 years, then it would require about twice this length of time, or 140 years, for an area equal to the entire landscape to burn. Thus, our best estimate of the fire rotation period in an aspen-dominated landscape during the period of indigenous settlement is about 140 years.

We conclude from this analysis that within this aspen dominated landscape during the period from the mid-1700s to the late 1800s, approximately half of the aspen forest consisted of relatively young stands developing after fires within the preceding 70 years, and that half of the stands had escaped fire for more than about 70 years. Fires occurred somewhere within the 76 km^2 study area nearly every decade, but it required more than a century for an area equal to the entire study area to be burned. Some stands probably were re-burned at relatively short intervals (<70 years), but many others persisted for more than a century without burning.

Caveats

Three important weakness of this fire history study should be acknowledged. First, we cannot say in which exact years fires occurred, because dating fires from postfire age cohorts is inherently less precise than dendrochronological dating based on fire-scarred trees. However, because fire scars are so rare in aspen forests, the decade-level precision that we achieved is probably about the best that can be done in aspen-dominated landscapes of the southern Rocky Mountains. A second weakness of our method is that it cannot distinguish between two or more fires within the same decade, nor can it depict actual sizes or shapes of patches created by individual fires. Finally, it is important to note that we probably detected only the relatively large fires that occurred in the past. Many smaller fires undoubtedly occurred in places between the locations of our sample points and were not detected. This may not be a serious error from the standpoint of interpreting past fire effects, however, because a few large fires probably were responsible for most of the burned area; this is the case today in boreal forest and several other types of fire-dominated landscapes (Johnson 1992; Moritz 1997; Romme et al. 1998).

It is also important to recognize that we have created a "snapshot" of the structure of the aspen forest mosaic at a single time at the very end of the period preceding extensive EuroAmerican land use changes, viz., the 1880s. We do not know just how representative this particular decade was of the period of several centuries before the 20th century. The landscape mosaic in 1880 probably was similar in its broad features to earlier mosaics, but there must have been fluctuations over time. Thus, in earlier periods, the median stand age probably was greater or less than the 70 years that we determined for the mid 1880s. Note, for example, the period in the late 1700s and early 1800s, a time when apparently few aspen stands were regenerated by fire in our study area (table 1). This was a period of reduced fire activity throughout the Southwest (Swetnam and Betancourt 1998; Swetnam et al. 1999), when the age structure of aspen forest mosaics in many areas probably shifted toward a predominance of older stands. In contrast, the middle and late 1800s was a time of greater fire frequency throughout the Southwest, when the aspen landscape mosaic may have been dominated by younger stands. Therefore, in evaluating today's age structures and developing desired future conditions, the 70-year median stand age that we determined for the 1880s should be viewed only as an approximate characterization of the conditions during the pre-1900 reference period.

Finally, we note that our study area in the western San Juan Mountains is located on a broad expanse of gently sloping terrain, with little topographic complexity and therefore few barriers to extensive fire spread under dry windy conditions. In other parts of the Rocky Mountains, where the terrain is more rugged or dissected, pre-1880 fire intervals probably were longer and the 1880 landscape structure probably contained a higher proportion of older stands than is depicted in figure 2.

Comparison of current conditions

Patch clearcutting now has replaced fire as the dominant disturbance agent in our study area (Crouch 1983; Shepperd 1993). However, the landscape mosaic still resembles the pre-1900 mosaic in its broad features, and overall, aspen appears to be thriving. Important practical questions remain about the optimal size and shape of logging units, and about differences between postfire and post-logging habitats (e.g., snags and coarse woody debris; Romme et al. 2000). However, aspen shows no serious decline and is in no danger of disappearing from this ecosystem (cf. Kay 1997).

In portions of the southern Rocky Mountains where no logging is allowed, the distribution of aspen stand ages is gradually shifting toward a preponderance of older age classes (Mueggler 1989). From an ecological standpoint, this is probably not a cause for concern, at least not in many areas (cf. Johnson 1994). Note in the age structure data from the Lime Creek burn (figure 1) that canopy stems are continuing to regenerate in most old stands, even after the original postfire cohort has largely disappeared. Nor is there evidence of replacement by conifers in many aspen stands of the San Juan Mountains (see below). Old aspen stems, especially those with decay, are extremely important for wildlife (DeByle 1985), and we see no obvious signs of diminished ecosystem function (e.g., gross productivity, decomposition, biodiversity) as these aspen stands age. Fire frequency likely will increase in the next century because of global warming (Graham et al. 1990), regardless of current management policies, and many old stands will be lost to wildfire. Therefore, rather than regarding late-successional aspen stands as a problem that needs to be fixed by returning them to younger states via logging or prescribed burning, we suggest that late-successional stands be regarded as valuable components of aesthetics and biodiversity, and worthy of preservation.

This case study may be representative of other areas on the western slope of Colorado and perhaps also portions of Utah and northern New Mexico, where aspen dominates mid-elevation portions of the landscape and fire was the principal agent of disturbance prior to EuroAmerican settlement.

Aspen, Elk, and Fire in Northern Yellowstone National Park

Only about 2% of the 140,000-ha ungulate winter range in northern Yellowstone National Park is classified as an aspen cover type (Hessl 2000). Aspen stands are mostly small, discrete patches within a landscape dominated by sagebrush (*Artemisia tridentata*) steppe and conifer forests of Douglas-fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta* var. *latifolia*). Aspen is largely restricted to a narrow elevation zone near the forest/steppe ecotone (Despain 1990).

Unlike the situation in southern Colorado, where stands have usually regenerated prolifically after disturbance, the extent and density of aspen stands in northern Yellowstone have clearly decreased during the 20th century (Wagner et al. 1995; Kay 1997; White et al. 1998). The current aspen decline is due largely to chronic heavy elk browsing. However, reconstructions of aspen age structures reveal that aspen overstory regeneration in northern Yellowstone may have been episodic even before the ecological changes that began with park establishment and EuroAmerican settlement of adjacent lands in the late 1800s. Most of the mature aspen found today in northern Yellowstone became established between 1871 and 1920 (Ripple and Larsen, in press[a]). A reanalysis of Warren's (1926) aspen data set indicates that aspen overstories were successfully regenerating, at least in places, from the 1750s through 1920s (Ripple and Larsen in press[a]). However, canopy regeneration may have been less widespread before 1870 than it was afterward, e.g., some photographs from the late 1800s show mostly sapling aspen stands apparently resprouting after recent fire. The late 1800s was a unique period in the ecological history of this area, when a combination of low elk numbers, recent fires followed by fire suppression, wolves, and moist weather allowed aspen stems to grow into large size classes over most of the ungulate winter range (Romme et al. 1995). This unique combination of conditions has not recurred since the early 20th century, and no significant aspen tree regeneration has occurred since that time (Ripple and Larsen, in press[a]). It is even possible that mature aspen were more abundant in the early 20th century, following the unique conditions of the late 1800s, than at any time in the previous century or centuries. As Singer et al. (1998) emphasize, the northern Yellowstone ungulate range must be viewed as a nonequilibrium system that exhibits wide variation in response to variability in climate and herbivore pressures (more on this below).

Question 2: Controls on Aspen Succession and Responses to Disturbance

Aspen stands may exhibit a variety of successional trajectories following disturbance. These trajectories are determined by local climate, soils, browsing pressures, and seed sources. Also, as we suggest below, contingent historical events that occurred before the most recent disturbance may have a powerful influence on successional dynamics. We examine two case studies that illustrate responses to two very different kinds of disturbance regimes, local histories, and successional responses. The first study is from the San Juan National Forest, Colorado, where past fires were followed almost always by aspen regeneration, but with highly variable densities of associated conifer species. The second study is from northern Yellowstone National Park, where the success of postfire aspen regeneration is strongly influenced by ungulate browsing pressure.

Seral Versus Stable Aspen Forests in the San Juan National Forest, Colorado

Aspen may be found in pure stands, without any other tree species, or as a seral species in stands going through succession toward eventual domination by conifers. The conifers that gradually replace aspen in seral stands of the southern Rocky Mountains usually are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, white fir (*Abies concolor*) and Douglas-fir at middle elevations, and ponderosa pine (*Pinus ponderosa*) at the lowest elevations. There is some controversy regarding the successional status of pure aspen stands. Some investigators argue that such stands really are not “climax,” but have been disturbed in the past and conifer replacement simply occurs over very long time periods (centuries or millennia). Other investigators suggest that pure aspen stands do in fact represent a stable vegetation type, independent of disturbance.

Regardless of the long-term successional status of pure aspen stands, it probably makes sense to regard them as a stable vegetation type within the intermediate time scales that managers have to deal with (Fetherolf 1917; Baker 1925; Langenheim 1962; Morgan 1969; Severson and Thilenius 1976; Mueggler 1985). For the remainder of this paper, we refer to pure aspen stands having little or no conifer component as “stable aspen.” We refer to aspen stands having enough conifers to dominate the stand once the current aspen canopy has died as “successional aspen.”

Stable aspen stands have an uneven age structure and lack conifers (Mueggler 1976, 1989; Betters and Woods 1981). They tend to be associated with certain combinations of elevation, topography, and substrate, but the patterns of association are weak. Baker (1925) reported that “heavy-soiled flats” are not favorable for conifers and support primarily aspen, whereas rocky soils favor conifers. Pfister (unpublished dissertation, cited in Mueggler 1976) reported that stable aspen stands were common at lower elevations, but that higher-elevation aspen stands tended to be seral to conifers. Similarly, K. T. Harper (personal communication, cited in Mueggler 1985) has observed that stable aspen communities are commonly found at mid-elevations and on southerly exposures, but that successional aspen communities predominate at higher elevations and on northerly exposures. Soils under stable aspen stands usually are richer than soils under a mix of aspen and conifers, but this may be a result of aspen dominance rather than a cause (Parker and Parker 1983; Cryer and Murray 1992). To better understand the environmental controls on aspen forest succession, we studied successional versus stable aspen stands in the San Juan National Forest, Colorado.

Methods

We located 65 mature aspen stands in a study area centered on the fire history study area described above, but also including some surrounding lands in the western portion of the San Juan National Forest. The stands were selected from topographic maps and field observations to represent the full range of elevation, substrate, topographic conditions, and conifer densities found in this portion of the San Juan Mountains. In each stand (about 1 ha in extent) we measured conifer density in a belt transect placed through the center of the stand, collected 10 increment cores from dominant canopy aspen trees, measured soil pH and hue at five points along the central transect, and recorded elevation, substrate, slope aspect, slope position, and steepness. After computing conifer densities in all stands, we defined stable stands as those having <200 conifer stems/ha and successional stands as those having 200 or more conifer stems/ha. In fact, most of the stands classified as stable had no conifers at all, but the broader definition was necessary to provide adequate sample sizes for chi-square analyses.

Results

The observed frequency of stable stands was significantly greater than expected at elevations below 8,000 feet, and was less than expected above 8,000 feet (chi-square test, $P = 0.02$, table 2). Thus, stable aspen stands in the western San Juan Mountains tend to be associated with lower elevations, consistent with other observations (cited in Mueggler 1976), although successional stands also are common at lower elevations. Aspen stands at higher elevations tend to be successional, although we found some stable stands at all elevations up to 10,500 feet.

Stable aspen stands also were significantly ($P < 0.05$) associated with shale substrates rather than sandstones or igneous rocks, consistent with Baker (1925), but the pattern in our San Juan National Forest study area was weak and probably not ecologically meaningful (data not shown). Chi-square tests revealed no significant patterns in frequency of stable versus successional aspen stands with respect to soil hue, soil pH, aspect, slope position, or slope steepness. There was a significant association between stable versus successional aspen stands and stand age, i.e., older stands tended to be successional and younger stands tended to be stable (data not shown). However, older stands also were significantly associated with higher elevations and younger stands with lower elevations, so elevation appears to be the most important underlying variable associated with aspen successional patterns in this area.

Interpretation

These results suggest that the occurrence of stable versus successional aspen forests in the western San Juan National Forest is explained not by deterministic climatic or topographic gradients, but by local historical contingencies. Many of the stable aspen stands are located adjacent to a zone of ponderosa pine that

Table 2—Frequency of stable aspen stands (<200 conifers/ha) in relation to elevation in the western San Juan National Forest, Colorado. The pattern is significantly different from the null model (chi-square = 10.27, 3 degrees of freedom, $P = 0.0164$, n = 65).

Elevation	Observed	Expected
feet		
6,000–7,000	21	15
7,001–8,000	16	10
8,001–9,000	21	29
9,001–10,500	7	11

covers an extensive plateau area just to the west and at lower elevations than the aspen zone. Median fire intervals before 1880 in the ponderosa pine zone were five to 15 years (Romme et al. 1999), because of frequent summer dry periods and highly flammable litter. Fires that were ignited in the ponderosa pine zone probably often spread into the adjacent aspen forests. The resulting fire intervals in the low-elevation aspen forests probably were longer than in the pine forests, because of the low flammability of aspen fuels, but were shorter than the time required for conifer seedlings to reach reproductive age. Consequently, conifer seed sources were locally eliminated in many stands. However, the aspen responded to frequent fire by resprouting from the roots, thus maintaining its local dominance.

In contrast, median fire intervals in aspen forests at the higher elevations, remote from the ponderosa pine zone, were substantially longer than in aspen at lower elevations. For example, median fire intervals prior to 1900 were >150 years in spruce-fir forests of the San Juan Mountains (Romme et al. 1999). Hence, conifer seed sources persisted at the higher elevations, and most aspen stands remained successional. Baker (1925) similarly suggested that recurrent fires (at about a 50-year rotation) may help maintain pure aspen forests by eliminating conifer seedlings and saplings. Thus, we hypothesize that many stable aspen stands in the southern Rocky Mountains and perhaps elsewhere, especially those at lower elevations, developed primarily in response to very short fire intervals in the past. These stands now persist without conifer invasion even in the absence of fire, because local conifer seed sources have been eliminated.

Effects of Fire and Ungulate Browsing on Aspen in Yellowstone National Park

The large fires of 1988 burned nearly a quarter of the northern Yellowstone winter range. However, even though the fires stimulated abundant sucker production in most of the burned aspen stands, almost none of those suckers are growing into new canopy stems today (Romme et al. 1995; Kay 1997). Why is aspen responding to this recent disturbance by fire in a fundamentally different manner than it did a century ago? The principal reason appears to be chronic heavy browsing by elk. The browsing is clearly preventing the aspen sprouts from growing taller than about 0.5 m and also may be gradually reducing the density and overall vigor of the sprouts and of the underlying aspen root system (White et al. 1998). Whereas fire formerly stimulated aspen tree regeneration in this region, current heavy browsing pressure has "uncoupled" the beneficial effect of recent fires on aspen (Hessl 2000). The warmer and drier climatic conditions of the 20th century also may have stressed the aspen and made them less resilient to browsing (Coughenour and Singer 1991).

We suggest that Yellowstone's northern winter range is representative of other areas in the West where aspen has always been a somewhat marginal species, because of suboptimal climate and soils coupled with heavy ungulate browsing pressures. A similar 20th century decline in aspen has been documented on elk winter ranges in Rocky Mountain National Park, Colorado (Olmsted 1979; Baker et al. 1997), in the Jackson valley, Wyoming (Krebill 1972; Bartos et al. 1991; Hessl 2000), and in Banff, Jasper, Yoho, and Kootenay National Parks in Canada (White et al. 1998). Aspen probably is most vulnerable to decline in this kind of ecological setting—in response not only to chronic heavy browsing, but also to drought and changes in the fire regime.

However, it is premature to predict a certain loss of aspen even in these landscapes where it is most vulnerable to decline. In the same national parks listed above, but outside the ungulate winter ranges, and in places like southwestern Colorado where climate and soils apparently are optimal for aspen, there is little or no evidence of aspen decline (Suzuki et al. 1999; Romme et al. 1999). Even within the elk winter range of the Jackson valley, Wyoming, Hessl (2000) found some stands that were regenerating adequately after prescribed fires, perhaps because of unique genetic characteristics or other subtle factors not immediately obvious. Moreover, aspen clones can persist for a very long time, even when subjected to intense browsing or competition from conifers (Despain 1990; Peterson and Peterson 1992). White et al. (1998) observed in Jasper National Park that aspen began to regenerate again after wolves were reestablished in the 1970s. With the recent reintroduction of wolves in Yellowstone, it is possible that predation pressure will reduce elk densities and modify elk foraging behavior in such a way that aspen will be able to escape browsing pressure and regenerate in portions of the northern range where no significant regeneration has occurred in the last 80 years (Ripple and Larsen, in press[a). Ripple and Larsen (in press[b]) also report that "jackstraw piles" of fallen conifers killed by the 1988 fires provided aspen sprouts with at least partial protection from elk browsing in northern Yellowstone National Park.

Question 3: Aspen Life History Traits, Reproductive Mechanisms, and Resilience

As a long-lived clonal species that reproduces primarily via vegetative sprouting, aspen responds very effectively to local disturbances that fall within the recent historic range of variation in disturbance kind and severity. Thus, in the San Juan Mountains study area, fire poses no serious threat to the long-term persistence of extensive aspen stands, even if fire frequency increases in the next century in response to global climate change. Similarly, aspen in the San Juan Mountains should be able to withstand reasonable logging and grazing programs, especially if those programs are designed to mimic the disturbance regime of the pre-1900 period as much as possible (Romme et al. 2000).

The situation is less clear in northern Yellowstone, where current browsing intensity may exceed historic levels—not with respect to acute browsing intensity (which must have been occasionally intense at many times in the past) but possibly with respect to the chronic heavy browsing pressure now occurring. Nevertheless, aspen's long genet life span, extensive root systems, and ability to produce new stems asexually have enabled it to persist throughout a century of heavy browsing pressure and may maintain the species well into the next century even under the current disturbance regime (Despain 1990).

However, asexual reproduction via root sprouting is not enough. To be able to cope with broad-scale climate change or habitat alterations that exceed the range of variation experienced during the last several centuries, aspen must be able to maintain genetic diversity through sexual reproduction and to produce new genetic individuals through seedling establishment (Eriksson 1992; Mitton and Grant 1996). Climate simulations under doubled-CO2 scenarios suggest that climatically suitable geographic ranges for many species will shift substantially during the next century, and that conditions within species' ranges may be altered (Romme and Turner 1991; Bartlein et al. 1997). Moreover, most individual aspen genets that we see on the landscape today may have established during cooler climates in the past, e.g., during the Little Ice Age or even in the early Holocene (Baker 1925; Cottam 1954; Barnes 1966; Tuskan et al. 1996), and hence may not be genetically well equipped to cope with the warmer climates and other environmental changes expected in the next century.

Aspen seedlings have been notoriously rare in the West throughout the 20th century, but genetic studies within mature populations indicate that occasional seedling establishment has occurred during previous centuries (Jelinski and Cheliak 1992). The most recent episode of sexual reproduction in aspen occurred following the 1988 Yellowstone fires (Kay 1993; Romme et al. 1997). The 1988 fires burned about 300,000 ha in and around Yellowstone National Park and were the largest fires in this region in the last 300 years (Romme and Despain 1989). Extensive surveys conducted in 1993 revealed that aspen seedlings were restricted to burned areas and varied greatly in local density, with maximum densities of >300 stems/ha (Romme et al. 1997). Notably, aspen seedlings were abundant in many areas well outside the pre-1988 distribution of aspen, as well as within the pre-1988 distribution. What does this unexpected response to the extensive fires of 1988 indicate about aspen's resilience to the environmental changes expected in the next century? We address this broad question by posing three smaller questions:

Why Did Extensive Aspen Seedling Establishment Occur After the 1988 Fires?

Establishment of new aspen genets in the West apparently has been infrequent and episodic (Jelinski and Cheliak 1992), principally because aspen seedlings are extremely intolerant of desiccation or competition (Moss 1938; McDonough 1979). A rare "window of opportunity" for seedling establishment occurred after 1988, due to a combination of unusually moist and cool weather in early summer, the occurrence of extensive bare substrate where competition from other plants was greatly reduced, and prolific seed production by mature aspen individuals that survived the fires. For instance, May precipitation in Yellowstone National Park was 139–197% of average in 1989–1991, and total plant cover in burned forests was 2–53% of cover in unburned forests (Romme et al. 1997).

The next century is likely to bring more extensive fires (Graham et al. 1990), which could mean more episodes of aspen seedling establishment if the concurrent weather conditions are cool and moist. However, if the fires of the next century are associated with drought and high temperatures, then aspen may be unable to establish new genets, and increased fire activity instead may lead to local extirpation of some old clones without establishment of new genets—especially in areas of chronic heavy ungulate browsing or other stresses on aspen.

What Are the Patterns of Genetic Diversity in the Aspen Seedlings?

Seedling populations sampled in 1993 exhibited greater overall genetic diversity than adult populations sampled on Yellowstone's northern range (Tuskan et al. 1996). However, as of 1997, there were no strong spatial patterns in the genetic structure of seedling populations across the Yellowstone Plateau (Stevens et al. 1999). This suggests that intense selection pressures have not yet occurred in the seedling populations, i.e., that we still see a more-or-less random distribution of genetic composition across the landscape reflecting vagaries of seed source and seed dispersal. Stevens et al. (1999) hypothesize that selective mortality will occur over the next few decades, and that local genetic diversity in seedling populations will decrease as one or a few genotypes come to dominate individual sites.

It seems logical that this infusion of new individuals with unique genetic recombinations into the aspen populations of the Greater Yellowstone area will enhance the species' ability to survive or even thrive in the face of impending climatic and environmental changes. However, we are in only the earliest stages of what will be a long-term population process. The rare episode of aspen seedling establishment that occurred after the 1988 Yellowstone fires provides a unique opportunity to document the establishment of new aspen individuals and genetic structure in a natural setting.

What Will Be the Long-Term Ecological Role of the New Aspen Genets?

Based on the resampling of permanent plots from 1996–1998, aspen seedling densities are decreasing across most of the Yellowstone Plateau (M.G. Turner and W. H. Romme, in preparation). Causes of mortality appear to include heavy browsing by elk as well as locally adverse microclimate and soils conditions. Over much of Yellowstone National Park, many or even most of the new aspen individuals that appeared after 1988 seem destined to disappear over the next few decades, leaving no lasting ecological legacy.

However, some of the new aspen genets are thriving and appear likely to become well established and to persist indefinitely. For example, in one study area in west-central Yellowstone National Park, aspen genets that germinated in 1989 were >1 m tall in 1999 and had a single dominant stem. These individuals were growing in a dense tangle of fallen pine stems killed by the 1988 fires, which probably protected the aspen seedlings from excessive elk browsing. Thus, even though most of the aspen seedlings that established soon after the 1988 fires may perish, enough may survive to increase overall genetic diversity of the species and to establish new genets in new locations. Tuskan et al. (1996) suggest that episodes of new aspen genet establishment may typically exhibit just such a pattern of initially high seedling densities, followed by extensive mortality with survival of a few individuals that are best adapted to local conditions and which go on to produce clonal structures. Additional seedling establishment events of this kind in the future may be crucial to long-term survival of aspen in the Yellowstone region if climate change in the next century shifts the elevational zones of tolerance for plant species (Romme and Turner 1991; Bartlein et al. 1997) and if continued browsing pressure combined with drought and other stresses causes local extirpation of some old aspen clones.

Conclusions and Management Implications

1. Aspen plays a variety of roles in western landscapes, depending on the ecological context. We urgently need more detailed, local case studies of aspen ecology, disturbance regimes, responses to disturbance, landscape patch dynamics, and genetic and population structure to further illustrate its different roles and to provide a reliable basis for making useful generalizations. For example, our understanding of the very different pre-1900 disturbance regimes in aspen forests of the San Juan National Forest and northern Yellowstone National Park helps to explain the very different responses to recent disturbance that have been observed in the two systems.

2. Long-term persistence of aspen may be threatened, especially in the face of broad-scale global change, in settings like Yellowstone's northern range, where (a) aspen stands have always been patchy and restricted to limited portions of the landscape, probably due in part to locally marginal climate and soils conditions, and (b) ungulate browsing is intense, concentrated, and chronic.
3. Long-term persistence of aspen probably is not threatened, even in the face of global change, in settings like the San Juan National Forest where (a) aspen stands are extensive and cover a wide range of elevations and topographic positions, probably due in part to locally favorable climate and soils conditions, (b) fire was the principal disturbance agent in the past, and (c) ungulate use is relatively light or widely dispersed.
4. In settings like the San Juan National Forest, conifer invasion of aspen stands is a natural successional process that has always occurred in some stands during long fire-free intervals, and there have always been some long fire-free intervals. For example, the paucity of fire in the 20th century somewhat resembles the reduced fire activity of the late 1700s and early 1800s in the Southwest. The relatively high proportion of old aspen stands that we see in some unlogged landscapes today probably is not far outside the historic range of variability in landscape patch structure.
5. Old aspen stands in the southern Rockies, with or without conifer invasion, are extremely valuable for wildlife and aesthetics and show no obvious decline in ecosystem function. Because the next century is likely to bring increased fire frequency, similar to what occurred in the late 1800s or even exceeding the fire frequency of that period, old aspen stands probably will become less abundant in the future—regardless of current management decisions.
6. Although aspen reproduces primarily via asexual root sprouting, it also periodically produces new genetic individuals via sexual reproduction and seedling establishment. Seedling establishment is associated with large-scale disturbances (e.g., fire) that coincide with cool moist climatic conditions. The resulting genetic recombination and establishment of new individuals in new geographic locations may enhance aspen's ability to tolerate the broad-scale climate and habitat changes anticipated in the next century.

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Biodiversity: Aspen Stands Have the Lead, But Will Nonnative Species Take Over?

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Abstract—*We investigated vascular plant and butterfly diversity in Rocky Mountain National Park. We identified 188 vascular plant species unique to the aspen vegetation type. The slope of the mean species-area curve for the aspen vegetation type was the steepest of the 10 types sampled, thus, an increase in aspen area could have much greater positive impacts on plant species richness than other vegetation types. Aspen plots contained the greatest number of butterfly species and ranked highest with all diversity indices tested. However, aspen plots were the most heavily invaded by nonnative plant species, which could have negative effects on native plant and butterfly species diversity.*

The importance of aspen (*Populus tremuloides* Michaux) for maintaining biodiversity in western landscapes is well introduced in DeByle et al. (1985), where aspen stands are noted for their own genetic diversity, as well as providing habitat for insects, birds, and mammals. Stohlgren et al. (1997a,b) found a disproportionately high number of vascular plant species in aspen stands in relation to their coverage in the Beaver Meadows area (750 ha) of Rocky Mountain National Park, Colorado. There, aspen covered only 1.2% of the landscape, but it contained 45% of the plant species sampled.

Resource managers in Rocky Mountain National Park (the Park) are concerned that elk (*Cervus elaphus* Nelsoni) may be harming vegetation in portions of the Park (Berry et al. 1997). Localized studies have reported little or no aspen regeneration in elk winter range (Baker et al. 1997; Olmstead 1997), while a more extensive study did find successful regeneration at landscape scales in areas of low elk use (Suzuki et al. 1999). Similar concern and controversy over regeneration exists in the Greater Yellowstone Ecosystem (Barnett and Stohlgren 2000; Bartos et al. 1991; Gruell and Loope 1974; Krebill 1972; Romme et al. 1995; Weinstein 1979). Another potential harmful effect on aspen stands and the diversity that they support is invasion by nonnative plant species. Work in other species-rich habitat types has found that hotspots of native plant diversity are being invaded by nonnative plant species (Stohlgren et al. 1998b, 1999a,b,c). These invasions may have long-term, negative consequences for native diversity, especially in vegetation types such as aspen that are small, scattered, and rare on the landscape in parts of their range.

Our objective was to assess a variety of vegetation types' contributions to plant and butterfly species richness. We used species-log(area) curves (Gleason 1925; Rejmanek and Ejvind 1992; Shmida 1984) to compare the relative contributions to vascular plant species richness made by 10 different vegetation types in the Park. Species-area curves allow comparisons across vegetation types, and even other studies, because the slopes of the curves can be calculated and compared without the difficulties posed by other diversity indices that often require abundance data (for evenness) and vary greatly depending on study design (Ludwig and Reynolds 1988). In addition, species-area models allow one to estimate the number of species expected in an area larger than the area

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sampled. These estimates may also be used as an index of diversity (richness). We also examine the number of species that only occur in one vegetation type (unique to a vegetation type) and the number of nonnative plant species found in a set of vegetation plots.

To test the use of plant richness to predict the diversity of other taxonomic groups, we investigated the significant contributions of aspen to butterfly species diversity and the relations between butterfly species richness and plants in the Beaver Meadows area (Simonson et al. 2000).

Our results should place renewed emphasis on the need to maintain aspen on the landscape to maintain landscape-scale biodiversity. In addition to managing natural processes such as elk herbivory and fire, resource managers may need to detect invasive species early, monitor their effects, and control nonnative plant invasions to maintain the native diversity supported by aspen.

Methods

Study Sites

From 1995 through 1998, 104 Modified-Whittaker plots (20 m x 50 m or 10 m x 25 m; figure 1) were established (using stratified, random sampling) in 10 vegetation types in a 54,000 ha portion of Rocky Mountain National Park, Colorado (after Stohlgren et al. 1997b). Vegetation cover types were identified on aerial photos (1987, color; 1:15840 scale) and included aspen (*Populus tremuloides* Michaux), willow (*Salix* spp.), dry meadow (various species), wet meadow (various species), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*Pinus contorta* Dougl.), mixed conifer (various species), subalpine (various species), alpine tundra (various species), and spruce/fir (*Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt). Twenty of the aspen plots were located based on a previous bird study (stands were similarly randomly located; Natasha Kotliar, U.S. Geological Survey, personal communication). Butterfly data were collected in 1996 on the 24 Modified-Whittaker plots (four plots in each of six vegetation types: aspen, burned ponderosa, dry meadow, lodgepole pine, ponderosa pine, and wet meadow) in the 750 ha Beaver Meadows study area (Simonson et al. 2000).

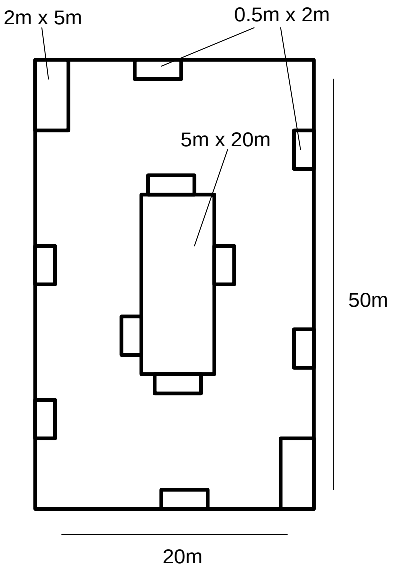

Figure 1—The Modified-Whittaker plot (not to scale). The main plot is 20 m x 50 m and contains ten 1-m^2 subplots (0.5 m x 2 m, six inside the perimeter of the main plot and four outside the perimeter of the 100-m^2 subplot), two 10-m^2 subplots (2 m x 5 m, in opposite corners of the main plot), and one 100-m^2 subplot (5 m x 20 m in plot center). Sampling at multiple spatial scales (1-m^2, 10-m^2, 100-m^2, and 1000-m^2) allows the construction of a species-area curve (figure 2). Plots that measured 10 m x 25 m (four vegetation plots) had the same plot design, but all dimensions were halved.

Plot Designs

The Modified-Whittaker plot for vegetation sampling consists of ten 1-m^2 subplots, two 10-m^2 subplots (in opposite corners), and one 100-m^2 subplot (in plot center) all contained within the 20 m x 50 m plot (figure 1). The original plot design placed the ten 1-m^2 subplots around the inside of the plot perimeter (Stohlgren et al. 1995). However, after 1996, four of the 1-m^2 subplots were moved to the outside perimeter of the 100-m^2 subplot to decrease the linearity of the 1-m^2 subplots. The 1-m^2 subplots were placed to maximize the distance between them while allowing for easy relocation where long-term monitoring was an objective (Stohlgren et al. 1998a). Within each 1-m^2 subplot, we identified all vascular plant species, recorded their average height, and estimated their cover to the nearest percent. In the 10-m^2 subplots and the 100-m^2 subplot we recorded species presence. Finally, the entire 1,000-m^2 plot was surveyed and any previously unrecorded (in the subplots) species were recorded.

For butterfly sampling, the 20 m x 50 m plot contained six 10-m^2 subplots around the inside of the plot perimeter and one 100-m^2 subplot in the plot center (Simonson 1998). The butterfly plot was overlain directly on the vegetation plot. Butterfly diversity was measured based on systematic surveys of the subplots and plot, under minimum weather conditions (Simonson 1998). Butterflies were identified to species, and abundances were also recorded.

Analyses

Species lists were compiled for plants and butterflies to determine the total numbers of species found in each vegetation type as well as the species unique to a vegetation type. Nonnative plant species were noted. All plant specimens identified to species follow the National Plants Database nomenclature (USDA NRCS 1999). Some plants could not be identified to species because of phenology or condition, so they were labeled with a unique identifier. If these “unknowns” could be identified to genus, then the genus was included in the descriptive name. For analyses, we erred on the side of caution by lumping difficult unknown species together (e.g., many grasses and small, basal rosettes of composites).

Species-log(plot size) curves, hereafter called species-area curves, were constructed using the mean number of plant species found in each subplot for the 1-m^2 and 10-m^2 subplots and the total number of plant species found in the 100-m^2 subplot and the full 1,000-m^2 plot. These curves are the result of linear regression where the number of species is dependent on the area sampled (figure 2). Thus, the curve rises more rapidly in species-rich habitat types because more species are encountered as area is increased (the slope of the line is steeper). Species-area curves were developed for each vegetation type based on all the plots sampled in that type. Butterfly data were analyzed using rarefaction curves, analysis of variance, diversity and evenness indices, and regression (Simonson et al. 2000).

Results

We identified 188 vascular plant species that occurred only in aspen plots (N = 32 plots) (appendix A). The remaining vegetation types (N = 72 plots) combined contained 264 species that only occurred in one vegetation type. The slope of the mean species-area curve for the aspen vegetation type was the steepest of the nine vegetation types sampled (table 1, figure 2). The slope indicates the rate of accumulation of new species as the area sampled is increased.

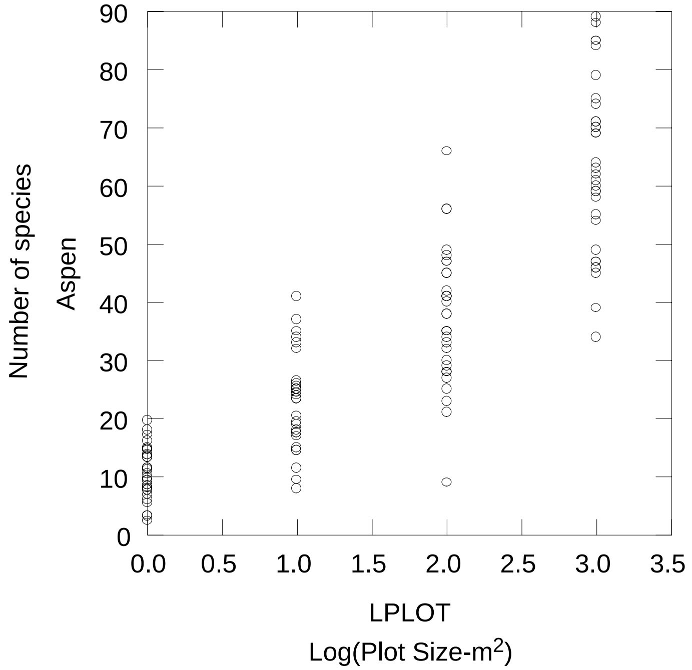

Figure 2—An example species-log(area) curve. Data are from 32 Modified-Whittaker plots placed in 32 aspen stands. The slope of the regression line is an index of species richness: the steeper the slope, the more new species are expected to be added as the area sampled increases. We used plot size (m^2) for area. The equation of the aspen regression is: N = 17.18(log(area)) + 7.85 (adjusted $r^2 = 0.76$, $p < 0.01$), where N is the predicted number of species for a given area, the slope is 17.18, and the constant (i.e., intercept) is 7.85.

Aspen plots contained 38 of the 42 nonnative species identified in all plots, and 15 of the 38 were not found in any other vegetation type (appendix A).

In the Beaver Meadows portion of the Park, four plots were sampled for plant and butterfly diversity in each of six vegetation types. Aspen covered the smallest area with a total of 8.8 ha scattered throughout the 750-ha area. Thirty-three butterfly species, a total of 252 individuals, were recorded in aspen stands, and seven of those species were found only in aspen (Simonson 1998; appendix B). For both richness and diversity indices, aspen consistently ranked the highest of the vegetation types sampled for butterfly diversity (Simonson et al. 2000; table 2). Butterfly species richness was strongly positively correlated with native plant species richness ($r = 0.64$; $p < 0.001$), but the best predictors of butterfly species richness were exotic plant species richness ($r = 0.70$; $p < 0.0001$) and exotic plant species cover ($r = 0.70$; $p < 0.001$; Simonson et al. 2000).

Table 1—Species-area curves for vascular plant species in 10 vegetation types from a 54,000-ha portion of Rocky Mountain National Park, Colorado. We used SYSTAT (SPSS, Inc., 1998) for statistical analyses. We used the mean number of species in the 1-m^2 and 10-m^2 subplots and the total number of species in the 100-m^2 subplot and 1,000-m^2 plot. We used the log(plot size) for area. The equations follow the general equation of a line: N = m(x) + b, where N = the number of species; m = the slope of the line; x = log(plot size); and b is a constant (the intercept). Larger values of the slope (m) indicate a greater accumulation of species as area is increased. In all cases $p < 0.01$.

Vegetation	Equation	Adjusted R^2	# plots
Aspen	N = 17.18(log(area)) + 7.85	0.76	32
Willow	N = 15.11(log(area)) + 6.31	0.80	9
Dry meadow	N = 13.14(log(area)) + 8.20	0.75	9
Spruce/fir	N = 12.81(log(area)) + 5.78	0.74	4
Ponderosa	N = 12.47(log(area)) + 3.70	0.85	8
Tundra	N = 11.69(log(area)) + 14.40	0.86	4
Wet meadow	N = 11.60(log(area)) + 6.55	0.71	8
Mixed conifer	N = 9.36(log(area)) + 1.33	0.48	5
Lodgepole	N = 9.23(log(area)) + 2.82	0.74	8
Subalpine	N = 9.02(log(area)) + 3.80	0.66	8

Table 2—Richness and diversity indices for butterflies in aspen (A), wet meadow (WM), Ponderosa pine (PP), dry meadow (DM), burned conifer (BC), and lodgepole pine (LP) vegetation types in the Beaver Meadows study area, Rocky Mountain National Park, Colorado (Simonson et al. 2000).

Vegetation	A	WM	PP	DM	BC	LP
Richness						
Observed species	33	27	21	19	15	13
Estimated species[a]	19	15	14	11	14	13
Diversity						
Simpson's A	0.08	0.11	0.12	0.17	0.12	0.13
Shannon's H	2.92	2.56	2.29	2.10	2.32	2.16
Hill's N1	18.60	12.89	9.83	8.13	10.21	8.71
Hill's N2	12.27	9.54	6.45	5.96	8.55	7.80

[a] Based on rarefaction, which allows the comparison of species numbers between vegetation types where sample sizes (number of individuals observed) were unequal. This estimate provides an index of richness.

Discussion

Although aspen stands cover a small proportion of Rocky Mountain National Park (2% based on one Park map or 5% based on recent work by Kaye et al., this proceedings), they contribute a disproportionate amount to plant and butterfly species richness. For example, aspen comprised only 1.2% of the vegetation cover in the Beaver Meadows study area, yet the four plots sampled in aspen contained 150 plant species (45% of the plants observed on all 24 plots). Of the plant species, 50 were unique to the aspen type (25% of the unique species observed in the six vegetation types in that study; Stohlgren et al. 1997b). Beaver Meadows aspen contained more unique butterfly species than any other vegetation type. Thirty-three of the 49 butterfly species observed were seen in aspen, and seven of those were recorded only in the aspen type. In the Beaver Meadows study area (750 ha; Stohlgren et al. 1997b) and the larger study area (54,000 ha, present study) the slopes of species-area curves for plants in aspen were steeper than those for any other vegetation type sampled. Using slope steepness as an index of a vegetation type's contribution to species richness, aspen stands are clearly important for maintaining landscape biodiversity. Resource managers are justified in their concern about aspen's persistence on the landscape.

Managers must add invasive, nonnative species to their list of potential threats to the integrity of aspen ecosystems. We observed 42 nonnative plant species in the Park; 38 of those occurred in aspen stands, and 15 of those were not found in the plots in any other vegetation type. This is partially explained by the large number of plots in aspen (N = 32 plots), but it is still extremely high compared to the 72 nonaspen plots. Especially alarming was the presence of noxious, agricultural, and urban weeds (e.g., field bindweed, *Convolvulus arvensis* L.) in seemingly remote, undisturbed aspen stands. None of our sites that appeared relatively undisturbed had high cover of nonnative species, but their presence indicates that seed sources are available. With seed available, any disturbance is likely to result in increased cover of nonnative plant species. The ability of the nonnative species to form dense stands can prevent native plants from persisting or establishing (Whitson et al. 1996).

Other potential negative effects involve pollinator interactions between native and nonnative plants. For example, we observed many butterflies on the flowers of musk thistle (*Carduus nutans* L.) and Canada thistle (*Cirsium arvense* L.). Even though these nonnative species provide nectar, they are not suitable host plants for most butterfly larva, which often require specific native hosts. If nonnatives are being pollinated this may increase their invasion success. In addition, many native plants are believed to be pollinator-limited (Burd 1994) even without competition for pollinators from nonnatives. If pollination of natives is reduced and results in decreased reproduction, this will exacerbate their displacement and could impact butterfly diversity by reducing the populations of required host plants.

Attempts to manage for intact aspen stands as a component of forest ecosystems must consider the potential negative impacts of nonnative plant species on native species richness across taxonomic groups. Controlling invasive nonnative species in aspen stands must be carefully done because these areas contain more unique assemblages of native species. Researchers and managers must be especially attentive to processes that encourage aspen regeneration or establishment (e.g., fire, disturbance) because these processes also facilitate nonnative species establishment. Understanding the connectivity of aspen and other vegetation cover types in relation to nonnative plant species movement and establishment will be an essential component to proactive management of native species and aspen stands.

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Appendix A

Plant species listed were only found in aspen stands (32 plots), except for the nonnative species indicated by an "N*", which were found in other vegetation types as well. We only list plants that were identified to species (47 unknowns were not included). Please note that a portion of these species certainly occurs in other vegetation cover types, but they were not found in our plots in other types (N = 72). Species noted as "Rare" are listed by Spackman et al. (1997).

Status	Family	Scientific name	Common name
N*	Poaceae	*Agrostis gigantea*	Redtop
N	Poaceae	*Alopecurus pratensis*	Meadow foxtail
N*	Brassicaceae	*Alyssum alyssoides*	Pale madwort
N*	Brassicaceae	*Arabis glabra*	Tower mustard
N	Brassicaceae	*Brassica juncea*	India mustard
N*	Poaceae	*Bromus tectorum*	Cheatgrass
N*	Brassicaceae	*Camelina microcarpa*	False flax
N	Apiaceae	*Carum carvi*	Caraway
N	Asteraceae	*Carduus nutans*	Musk thistle
N*	Chenopodiaceae	*Chenopodium album*	Lambsquarters
N*	Asteraceae	*Cirsium arvense*	Canadian thistle
N	Convolvulaceae	*Convolvulus arvensis*	Field bindweed
N*	Apiaceae	*Conium maculatum*	Poison hemlock
N	Poaceae	*Cynodon dactylon*	Bermudagrass
N	Boraginaceae	*Cynoglossum officinale*	Gypsy flower
N	Poaceae	*Dactylis glomerata*	Orchardgrass
N*	Brassicaceae	*Descurainia Sophia*	Flixweed
N	Poaceae	*Elytrigia repens* var. *repens*	Quackgrass
N*	Poaceae	*Festuca ovina*	Sheep fescue
N*	Apiaceae	*Heracleum sphondylium*	Eltrot
N	Brassicaceae	*Lepidium campestre*	Field pepperweed
N	Brassicaceae	*Lepidium perfoliatum*	Clasping pepperweed
N*	Poaceae	*Lolium pratense*	Ryegrass
N	Fabaceae	*Melilotus officinalis*	Yellow sweetclover
N*	Poaceae	*Phleum pratense*	Timothy
N	Poaceae	*Poa compressa*	Canada bluegrass
N*	Poaceae	*Poa pratensis*	Kentucky bluegrass
N*	Polygonaceae	*Rumex acetosella*	Sheep sorel
N*	Polygonaceae	*Rumex crispus*	Curly dock
N	Caryophyllaceae	*Silene vulgaris*	Maidenstears
N*	Brassicaceae	*Sisymbrium altissimum*	Tall tumblemustard
N*	Asteraceae	*Taraxacum officinale*	Common dandelion
N*	Brassicaceae	*Thlaspi arvense*	Pennycress
N*	Asteraceae	*Tragopogon dubius*	Salsify
N*	Fabaceae	*Trifolium hybridum*	Alsike clover
N*	Fabaceae	*Trifolium repens*	White Dutch clover
N	Scrophulariaceae	*Verbascum thapsus*	Common mullein
	Poaceae	*Achnatherum lettermanii*	None listed
	Asteraceae	*Achillea millefolium* var. *occidentalis*	Western yarrow
	Poaceae	*Achnatherum nelsonii* ssp. *dorei*	Needle-and-thread
	Ranunculaceae	*Actaea rubra*	Baneberry
	Rosaceae	*Amelanchier alnifolia*	Saskatoon serviceberry

Appendix A, cont'd

Status	Family	Scientific name	Common name
	Ranunculaceae	*Anemone canadensis*	Meadow anemone
	Apocynaceae	*Apocynum androsaemifolium*	Spreading dogbane
	Ranunculaceae	*Aquilegia caerulea*	Colorado blue columbine
	Araliaceae	*Aralia nudicaulis*	Wild sarsaparilla
	Asteraceae	*Artemisia ludoviciana* ssp. *Mexicana*	Mexican white sagebrush
	Fabaceae	*Astragalus alpinus*	Alpine milkvetch
	Asteraceae	*Aster foliaceus* var. *parryi*	Parry's aster
	Asteraceae	*Aster laevis*	Smooth aster
	Asteraceae	*Aster novae-angliae*	New England aster
	Fabaceae	*Astragalus parryi*	Parry's milkvetch
	Asteraceae	*Aster porteri*	Porter's aster
	Fabaceae	*Astragalus sparsiflorus*	Front range milkvetch
	Asteraceae	*Brickellia californica*	California brickellbush
	Asteraceae	*Brickellia grandiflora*	Tasselflower brickellbush
	Poaceae	*Calamagrostis montanensis*	Plains reedgrass
	Cyperaceae	*Carex canescens*	Silvery sedge
	Cyperaceae	*Carex durinscula*	Needleleaf sedge
	Cyperaceae	*Carex foenea* var. *foenea*	Dryspike sedge
	Cyperaceae	*Carex lanuginosa*	Woolly sedge
	Cyperaceae	*Carex oreocharis*	Grassyslope sedge
	Cyperaceae	*Carex rostrata*	Beaked sedge
	Scrophulariaceae	*Castilleja miniata*	Scarlet paintbrush
	Rhamnaceae	*Ceanothus velutinus*	Snowbrush ceanothus
	Chenopodiaceae	*Chenopodium fremontii*	Fremont's goosefoot
	Asteraceae	*Cirsium canescens*	Prairie thistle
	Asteraceae	*Cirsium drummondii*	Dwarf thistle
	Ranunculaceae	*Clematis occidentalis*	Western blue virginsbower
	Scrophulariaceae	*Collinsia parviflora*	Smallflower blue-eyed Mary
	Orchidaceae	*Corallorhiza* sp.	Coral root
	Fumariaceae	*Corydalis aurea*	Golden smoke
	Pteridaceae	*Cryptogramma crispa*	Crisp rockbreak
	Boraginaceae	*Cryptantha fendleri*	Sanddune catseye
	Ranunculaceae	*Delphinium ramosum*	Mountain larkspur
	Brassicaceae	*Descurainia pinnata*	Western tanseymustard
	Primulaceae	*Dodecatheon pulchellum*	Darkthroat shootingstar
	Lamiaceae	*Dracocephalum parviflorum*	American dragonhead
	Poaceae	*Elymus elymoides*	Bottlebrush squirreltail
	Poaceae	*Elymus glaucus*	Blue wildrye
	Poaceae	*Elymus lanceolatus* ssp. *Albicans*	Montana wheatgrass
	Poaceae	*Elymus subsecundus*	Bearded wheatgrass
	Poaceae	*Elymus virginicus* var. *submuticus*	Virginia wildrye
	Onagraceae	*Epilobium brachycarpum*	Autumn willowweed
	Equisetaceae	*Equisetum laevigatum*	Smooth horsetail
	Asteraceae	*Erigeron subtrinervis*	Three-nerved fleabane
	Asteraceae	*Eucephalus engelmannii*	None listed
	Poaceae	*Festuca thurberi*	Thurber's fescue
	Rosaceae	*Fragaria vesca*	Woodland strawberry
	Polemoniaceae	*Gilia pinnatifida*	Sticky gilia

Appendix A, cont'd

Status	Family	Scientific name	Common name
	Orchidaceae	*Goodyera oblongifolia*	Western rattlesnake plantain
	Dryopteridaceae	*Gymnocarpium dryopteris*	Western oakfern
	Asteraceae	*Helianthella quinquenervis*	Five-nerve helianthella
	Asteraceae	*Heterotheca fulcrata*	Rockyscree false goldenaster
	Saxifragaceae	*Heuchera bracteata*	Bracted alumroot
	Asteraceae	*Hieracium albiflorum*	White hawkweed
	Rosaceae	*Holodiscus dumosas*	Rock spirea
	Juncaceae	*Juncus balticus*	Baltic rush
	Asteraceae	*Lactuca tatarica*	Large-flowered blue lettuce
Rare	Liliaceae	*Lilium philadelphicum*	Wood lily
	Orchidaceae	*Listera convallarioides*	Broadlipped twayblade
	Fabaceae	*Lupinus argenteus*	Silvery lupine
	Asteraceae	*Machaeranthera bigelovii* var. *bigelovii*	Bigelow's tansyaster
	Asteraceae	*Machaeranthera canescens*	Hoary aster
	Lamiaceae	*Monarda fistulosa*	Wild bergamot beebalm
	Poaceae	*Muhlenbergia asperifolia*	Alkali muhly
	Onagraceae	*Oenothera villosa* ssp. *Strigosa*	Hairy evening primrose
	Orobanchaceae	*Orobanche uniflora*	One-flowered broomrape
	Poaceae	*Oryzopsis asperifolia*	Roughleaf ricegrass
	Celastraceae	*Paxistima myrsinites*	Mountain-lover boxleaf myrtle
	Scrophulariaceae	*Pedicularis procera*	Grays lousewort
	Scrophulariaceae	*Penstemon rydbergii*	Rydberg's penstemon
	Solanaceae	*Physalis heterophylla*	Clammy groundcherry
	Rosaceae	*Physocarpus monogynus*	Mountain ninebark
	Orchidaceae	*Platanthera hyperborean* var. *hyperborean*	Northern green orchid
	Polygonaceae	*Polygonum aviculare*	Devils shoestrings
	Polygonaceae	*Polygonum douglasii* ssp. *Johnstonii*	Johnston's knotweed
	Rosaceae	*Potentilla nivea*	Snow cinquefoil
	Lamiaceae	*Prunella vulgaris*	Common selfheal
	Asteraceae	*Ratibida columnifera*	Upright prairie coneflower
	Asteraceae	*Rudbeckia laciniata*	Tall cone-flower
	Salicaceae	*Salix petiolaris*	Meadow willow
	Salicaceae	*Salix scouleriana*	Scouler's willow
	Apiaceae	*Sanicula marilandica*	Maryland snakeroot
	Selaginellaceae	*Selaginella densa*	Lesser spikemoss
	Selaginellaceae	*Selaginella underwoodii*	Underwood's spikemoss
	Asteraceae	*Senecio crassulus*	Thickleaf groundsel
	Asteraceae	*Senecio eremophilus* var. *kingii*	King's groundsel
	Asteraceae	*Senecio pudicus*	Bashful ragwort
	Asteraceae	*Senecio rapifolius*	Openwoods groundsel
	Asteraceae	*Senecio serra*	Butterweed
	Caryophyllaceae	*Silene drummondii*	Drummond's campion
	Caryophyllaceae	*Silene drummondii* var. *drummondii*	Drummond's campion
	Asteraceae	*Solidago simplex* ssp. *simplex* var. *simplex*	Mt. Albert goldenrod
	Rosaceae	*Sorbus scopulina*	Greene mountain ash
	Lamiaceae	*Stachys palustris*	Marsh hedgenettle
	Caryophyllaceae	*Stellaria calycantha*	Northern starwort
	Asteraceae	*Taraxacum officinale* ssp. *ceratophorum*	Fleshy dandelion

Appendix A, cont'd

Status	Family	Scientific name	Common name
	Caprifoliaceae	*Viburnum edule*	Mooseberry viburnum
	Violaceae	*Viola canadensis*	Canadian white violet
	Vitaceae	*Vitis riparia*	Riverbank grape
	Asteraceae	*Wyethia mollis*	Woolly wyethia

Appendix B

Butterfly species found in the aspen vegetation type in the 754-ha Beaver Meadows area of Rocky Mountain National Park (four 0.1-ha plots, each sampled four times; Simonson 1998).

Scientific name and authority	Unique to aspen plots
Parnassius smintheus Doubleday	
Papilio rutulus Linnaeus	
Papilio multicaudatus Kirby	X
Pontia protodice (Boisduval and Leconte)	X
Pieris marginalis (Scudder)	X
Euchloe ausonides (Lucas)	
Colias eurytheme Boisduval	
Colias philodice Godart	
Colias alexandra Edwards	
Lycaena helloides (Boisduval)	
Lycaena rubida (Behr)	
Callophrys spinetorum (Hewitson)	
Callophrys eryphon (Boisduval)	
Everes amyntula (Boisduval)	
Celastrina ladon (Cramer)	
Plebejus acmon (Westwood and Hewitson)	
Plebejus saepiolus (Boisduval)	
Agriades glandon (De Prunner)	
Glaucopsyche lygdamus (Doubleday)	X
Speyeria atlantis (Edwards)[a]	
Speyeria aphrodite (Fabricus)	
Speyeria edwardsii (Reakirt)	
Phyciodes pratensis (Behr)	
Polygonia faunus (Edwards)	X
Polygonia gracilis (Grote and Robinson)	
Nymphalis antiopa (Linnaeus)	
Limentis weidemeyerii (Edwards)	X
Coenonympha tullia (Edwards)	
Cercyonis oetus (Boisduval)	
Oeneis chryxus (Doubleday and Hewitson)	
Erynnis persius (Scudder)	
Oarisma garita (Reakirt)	
Polites draco (Edwards)	

[a] Complex, including *Speyeria hesperis* (Edwards).

Adaptations of Quaking Aspen for Defense Against Damage by Herbivores and Related Environmental Agents

Richard L. Lindroth[1]

***Abstract**—Quaking aspen (*Populus tremuloides*) employs two major systems of defense against damage by environmental agents: chemical defense and tolerance. Aspen accumulates appreciable quantities of phenolic glycosides (salicylates) and condensed tannins in most tissues and accumulates coniferyl benzoate in flower buds. Phenolic glycosides are toxic and/or deterrent to pathogens, insects, and small mammals, and coniferyl benzoate is toxic to ruffed grouse, but the functional significance of tannins remains unclear. Levels of secondary compounds are influenced by both genetic and environmental (e.g., resource availability) factors. Tolerance is less well understood but may play an important role as an adaptation to extensive damage during herbivore outbreaks. Critically needed is an assessment of the roles of chemical defense and tolerance in relation to the foraging ecology of large mammals such as cervids.*

Introduction

If geographic range, population density, and capacity to flourish in a diversity of habitat types are indicators of "ecological success," then quaking aspen (*Populus tremuloides* Michx.) must be considered one of the most successful of extant tree species. A primary contributor to such success has been the evolution of chemical and physiological defense systems that afford resistance or tolerance to a host of biotic and abiotic factors. The purpose of this paper is to provide a succinct summary of the defensive adaptations of aspen and how they are influenced by genetic and environmental factors, and to discuss implications for their efficacy against harmful environmental agents, particularly herbivores. (For more detailed information, refer to the review by Lindroth and Hwang [1996a].) One caveat must be stated up front: Nearly everything known about the defense systems of aspen is based on research conducted in Eastern North America. The same systems are likely important to Western aspen, although particular contexts will vary.

Plants have evolved arrays of chemical, physiological, and physical defenses against damage by environmental agents. For aspen, a growing body of literature has unveiled the critical importance of chemical defense mechanisms. Physiological defenses, such as tolerance, are less well understood but are generating increased interest. Physical defenses (associated with physical characteristics such as spines and silica) are unlikely of importance in aspen. In the context of this paper, secondary plant metabolites with demonstrated or putative protective roles will be considered "chemical defenses." Tolerance—the capacity to sustain growth and reproduction following damage—will be considered a "physiological defense."

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Chemical Defense

Secondary Metabolites

The dominant secondary metabolites of aspen are phenolic compounds, produced via the shikimic acid pathway. These include phenolic glycosides and condensed tannins, which occur in leaf, bark, and root tissues, and coniferyl benzoate, which occurs only in flower buds.

The signature secondary metabolites of aspen comprise a suite of salicylates generally known as phenolic glycosides (Lindroth et al. 1987; Palo 1984). The exact biosynthetic pathway is unknown, but the compounds are most likely derivatives of salicylic acid. They vary according to the type and position of benzoyl and similar functional groups, and these groups confer tremendous variation in terms of biological activity (Lindroth and Peterson 1988; Lindroth et al. 1988). Quaking aspen contains four phenolic glycosides, including salicin, salicortin, tremuloidin, and tremulacin (figure 1). Of these, salicin and tremuloidin generally occur in concentrations <1% leaf dry weight. Levels of salicortin and tremulacin, however, are much higher, typically 1 to 8% each, and occasionally attain 15% (Hemming and Lindroth 1995; Lindroth and Hwang 1996b; Osier et al. 2000a).

A second major class of phenolics produced in aspen is condensed tannins. These compounds are derived from 4-coumaric acid and accumulate to appreciable levels, up to nearly 30% of leaf dry weight (Hemming and Lindroth 1995; Lindroth and Hwang 1996b; Osier et al. 2000a). Aspen does not produce hydrolyzable tannins.

Coniferyl benzoate is a phenylpropanoid ester, also derived from 4-coumaric acid. Concentrations of this compound range from 0 to 7% dry weight in flower buds (Jakubas et al. 1993a,b).

Phytochemical Variation

Aspen exhibits tremendous variation in levels of foliar chemical defenses (Lindroth and Hwang 1996a). Research over the last 10 years has identified a complex of genetic and environmental factors, and interactions among them, that contribute to such variation. Moreover, the magnitude of influence of genetics and environment varies among different secondary metabolites. In contrast to a large accumulated literature for leaves, we know almost nothing about quantitative chemical variation in stem, bark, or root tissues.

Genetic variation

Striking genetic variation among clones is a hallmark characteristic of aspen, and no less so for levels of foliar secondary metabolites. Among clones in a common field habitat, levels of total phenolic glycosides vary from <1 to 16% dry weight, whereas levels of condensed tannins vary from 3 to nearly 30% dry weight (Hemming 1998; Lindroth and Hwang 1996a,b; Osier et al. 2000a). Measurements of chemical variation among clones in the field do not indicate true genotypic variation, however, as they may be confounded with differences among local (clone) environments. Sorting out true genotypic variation requires growing trees in a common environment.

To that end, we have conducted several common garden experiments with trees propagated from root cuttings of field clones. Quantification of phenolic glycoside and condensed tannin concentrations revealed virtually the entire range of concentrations reported for field clones (Hwang and Lindroth 1997, 1998).

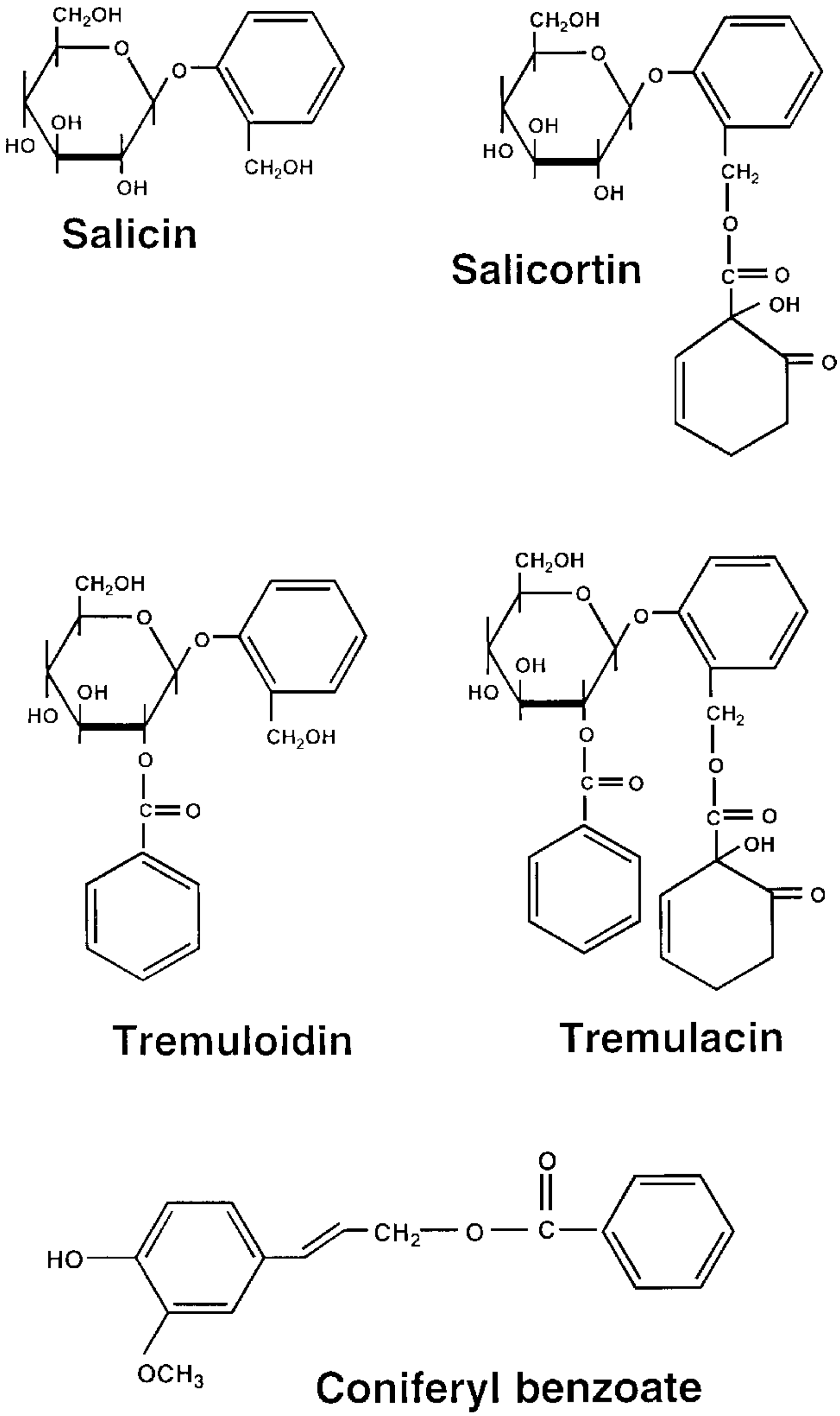

Figure 1—Phenolic glycosides and coniferyl benzoate, characteristic secondary compounds of quaking aspen.

Interestingly, levels of secondary metabolites appear to be much more variable among aspen genotypes than are those of primary metabolites or mineral nutrients. Our studies have generally shown that although concentrations of water, carbohydrates, and nitrogen (an index of protein) may differ significantly among clones, the magnitude of variation (both relative and absolute) is minimal in comparison with that of secondary metabolites (Hwang and Lindroth 1997, 1998). We have not evaluated levels of macronutrients in aspen foliage. Jelinski and Fisher (1991), however, assessed nutrient content of winter twigs and reported similar low levels of clonal variation for all macronutrients except calcium. If aspen secondary metabolites are effective deterrents to feeding by particular herbivores, these results suggest that clonal variation in herbivore preference or performance may be more strongly determined by secondary than primary chemical composition.

Temporal variation

Levels of foliar defense compounds exhibit temporal variation with respect to both development (ontogeny) and seasonal progression (phenology). A preliminary survey of foliar defense chemistry in seedling, juvenile (burned or browsed), and mature aspen in Yellowstone National Park suggested that levels of phenolic glycosides decline as aspen mature (Erwin et al. 2000). These results are consistent with the hypothesis of ontogenetic development of chemical defense against herbivores, which purports that early successional trees have evolutionarily adapted to substantial herbivory during juvenile stages by the expression of high levels of constitutive defenses (Bryant and Julkunen-Tiitto 1995).

Within a growing season, changes in levels of foliar phenolic glycosides differ among clones; increases, decreases, and no significant changes have been reported (Hemming 1998; Hwang and Lindroth 1998; Lindroth and Hwang 1996a; Osier et al. 2000a). In contrast, levels of condensed tannins generally increase during a growing season, with the most pronounced increases occurring during the period of leaf expansion (Hemming 1998; Hwang and Lindroth 1998; Lindroth and Hwang 1996a; Osier et al. 2000a).

Resource availability

Numerous studies have investigated the effects of resource (light, water, nutrients, carbon dioxide) availability on the chemical composition of aspen. As would be expected for a fast-growing species (Bryant et al. 1987a), aspen exhibits considerable plasticity in chemical response to changes in nutrient availability. In general, these changes accord well with predictions of the carbon-nutrient balance (Bryant et al. 1983) and growth-differentiation balance (Herms and Mattson 1992) hypotheses. According to these hypotheses, environmental conditions that increase carbon availability (e.g., high light, high CO_2) or decrease nutrient availability (e.g., low soil fertility) lead to a relative excess of carbohydrates and an increase in C-based secondary or storage compounds.

Indeed, levels of phenolic glycosides, condensed tannins, and starch generally increase in aspen grown under conditions of high light, high CO_2, and/or low nutrient availability (Hemming and Lindroth 1999; Lindroth et al. 1993; McDonald et al. 1999). The various compounds are not, however, similarly responsive to changes in resource availability. Concentrations of condensed tannins respond much more strongly to environmental changes than do concentrations of phenolic glycosides. Moreover, the magnitudes of chemical responses differ among clones (significant gene x environment effects).

Induction

Damage by herbivores or pathogens can elicit a host of plant responses that alter the susceptibility of remaining tissues to further damage (Karban and Baldwin 1997). Several research groups have investigated short-term induction of chemical defenses in aspen leaves. Mattson and Palmer (1988) reported an 18% increase in total phenolics following artificial defoliation of 50% leaf area. Clausen et al. (1989) found that levels of salicortin and tremulacin, but not salicin and tremuloidin, increased (slightly) within 24 hours of mechanical defoliation. Work by my research group has shown slight to no increases in phenolic glycoside levels immediately following mechanical or natural defoliation (Lindroth and Kinney 1998; Roth et al. 1998; Osier and Lindroth 2000). In contrast, levels of condensed tannins generally increase following natural or artificial defoliation, and the magnitude of increase is influenced by resource availability (Lindroth and Kinney 1998; Roth et al. 1998; Osier and Lindroth 2000).

Less is known about long-term (interannual) induced defenses in aspen. Clausen et al. (1991) reported increases in only one (tremulacin) of four phenolic glycosides 1 year after 50 and 100% defoliation. Osier and Lindroth (unpublished data) investigated the effects of 90% defoliation on several aspen genotypes grown in nutrient-deficient or nutrient-rich soil. We found no increases in phenolic glycoside concentrations and a slight increase in condensed tannin concentrations 1 year after defoliation. Responses did not differ significantly across clones or nutrient treatments.

To date, virtually all work with induced defenses in aspen has focused on folivory. Almost nothing is known about the impacts of browsing on expression of foliar defense traits in aspen. According to the resource-based model of Bryant et al. (1991), however, defoliation and browsing may cause very different outcomes for the quality of subsequent leaf tissue. Severe defoliation contributes to mortality of fine roots, leading to reduced nutrient absorption, reduced nutrient concentration per leaf, decreased leaf growth, increased leaf carbohydrate pools, and an increase in carbon-based secondary metabolites. In contrast, browsing reduces leaf numbers, leading to increased nutrient concentration per leaf, increased leaf growth, decreased carbohydrate pools, and a decrease in carbon-based secondary metabolites. This model suggests that insect outbreaks on aspen may elicit changes in foliar quality very different from those of browsing mammals.

Costs of Chemical Defense

If levels of aspen defense compounds are strongly genetically determined, and if the compounds are effective deterrents against herbivores, the question arises as to why genetic variation persists in field populations. The classic answer to this evolutionary problem is that costs of defense must exist, such that expression of defense is not advantageous in all environments at all times.

Recent research by Osier and Lindroth (unpublished data) documented significant costs of resistance in aspen. These were exhibited as tradeoffs (negative genotypic correlations) between growth and phenolic glycoside concentrations among aspen genotypes. The tradeoffs were strongest in low-resource (low light, low nutrient availability) environments. In high-resource environments, however, the tradeoff disappeared. Thus, expression of high levels of constitutive defense (phenolic glycosides) appears to exact a cost in terms of plant growth, except in high-resource environments.

Tolerance

Historically, investigations of defensive strategies of plants have focused on chemical systems. Recently the concept of tolerance has begun to generate theoretical and empirical attention. Tolerance refers to the capacity of plants to maintain fitness through growth and reproduction after herbivore damage (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999). Tolerance is considered to be an especially viable form of defense in plants with high intrinsic growth rates, large storage capacity, and substantial physiological (e.g., photosynthetic) plasticity. All such traits are characteristic of aspen. Tolerance is advantageous in situations where herbivore damage is so uniform and severe that even chemically resistant genotypes are heavily damaged. Under such conditions, tolerance would confer a fitness advantage even though resistance does not. Tolerance may be selectively advantageous in forest ecosystems in which outbreak folivores cause extensive and uniform damage during peak periods of defoliation (Mattson et al. 1991). Examples include outbreaks of forest tent caterpillars (*Malacosoma disstria*), gypsy moths (*Lymantria dispar*), and large aspen tortrix (*Choristoneura conflictana*) on aspen.

Results from studies by Osier and Lindroth (unpublished data) suggest that aspen does exhibit tolerance to defoliation and that tolerance differs among aspen genotypes and resource environments. Under low nutrient availability, defoliation suppressed growth in each of four genotypes. Under high nutrient availability, however, two of the genotypes compensated nearly entirely for damage.

Defense Against Abiotic Agents

Lindroth and Hwang (1996a) reported that exceedingly little is known about the roles of aspen secondary metabolites with respect to protection from physical factors. Five years later, the same holds true. Phenolic glycosides may confer protection from ultraviolet (UV) radiation (Lindroth and Hwang 1996). Evidence in support of that function includes the fact that phenolic glycosides absorb UV radiation (especially at 200-320 nm) and that several clones of aspen propagated from cuttings collected in alpine environments in Colorado (high incident UV) continued to express very high levels of phenolic glycosides when grown in a common garden in Wisconsin.

Defense Against Biotic Agents

That the defense systems of aspen are based on fairly simple phenolic chemicals, coupled with physiological adaptations for tolerance, seem all the more remarkable given their apparent efficacy against a host of potentially damaging organisms. The phenolic glycosides, in particular, appear to have broad-spectrum activity, reducing the performance of organisms as variable as fungi, insects, and vertebrates (table 1).

Pathogens

Aspen is subject to diseases caused by viruses, bacteria, and most importantly, fungi (Ostry et al. 1988; Perala 1990). Although the nature of the defense mechanisms mounted against these pathogens is mostly unknown, secondary metabolites play a role in some cases.

Hypoxylon mammatum stem canker is a serious fungal pathogen of aspen, particularly east of the Rocky Mountains (Perala 1990). Initially, Flores and Hubbes (1979, 1980) showed that phenolic glycoside "phytoalexins" (identity

Table 1—Organisms affected by secondary metabolites of aspen.

Species	Metabolite	Reference
Pathogenic fungi		
Hypoxylon (ascospores)	Unidentified “phytoalexin,” phenolic glycosides	Flores and Hubbes 1979, 1980; Kruger and Manion 1994
Alternaria (conidia and mycelia)	Unidentified “phytoalexin”	Flores and Hubbes 1979, 1980
Insects		
Gypsy moth (*Lymantria dispar*)	Phenolic glycosides	Hemming and Lindroth 1995; Lindroth and Hemming 1990; Hwang and Lindroth 1997; Osier et al. 2000b
Forest tent caterpillar *(Malacosoma disstria*)	Phenolic glycosides	Hemming and Lindroth 1995, 1999; Lindroth and Bloomer 1991; Lindroth et al. 1993
White-marked tussock moth (*Orgyia leucostigma*)	Phenolic glycosides	McDonald et al. 1999
Canadian tiger swallowtail (*Papilio canadensis*)	Phenolic glycosides	Hwang and Lindroth 1998
Big poplar sphinx moth (*Pachysphinx modesta*)	Phenolic glycosides	Hwang and Lindroth 1998
Large aspen tortrix (*Choristoneura conflictana*)	Phenolic glycosides	Bryant et al. 1987b
Aspen blotch leafminer (*Phyllonorycter tremuloidiella*)	Phenolic glycosides (?; marginal effect)	Auerbach and Alberts 1992
Vertebrates		
Ruffed grouse (*Bonasa umbellus*)	Coniferyl benzoate	Jakubas et al. 1993a,b
Snowshoe hare (*Lepus americanus*)	Unidentified “phenolic and terpene resin”	Bryant 1981
Beaver (*Castor canadensis*)	Unidentified “phenolic”	Basey et al. 1990

unknown) could be isolated from aspen twigs following inoculation with *Hypoxylon*; these compounds inhibited germination of *Hypoxylon* ascospores and Alternaria conidia, and growth of *Alternaria* mycelia. Later, Kruger and Manion (1994) showed that the phenolic glycosides salicin and salicortin, and the simple phenolic catechol, inhibit *Hypoxylon* ascospore germination.

Insects

Aspen serves as a host to over a hundred species of insects, including nine species of expansive outbreak folivores (Baker 1972; Furniss and Carolin 1977; Mattson et al. 1991; Perala 1990). Some of the latter defoliate trees on a scale rarely seen for other insect pests in North America. For example, annual defoliation by the forest tent caterpillar (*Malacosoma disstria*) and large aspen tortrix (*Choristoneura conflictana*) for the period 1957–1987 averaged 935,000 and 246,000 ha, respectively, with tent caterpillar outbreaks as large as 13.5 million ha observed (Mattson et al. 1991). With the exception of the gypsy moth (*Lymantria dispar*), all the major insect pests of aspen are native species.

Numerous studies have evaluated the role of chemistry pertaining to the performance of aspen-feeding insects (table 1). These studies have included specialists and generalists, as well as outbreak and nonoutbreak species, and have been conducted under laboratory and field conditions. In nearly every instance, phenolic glycosides were of singular importance with respect to influence on insect performance (survival, development, growth, feeding, reproduction). Phenolic glycoside concentrations typically account for 60 to 98% of the variation in insect performance parameters. Results from correlative studies have been substantiated by experimental studies in which purified phenolic glycosides were incorporated into insect diets (Hemming and Lindroth 1995; Lindroth and Bloomer 1991; Lindroth and Hemming 1990). The only study published to date that does not suggest a major role of phenolic glycosides in insect resistance in aspen is that of Auerbach and Alberts (1992) for aspen blotch leafminers (*Phyllonorycter tremuloidiella*).

Surprisingly, several studies have shown that condensed tannins have no deleterious effect on the performance of aspen-adapted insects (Ayres et al. 1997; Bryant et al. 1987b; Hemming and Lindroth 1995; Hwang and Lindroth 1997, 1998). Indeed, presence of moderate to high levels of tannins can actually increase consumption rates, perhaps as a consequence of the dilution of critical foliar nutrients (Osier and Lindroth 2000).

The efficacy of chemical defense appears to change during the course of insect (e.g., gypsy moth, forest tent caterpillar) outbreaks on aspen. At moderate to high insect population densities, aspen clones are not uniformly susceptible to defoliation; rates may vary from 20 to 90% of leaf area removed for clones in a common habitat (Lindroth, personal observation). Differential defoliation is likely due to genotypic differences in levels of phenolic glycosides, although this has yet to be confirmed experimentally. At very high population densities, however, all aspen are heavily defoliated, apparently irrespective of chemical variation. Traits conferring tolerance to damage would be particularly beneficial in these situations.

Vertebrates

Given the importance of aspen as a food source for a variety vertebrate species, surprisingly little is known about the role of particular defense characteristics in mediating those interactions. The most detailed assessment of the impact of aspen chemistry on a vertebrate herbivore was conducted for ruffed grouse (*Bonasa umbellus*). A series of studies by Jakubas and colleagues (Jakubas and Gullion 1991; Jakubas et al. 1989, 1993a,b) revealed that coniferyl benzoate, rather than phenolic glycosides or tannins, strongly influences selection of buds and catkins. These tissues can comprise from much to nearly all of the diet of grouse during winter and spring. Ingestion of high levels of coniferyl benzoate causes loss of nitrogen, reductions in metabolizable energy, and acidosis from production of acidic detoxication products.

Less is known about the roles of aspen defenses with respect to herbivory by mammals. Winter browsing by snowshoe hares (*Lepus americanus*) may be influenced by aspen chemical composition, as adventitious shoots contain high levels of phenolic and terpene resins and are unpalatable to hares (Bryant 1981). 6-Hydroxycyclohex-2-ene-1-one and salicaldehyde, derivatives of phenolic glycosides such as salicortin and tremulacin, protect internodes of juvenile balsam poplar (*Populus balsamifera*) from browsing by hares (Reichardt et al. 1990). Related work with other poplars and willows has shown that phenolic glycosides deter feeding by opossums (*Trichosurus vulpecula*) in New Zealand (Edwards 1978) and mountain hares (*Lepus timidus*) in Scandinavia (Tahvanainen et al. 1985).

Aspen chemistry also appears to play a role in defense against feeding by beaver (*Castor canadensis*). Aspen trees cut by beaver will resprout with a juvenile growth form, which is avoided by beaver when mature growth-form plants are available (Basey et al. 1990). Food selection is not influenced by phenolic glycoside levels, but by levels of an unknown phenolic constituent that occurs in high concentrations in juvenile tissue.

Almost nothing is known about the effects of aspen chemical composition on foraging by cervids. Given the importance of aspen as a browse species for deer (*Odocoileus hemionus*, *O. virginianus*), elk (*Cervus elaphis*), and moose (*Alces alces*), this represents a significant gap in our understanding of cervid foraging ecology. Because accessible aspen are heavily browsed by cattle and cervids (especially elk) throughout much of Western North America, the argument could be made that chemical defenses are ineffective in reducing herbivore damage. Although such may be the case now, it is likely an artifact of artificially sustained high densities of browsing mammals. Such high densities were likely rare throughout most of the evolutionary history of aspen (C. Kay, this proceedings). The potential error of the deduction of "ineffective defense" becomes clear as one considers the analogous situation with outbreak insects. At low to moderately high herbivore densities, marked differences in susceptibility to defoliation exist (advantages of chemical defense are obvious), but these differences disappear under conditions of exceptionally high herbivore feeding pressure. In situations during which chemical defenses are rendered ineffective, aspen likely relies on tolerance. But tolerance is a relatively short-term defense. It cannot be sustained during extended periods of heavy browsing, as now exist throughout much of the western range of aspen. Clearly, much remains to be learned about the roles of chemical and physiological mechanisms as mediators of aspen-mammal interactions in Western North America.

Conclusions

Much of the ecological success of aspen can be attributed to the defense systems it employs against potentially damaging agents in the environment. The dominant defense system is chemical, and phenolic glycosides are the signature compounds. Tolerance is also likely to be an important defense system, although less is known about this system than is known about chemical defenses. Commitment to chemical defense varies strikingly among aspen genotypes. Such variation is likely maintained due to the "costs" of defense; negative genetic correlations exist between growth and defense, and these are strongest under conditions of low resource availability. Chemical defense systems have been demonstrated to negatively affect the performance of a variety of aspen pathogens and herbivores. That work focused, however, on interactions between aspen and insect herbivores in the Great Lakes region. Critically needed is an evaluation of (1) the relevance of chemical defense and tolerance to herbivory by large browsing mammals and (2) implications thereof for the long-term health of aspen in Western North America.

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Mycorrhizal Fungi of Aspen Forests: Natural Occurrence and Potential Applications

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Abstract—*Native mycorrhizal fungi associated with aspen were surveyed on three soil types in the north-central Rocky Mountains. Selected isolates were tested for the ability to enhance aspen seedling growth in vitro. Over 50 species of ectomycorrhizal fungi occur with* Populus tremuloides *in this region, primarily basidiomycete fungi in the Agaricales. Almost one-third (30%) were ubiquitous with aspen and were found on all three soil types. Over one-third (37%) were restricted to the acidic, sandy soil of the smelter-impacted Butte-Anaconda area, revealing a subset of fungi that tolerate these conditions. Mycorrhizal fungi were screened for their ability to enhance aspen growth and establishment. Of nine selected isolates, all but one increased the biomass of aspen seedlings 2–4 times. Stem diameter, height, and number of root tips increased with inoculation of some fungi. The native species* Paxillus vernalis, Tricholoma scalpturatum, Hebeloma mesophaem, Thelephora terrestris, *and* Laccaria s*pp. were most promising for further study.* Pisolithus tinctorius *(available as commercial inoculum) formed prolific mycorrhizae and stimulated plant growth but does not occur with aspen in the Rocky Mountains.*

Introduction

Over 80% of plant families are mycorrhizal, and this mutualistic association between plant roots and fungi are the rule in nature, not the exception (Malloch et al. 1980). Most terrestrial ecosystems depend on mycorrhizae, which promote the establishment, growth, and health of plants. Mycorrhizal fungi are particularly crucial in forest systems where they benefit trees by augmenting inorganic nutrient uptake and providing protection from heavy metals, drought, pathogens, grazers, and other organisms (Fogel 1980). Seven mycorrhizal "types" have been defined by the morphology of the root structures formed and the organisms involved (see Smith and Read 1997 for a review). The Pinaceae (pine family), Betulaceae (birch family), Salicaceae (willow and aspen family), Fagaceae (oak family), and Myrtaceae (eucalyptus family) are primarily *ecto*mycorrhizal and associate mostly with basidiomycete fungi, which produce mushrooms as reproductive structures (Malloch et al. 1980). Mushrooms produced by mycorrhizal fungi can be observed near host trees at certain times of the year and are evidence of mycorrhizae in the soil. It should be kept in mind that not all mushroom-producing fungi are mycorrhizal, and forests also host a diverse array of large, fleshy fungi that are saprophytic, parasitic, or mutualistic in other ways (Pilz and Molina 1996).

Aspen (*Populus tremuloides* Michx.) is predominantly ectomycorrhizal (Cripps and Miller 1993; Fontana 1963; Vozzo and Hackskaylo 1974). The prefix "ecto" refers to the intercellular nature of the fungal hyphae that remain external to the plant root cells. Hyphae form a layer over individual roots tips (mantle) and surround individual cortex cells (Hartig net) where nutrient exchange takes

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place, but they do not invade the root cells. The fungal mycelium proliferates into the soil, essentially extending the root system and enhancing the uptake of inorganic nutrients, primarily of phosphorus and nitrogen, which is considered a main benefit to the plant. In return, fungi subsist on carbohydrates from the plant, which are converted to fungal sugars. There are reports of *Populus tremuloides* associating with arbuscular mycorrhizal (AM) fungi that invade the root cells forming a type of endomycorrhizae, but we have found this to be rare. Other species of *Populus* are more likely to associate with AM fungi, and some are also ectomycorrhizal (Vozzo and Hackskaylo 1974).

There were two main objectives in the present study. The first was to survey the mycorrhizal fungi associated with aspen on three different soil types in the north-central Rocky Mountains and identify species with a narrow or broad range. The second objective was to evaluate the effectiveness of several mycorrhizal species in enhancing the growth of aspen seedlings. The second goal has potential application in mined-land reclamation.

In nature, an individual tree typically supports numerous species of mycorrhizal fungi simultaneously, and this mycoflora is dynamic, changing over the life of the tree. The potential number of fungal associates varies with the plant species. For example, Douglas-fir (*Pseudotsuga menziesii*) is capable of forming mycorrhizae with over 2,000 species of fungi (Trappe 1977), while alder (*Alnus* spp.) is limited to only a few (Brunner et al. 1990). In Montana and Idaho, we previously reported over 50 species of mycorrhizal basidiomycete fungi in aspen stands (Cripps and Miller 1993; Cripps 1997). That list has now been extended and refined with additional species determinations, particularly in the Cortinariaceae, a dominant family with aspen in terms of species richness. Ectomycorrhizal fungi exhibit various levels of specificity in plant-fungus interactions. Some fungi are restricted to one or a few hosts, while others have a preference for conifers or broad-leaf hosts. Some are known to occur with a wide range of trees. For example, *Suillus* occurs primarily with pine, occurs to a lesser extent with larch and Douglas-fir, and is rare with other trees. The genus *Gomphidius* appears restricted to pines, and *Lactarius controversus* to aspen and birch. The role that soil and other factors play in determining the mycobionts of a particular forest is only beginning to be understood. In Europe it is common to refer to a particular mycorrhizal fungus's preference for mull or mor soil, while in North America we know so little about the distribution of mycorrhizal fungi that patterns are yet to be completely discerned. Aspen occur in large, pure stands on many soil types and offer an opportunity to examine the role soil factors play in the distribution of mycorrhizal fungi on one host. Mycorrhizal fungi with aspen were surveyed on three very different soil types in Montana and adjacent areas of Idaho to determine if mycofloras varied or if the same subset of mycorrhizal fungi occurred in all stands. Some results have been reported in Cripps and Miller (1993). The updated list is given here along with the specifics of soil characteristics.

Potential Application of Mycorrhizal Fungi

The smelter-impacted area of Butte-Anaconda was of particular interest, because soils are acidic and high in concentrations of copper, iron, and zinc. Heavy metals such as cadmium have been found in aspen leaves on this Superfund site (Bissell 1982). The role of aspen as a pioneering tree in the recovery of smelter-impacted sites in this region is generally unrecognized, and reclamation efforts are typically focused on imported plants. The backside of the Anaconda smelter hill supports a vibrant aspen stand, and young aspen are found within a few hundred feet of the smelter stack itself (Cripps 1996). Dotting the extensive moonscape of tailings waste, small isolated aspen appear to be healthy and thriving. Although their longevity is in question, the survival of even one is significant given aspen's clonal nature and potential to proliferate. At the smelter site in Kellogg, Idaho, a thriving natural aspen stand rises above the planted yellowing conifers. In Trail, British Columbia, where the smelter is still in operation, numerous *Populus* spp. line the banks of the Columbia River downwind of the smelter stack.

Whether aspen has seeded in or regenerated from protected pockets of aspen is an open question. It is difficult to account for the occurrence of isolated aspen trees located on tailings 10 m deep and surrounded by hectares of dumped tailings except by seeding, although this has not been verified. All of the roots examined at these sites were mycorrhizal and several species of fungi have been identified. Ectomycorrhizal fungi are crucial to aspen's survival in these areas, and their potential to expedite aspen colonization on these sites has not been examined. With this in mind, the effects of mycorrhizal fungi on early seedling growth of aspen were studied as an initial screening for native and nonnative fungi, which might be useful in aspen establishment and health and for mined-land reclamation. The parameters examined were the ability of the mycorrhizal fungi to (1) grow in vitro, (2) form mycorrhizae with aspen in vitro, and (3) affect biomass, height, stem diameter, and general health of aspen.

Methods

Sites

The three study areas are located in the north-central Rocky Mountains of southwestern Montana and southeastern Idaho at latitude 45° N, longitude 110–112° W, and elevations of 1,800 to 2,000 m (figure 1). The Butte-Anaconda (B) area lies near the towns of those names in Montana at an elevation near 1,800 m. Fumes from previously operating copper smelters killed much of the vegetation in the late 1800s and early 1900s, and aspen have colonized large areas within the last 70 years. The soil is a nutrient-poor sand (over 70%), with pH's from 4.3 to 5.7, and contains high concentrations of metals, particularly copper. The Cinnabar site (C) just north of Yellowstone National Park supports an older aspen stand with trees up to 114 years old that is gradually being invaded by conifers. The moist area is in a mountain basin, and the soil is a gravelly glacial till, high in P, Ca, and Mg. The large aspen stands of the Teton (T) area in SW Idaho lie on rolling uplands of well-drained soils formed from deep loess and composed of 75% silt. The soil is relatively fertile as attested to by adjacent agricultural land, and aspen tend to persist in this area without conifer replacement. Soil characteristics for the sites are shown in tables 1 and 2.

Mycorrhizal Synthesis and Growth Studies

Native and nonnative fungi that grew well in culture were selected for in vitro growth studies to examine the effects of individual fungal species on early aspen growth. Sterile technique was used to ensure that effects were due to the mycorrhizal fungi and not to extraneous organisms. Pot and field studies will be necessary to further examine effects of mycorrhizal inoculation under greenhouse conditions and for outplantings. Our purpose was to restrict each experimental unit to one mycobiont and one plant host (aspen). Sporocarp

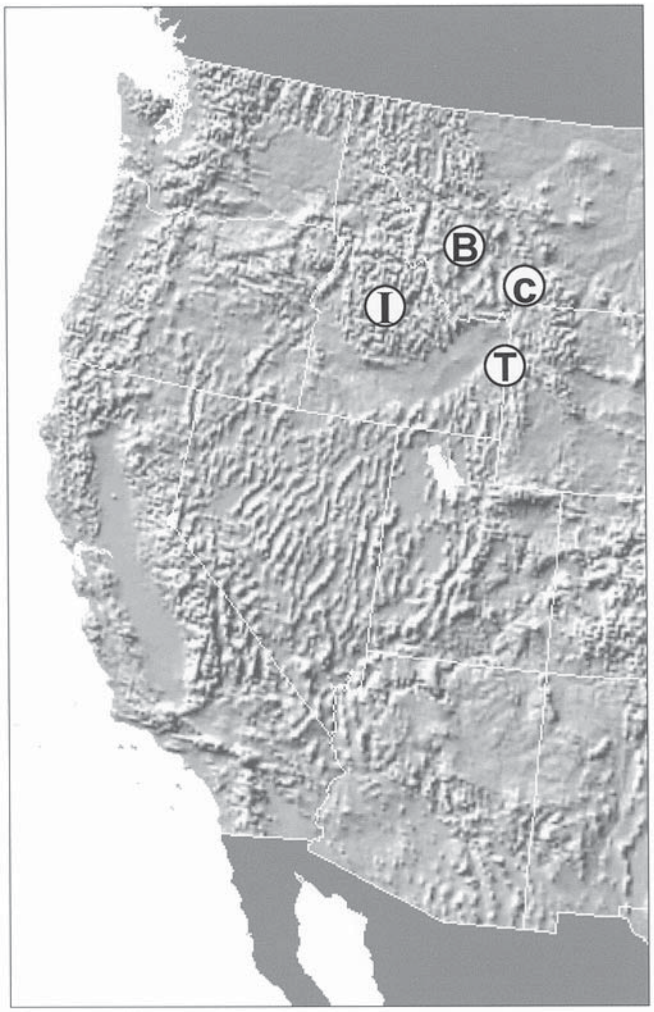


Figure 1—Location of aspen forests in study. B = Butte-Anaconda smelter-impacted area. C = Cinnabar Basin north of Yellowstone Park. T = Teton foothills. I = the town of McCall, ID. Map courtesy of Ray Steiner, John Hopkins University.

Table 1—Soil characteristics of aspen sites in relation to depth. OM = organic matter, CEC = cation exchange capacity.

Soil depth	Sand	Silt	Clay	pH	Exchangeable Ca in ppm	OM	Base saturation	CEC
cm	*- - - - - - - - - Percent*			*- - - - - - - - -*		*- - - - Percent*	*- - - -*	
Butte								
8	82	15	3	5.3	1.46	1.9	45	0.46
15	81	13	5	4.3	1.04	3.2	15	0.15
20	70	20	9	4.5	1.53	4.8	11	0.11
58	74	17	8	4.9	3.03	2.7	28	0.28
97	84	6	10	5.6	5.92	2.1	77	0.77
Cinnabar								
8	65	27	7	5.5	12.60	7.2	63	0.63
15	63	28	9	5.7	11.80	5.7	66	0.66
20	58	31	11	5.8	13.70	5.5	65	0.65
58	70	24	6	6.4	7.40	1.1	86	0.86
94	67	24	9	6.5	6.89	1.1	93	0.88
Tetons								
15	15	77	8	5.5	8.00	2.4	84	0.84
36	12	79	9	6.0	6.37	1.7	73	0.73
56	12	79	9	6.1	5.92	1.2	71	0.71
84	11	67	21	6.3	10.2	1.0	82	0.83
122	42	44	14	6.3	7.90	0.7	79	0.79

Table 2—Exchangeable macro- and micronutrients (ppm) of soil on aspen forest sites.

Soil depth	P	Ca	Mg	Zn	Fe	Al	Cu
cm							
Butte							
8	62	404	53	10.7	31.6	155	43
15	54	252	34	7.7	72.4	264	116
20	94	386	37	19.7	35.2	588	142
58	63	803	61	72.9	9.9	388	3.5
97	40	1,377	68	1.7	3.2	71	0.3
Cinnabar							
8	78	2,048	303	4.7	12.3	135	0.2
15	67	2,128	312	3.6	10.2	138	0.2
20	64	2,260	332	3.5	9.3	138	0.2
58	130	1,487	312	0.6	22.3	131	0.4
94	119	1,360	295	0.6	25.2	122	0.6
Tetons							
15	62	1,502	111	3.3	15.8	128	0.5
36	56	1,190	105	2.6	14.2	117	0.7
56	62	1,032	97	1.9	19.1	111	1.3
84	113	1,523	164	1.3	28.1	157	3.8
122	32	977	124	0.8	20.3	133	1.9

tissue of native fungi and mycelium of nonnative fungi was cultured according to the sterile technique described by Molina and Palmer (1982) and grown on Hagem's medium modified by Van Cotter (1987, unpublished): 4 g malt extract, 1 g yeast extract, 5 g d-glucose, 0.5 g NH_4Cl, 0.5 g KH_2PO_4, 0.5 g $MgSO_4 \cdot 7H_2O$, 0.5 ml $FeCl_3$ (1% aqueous), 100 ml biotin (0.5 mg biotin/ml aqueous), and 100 ml thiamine-HCl (1 mg thiamine/ml aqueous) added to 1,000 ml of distilled H_2O. Eleven grams of agar/L were added to solidify the medium, which was autoclaved for 20 minutes. Cultures were incubated in the dark at 20 °C for a minimum of 1 month and used to inoculate 250 ml flasks containing 75 ml of liquid Cotter's modified Hagem's without agar.

Fresh aspen seeds were stored in a dry place at 0 to 5 °C. Seeds stored too long lose viability and the risk of contamination increases. Seeds were gently agitated in a 15% Clorox™ solution for 15 minutes and rinsed three times (10 minutes each) in double-distilled H_2O (Cripps and Miller 1995). Two drops of the detergent Tween™ were added to the first two solutions to reduce surface tension. Seeds were placed in petri dishes containing Cotter's modified Hagem's made with 11 g/L of agar and placed in a growth chamber under incandescent and fluorescent lights for 16 hours a day followed by 8 hours of dark. Seedlings that showed no signs of contamination were planted in synthesis tubes 23 days later.

Molina and Palmer's tube method of synthesis (1979) was followed using 10 ml peat, 90 ml of vermiculite, and 70 ml of Cotter's modified Hagem's (without agar) for each 200 ml synthesis tube. Five ml of mycelial slurry was added to each tube, which was autoclaved, and the lower part encased in aluminum foil. Ten replicates were used for each fungus and the uninoculated controls. After mycelium colonized the peat-vermiculite medium for 2 weeks, sterile seedlings were introduced and tubes were placed in a growth chamber. Tubes were periodically checked for mycorrhization and seedlings harvested after 3 months. At that time, the general condition of the aspen seedlings was noted, particularly leaf color. The stem diameter and height were measured. Roots were carefully washed and percent mycorrhization determined by counting the number of mycorrhizae per total number of root tips.

Seedlings were dried at 65 °C for 48 hours and weighed. The nonparametric Kruskal-Wallis *t*-test was used to compare responses in control seedlings versus those inoculated with individual fungi.

Results

Mycorrhizal Associates of Aspen

Over 54 species of ectomycorrhizal fungi occurred with aspen on the three study sites and additional aspen stands sampled in Montana and Idaho (table 3). The fungi are all Basidiomycota, primarily Agaricales (gilled mushrooms and boletes), and one Aphyllophorales (*Thelephora terrestris* Fr.). The fungi are distributed in seven families: Amanitaceae, Russulaceae, Tricholomataceae, Cortinariaceae, Paxillaceae, Boletaceae, and Thelephoraceae (figure 2). The dark-spored Cortinariaceae is the most diverse family, with 25 species of *Cortinarius, Inocybe*, and *Hebeloma* occurring in aspen stands. In casual observation, *Leccinum* species often dominate in terms of sheer biomass, with sporocarps occurring in large numbers. *Leccinum insigne* (orange-capped bolete) is considered one of the most characteristic species of aspen stands.

Two major categories of ectomycorrhizal fungi became apparent in the study. Nearly one-third (30%) of the ectomycorrhizal species occurred on all three soil types with *Populus tremuloides*. This percentage increased each year of the study as species fruited on additional sites, as is typical in fungal studies. In the second group, over 37% of the mycorrhizal species occurred only on the smelter-impacted, sandy, acidic soil of the Butte-Anaconda area, suggesting that there is a subset of mycorrhizal fungi more restricted to, or more tolerant of, these abiotic conditions.

Effect of Mycorrhizal Fungi on Aspen Seedling Growth

General condition of aspen

About half of the mycorrhizal fungi isolated grew in culture, and fewer grew well enough to be tested. Of the six native and three nonnative fungi selected for testing, all formed mycorrhizae with aspen, except *Chalciporus (Boletus) piperatus* (Bull.:Fr.) Singer. *Piloderma* formed a mantle, but no Hartig net. The general condition of plants at the end of the experiment is shown in table 4. None of the uninoculated control seedlings died, and leaves remained completely green throughout the experiment. This was also true for inoculation with four native fungi, *Amanita muscaria* v. *formosa* (Pers. Per Fr.) Bert.*, Amanita pantherina* (DC Per Fr.) Krombh., *Paxillus vernalis* Watling, and *Tricholoma scalpturatum* (Fr.) Quel. In contrast, all plants inoculated with *Inocybe lacera* (Fr:Fr) Kummer became necrotic after forming a few mycorrhizae; the black leaves abscissed and dropped off, and the plants died. *Chalciporus piperatus* inoculated plants did not form mycorrhizae, but leaf color was affected. Leaves of seedlings inoculated with *Paxillus vernalis* developed red, yellow, and black coloration, but plants remained in good condition. With the exception of *Inocybe lacera,* which produced 100% mortality in aspen seedlings, and one plant with *B. piperatus*, all plants inoculated with native mycorrhizal fungi were alive at the end of the experiment. However, mycorrhizae were slow to form under these conditions with native fungi.

Seedlings inoculated with nonnative fungi had a higher mortality rate (10–20%), and extreme leaf tips turned black. While *Cenoccocum* and *Piloderma*-inoculated plants turned a pale yellow-green color, those with

Table 3—Ectomycorrhizal fungi occurring with *Populus tremuloides* in the north-central Rocky Mountains, U.S.A. B = Butte, C = Cinnabar, and T = Teton site.

Ectomycorrhizal fungi with *Populus tremuloides* in the north-central Rocky Mountains	State	Acidic, sandy infertile soil (Butte-Anaconda)	Calcareous, sandy loam (Cinnabar)	Calcareous silty soil (Tetons)	Soil types	Growth in vitro[a]
AMANITACEAE						
Amanita alba Gill.	MT, ID		+		C	–
Amanita fulva (Schaeff.) per Pers.	ID			+	T	–
Amanita muscaria v. *alba* Peck	ID				?	+
Amanita muscaria v. *formosa* (Pers per Fr.) Bert.		+	+	+	BCT	+
Amanita pantherina (DC. Per Fr.) Krombh.	MT, ID	+	+	+	BCT	+
Amanita vaginata (Bull. Per Fr.) Krombh.	MT, ID		+	+	CT	–
RUSSULACEAE						
Lactarius controversus (Fr.) Fr.	ID, MT	+	+	+	BCT	+
Lactarius cf*. zonarius* Fr.	MT, ID		+	+	CT	?
Russula aeruginea Lindbl.:Fr.	MT, ID	+	+	+	BCT	–
Russula claroflava Grove	MT	+			B	–
Russula cf. *krombholtzii* Kromb.	MT	+		+	BT	–
Russula foetenula Peck	MT	+	+		BC	–
Russula cf*. velenovskyi* Mlz-Zv.	MT	+	+	+	BCT	–
Russula xerampelina (Schaef.:Secr.) Fr.	MT		+		C	–
TRICHOLOMATACEAE						
Laccaria laccata v. *pallidifolia* (Peck) Peck	MT	+			B	+
Laccaria proxima (Boud.) Pat	MT	+			B	+
Laccaria tortilis (Bolt.) Cooke	MT	+	+		BC	?
Tricholoma flavovirens (Pers. Ex Fr.) Lun & Nan	MT	+			B	?
Tricholoma populinum Lge.	MT	+			B	+
Tricholoma scalpturatum (Fr.) Quel.	MT, ID	+	+	+	BCT	+
CORTINARIACEAE						
Cortinarius alboviolaceous (Pers.:Fr.) Fr.	MT		+		C	–
Cortinarius hedyaromaticus Cripps & Miller	MT		+		C	+
Cortinarius ochrophyllus Fr.	MT	+			B	–
Cortinarius subbalaustinus R. Hry.	MT, ID	+	+	+	BCT	–
Cortinarius talus Fr.		+			B	+
Cortinarius trivialis Lge.	MT, ID	+	+	+	BCT	–
Cortinarius cf *stuntzii* Rehner and Ammirati	MT	+			B	?
Cortinarius cf *sertipes*	MT		+		B	?
Hebeloma insigne Smith, Evenson & Mitchell	MT	+	+	+	BCT	+
Hebeloma mesophaeum (Fr.) Quel.	ID, MT	+	+		BC	+
Hebeloma populinum Romagn.	MT	+	+	+	BCT	+
Hebeloma spp. 1, 2, 3	MT				?	+
Inocybe dulcamara (Alb. & Schw:Pers) Kummer	MT	+	+		BC	+
Inocybe flavella v. *flavella* P. Karst	MT, ID	+	+	+	BCT	?
Inocybe flocculosa (Berk) Sacc. v. *flocculosa*	MT, ID	+	+	+	BCT	–
Inocybe geophylla (Fr.:Fr.) *Kumm.* v. *geophylla*	MT	+			B	–
Inocybe griseolilacina Lge.	MT		+		C	–
Inocybe lacera (Fr:Fr) Kummer v. *lacera*	MT, ID	+			B	+
Inocybe longispora Lge.	MT	+			B	–
Inocybe mixtilis (Britz.) Sacc.	MT	+	+		BC	–
Inocybe nitidiuscula (Britz.) Sacc.	MT	+	+		BC	–
Inocybe phaeocomis (Pers.) Kuyper v. *major*	MT	+			B	–
Inocybe rimosa (Bull:Fr.) Kummer	MT, ID	+			B	+
Inocybe squamata Lge	MT	+			B	?
Inocybe sindonia (Fr.) P. Karst	MT	+			B	–
Inocybe whitei (B & Br) Sacc. v. *whitei*	MT	+	+	+	BCT	–
PAXILLACEAE						
Paxillus vernalis Watling	MT, ID	+	+	+	BCT	+
BOLETACEAE						
Chalciporus piperatus (Bull.:Fr.) Singer	MT, ID		+	+	CT	+
Leccinum aurantiacum (Bull:St.Amans) SF Gray	MT, ID	+	+	+	BCT	+
Leccinum holopus *(Rostk.) Watl.*	*ID*				*?*	*?*
Leccinum insigne Smith, Thiers & Watling	MT, ID	+	+	+	BCT	+
Phylloporus rhodoxanthus (Schw.) Bres.	MT	+			B	?
Xerocomus spadiceus Fr.	MT	+			B	+
THELEPHORACEAE						
Thelephora terrestris Fr.	MT, ID	+			B	+

[a] (+) fungus grew on MMN, (–) fungus showed no growth on MMN, (?) fungus was not tested on MMN. MMN is Melin-Norkrans media (Molina and Palmer 1982).

Figure 2—Ectomycorrhizal fungi associated with aspen. Row 1: *Amanita muscaria, Amanita pantherina, Laccaria proxima*. Row 2: *Lactarius controversus, Russula aeruginea, Cortinarius trivialis*. Row 3: *Cortinarius subbaulaustinus, Inocybe squamata, Inocybe lacera*. Row 4: *Leccinum insigne, Boletus piperatus, Paxillus vernalis*.

Table 4—General condition of aspen seedlings inoculated with mycorrhizal fungi after 3 months. Native fungi were isolated from aspen stands in Idaho and Montana. Nonnative fungi are from VPI culture collection and origins are unknown.

	Seedling mortality	Leaf color general condition	Mycorrhizal	Average biomass as % of control
	Percent		*Percent*	*Percent*
Control	0	Green	0	100
Native fungi				
Amanita muscaria	0	Green	15	400
Amanita pantherina	0	Green	11	250
Boletus piperatus	10	Green with black tips	0	430
Inocybe lacera	100	Most black	1	100
Paxillus vernalis	0	Red/yellow/green/black	12	300
Tricholoma scalpturatum	0	Green	1	430
Nonnative fungi				
Cenococcum graniforme	20	Yellow-green, black tips	5	275
Piloderma croceum	10	Yellow-green, black tips	1	300
Pisolithus tinctorius	20	Dark green, black tips	86	350

Pisolithus tinctorius were a healthy looking dark green. Mycorrhizae were slow to form with the first two, but the root systems of aspen inoculated with *P. tinctorius* (PT) were heavily colonized by the fungus in a short period of time (table 4).

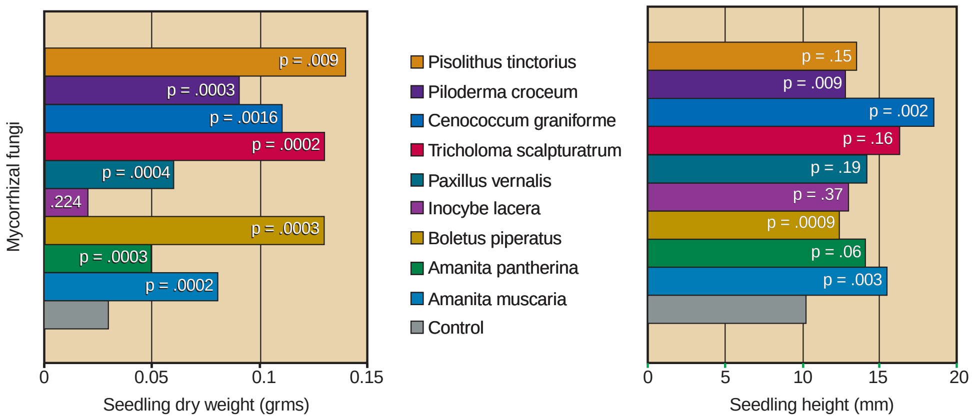
Aspen biomass, stem diameter, height, number of root tips

All of the inoculated aspen seedlings (except those with *I. lacera*) showed a significant increase in total plant biomass over uninoculated controls (figure 3a). In most cases, the increase in average biomass was substantial, and as a percent of the controls the biomass was 430% for *Tricholoma scalpturatum* and *Boletus piperatus*, 400% for *Amanita muscaria*, 350% for *Pisolithus tinctorius*, 300% for *Paxillus vernalis* and *Piloderma croceum*, 275% for *Cenococcum graniforme*, and 250% for *Amanita pantherina*. The biomass of aspen inoculated with *Inocybe lacera* was not significantly different from the control, and plants were in poor condition.

Stem diameter in aspen seedlings increased significantly with the addition of all the mycorrhizal fungi, except *I. lacera* (figure 3d). While the average height of aspen seedlings was increased by inoculation with some fungi, this was only marginally significant for others (figure 3b). Inoculation also affected leaf shape, size, and number differentially, with a general increase of surface area, but the details are not reported here. The average number of root tips doubled with inoculation for most fungi, even those with *Boletus piperatus* that did not form mycorrhizae (figure 3c). *Inocybe lacera* eventually killed the seedlings. The average number of root tips after inoculation with *Pisolithus tinctorius*, *Cenococcum graniforme*, and *Tricholoma scalpturatum* was generally four times that of the control (figure 3c).

a) Effect on aspen biomass

b) Effect on aspen height



c) Effect on number of aspen root tips

d) Effect on aspen stem diameter

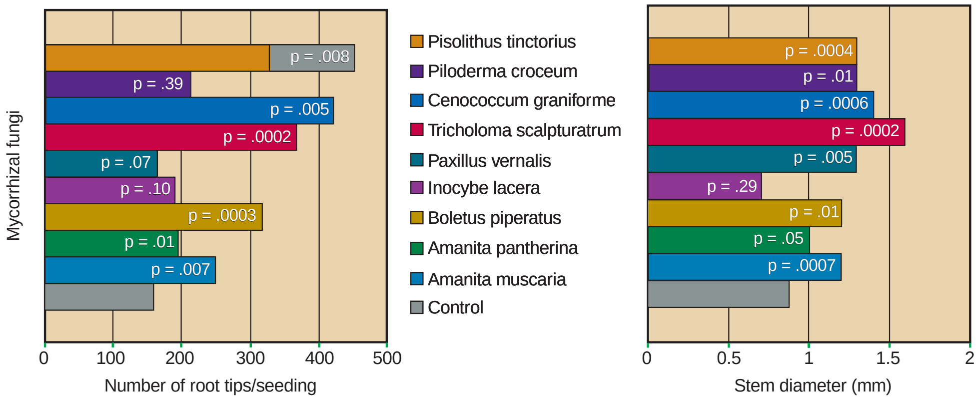


Figure 3—Effect of ectomycorrhizal fungi on early seedling growth of aspen. First three fungi are nonnatives, followed by six native species occurring with aspen in Montana and Idaho. A p-value of less than 0.05 is considered significantly different from the control.

Discussion

Mycorrhizal Associates of Aspen

Quaking aspen is now known to be associated with over 54 species of ectomycorrhizal fungi in the north-central Rocky Mountains and more species of fungi are yet to be identified, particularly in the *Russulaceae*. Aspen's ability to form a mutualistic association with such a diverse array of fungi could help account for its wide geographic range and its ability to proliferate in many different habitats (Cripps and Miller 1993). All of the mycorrhizal fungi are Basidiomycetes and members of the Agaricales (gilled mushrooms), except *Thelephora terrestris* (Aphyllophorales). Many of the same species have been reported with aspen in Canada and their mycorrhizae synthesized in the lab (Godbout and Fortin 1985). In that study, aspen formed mycorrhizae with several species of *Scleroderma,* which is of interest because of its use as a commercial inoculum (but not recorded for our study). Aspen did not form mycorrhizae with *Rhizopogon,* also used as a commercial inoculum, which occurs naturally with conifers. Sister species *Populus tremula* L. in Europe is mycorrhizal with the same fungal genera, and often with the same or related species (Anselmi et al. 1990; Heslin and Douglas 1986; Pirazzi et al. 1989). Many groups of mycorrhizal fungi found in conifer forests are absent from the aspen stands of Montana and Idaho. Mycorrhizal members of whole families such as the Sclerodermataceae, Hydnaceae, Clavariaceae, Cantharellaceae, Hygrophoraceae, Corticiaceae, and hypogeous (subterranean) Ascomycota and Basidiomycota, i.e., the truffle-like fungi, were not recorded in Rocky Mountain aspen forests. Conversely, many of the mycorrhizal fungi found in aspen forests are infrequent or absent from conifer forests.

The Cortinariaceae are a dominant group in terms of species richness, but many of the dark-spored species do not grow well in culture and are not useful for growth studies. *Inocybe* species are particularly diverse with aspen (Cripps 1997), as are *Cortinarius* species. Perhaps the most characteristic fungi of aspen stands are the *Leccinum* species (rough-stemmed boletes), which often fruit in abundance in mid-summer after significant amounts of rain.

Almost one-third (30%) of the mycorrhizal fungi occurred on all three diverse soil types examined, including (1) a nutrient-poor sandy soil, (2) a fertile gravelly loam/glacial till, and (3) a deep silty loess. Interestingly, these fungi appear to be those most closely allied with aspen. For example, the following fungi are almost strictly with aspen (or birch) and are extremely rare in conifer forests and possibly absent altogether: *Lactarius controversus* (Fr.)Fr.; *Russula aeruginea* Lindbl.:Fr.; *Cortinarius trivialis* Lge.; *Cortinarius subbalaustinus* R. Hry.; *Hebeloma insigne* Smith, Evenson, and Mitchell; *Hebeloma populinum* Romagn.; *Paxillus vernalis* Watling; *Leccinum aurantiacum* (Bull:St.Amans) SF Gray; and *Leccinum insigne* Smith, Thiers & Watling. This close alliance, regardless of soil type, appears more characteristic of older aspen stands with sufficient organic matter and nutrient availability. *Amanita* species are the exception, occurring also in conifer woods, and could possibly be "crossover" species in successional processes.

Over one-third (37%) of the mycorrhizal fungi were found only on the acidic, sandy, nutrient-poor soil of the Butte-Anaconda site, where smelters have impacted the area, and high concentrations of copper, lead, and zinc are present. This subset of aspen's mycorrhizal flora prefers or tolerates these conditions. Many of these species are rather nonspecific in regard to host plant, and are considered "early colonizers" occurring with many species of young trees.

Thelephora terrestris Fr., *Laccaria laccata* Peck, *Laccaria proxima* (Boud.) Pat, *Hebeloma mesophaeum* (Fr.) Quel., and *Inocybe lacera* (Fr.:Fr) Kummer have all been observed on smelter sites, in coal spoils, and with many species of young trees in open habitats. These same fungi have been observed with aspen on smelter sites in Kellogg, Idaho, and Trail British, British Columbia (Cripps 1996). Since aspen is often the pioneering species in smelter-impacted areas of Montana and Idaho, these fungi have a potential value for use in reclamation. In contrast, many species of ectomycorrhizal fungi are inhibited by low pH and high metal content in soils (Harris and Jurgensen 1977; Hung and Trappe 1983; McCreight and Schroeder 1982). Other mycorrhizal species are believed to ameliorate effects of heavy metals in plants (Hartley et al. 1997).

For birch, the succession of mycorrhizal fungi on a tree is predictable, with early stage fungi colonizing young seedlings, followed by the prevalence of late stage fungi with older trees (Last et al. 1987). The succession of mycorrhizal fungi on aspen in the study area appears to start with the early colonizers listed above, which are eventually replaced by fungi more restricted to aspen. Given aspen's clonal nature, microhabitat could play more of a role in species distribution. Early colonizers often occurred in young aspen stands or with young roots on the edge of older clones. Late colonizing fungi preferred the interior of aspen stands with a relatively well-developed soil and understory. It should be kept in mind, however, that fungal sporocarps are not necessarily indicative of the predominance of a fungus in the soil and on the plant roots.

Screening native mycorrhizal fungi as inoculum for aspen

Only a limited number of mycorrhizal fungi were examined for their effect on aspen seedlings because many of the species do not grow or grow well in culture. Others with a high potential for use as mycorrhizal inoculum such as *Hebeloma*, *Laccaria*, *Thelephora*, and some *Tricholomas* are yet to be tested. Although mycorrhizal fungi enhanced the growth of young aspen, sometimes remarkably so, with a two- to four-fold increase in biomass, this is not necessarily indicative of enhanced establishment and survival of aspen seedlings under natural conditions. Field and pot experiments need to follow this in vitro study to evaluate inoculated aspen as outplantings and in greenhouse conditions. Anselmi et al. (1990) did report a significant increase in aspen volume with fungal inoculation of most species in pot cultures. In our study, stem diameter and height increased with inoculation of about half of the fungal species. How growth parameters translate into increased fitness of aspen is another question.

What may not be obvious from our results is that each mycobiont affected the morphology of aspen in a recognizable manner for the given conditions. For example, inoculation with *Cenococcum* produced tall, pale seedlings with long, narrow leaves and long petioles. Aspen inoculated with *Tricholoma* had leaves that were two times as wide and long as the control, and plants in general were a deep rich green. Whether morphological changes produced by mycorrhizal fungi translate into form differences in older trees is not known but is an intriguing idea. The fact that various mycorrhizal fungi differ in their effect on aspen suggests that the physiology of each union is unique and that each fungus plays a particular role in the ecology of a host plant. For example, *Cenococcum* is known to tolerate drought conditions that inhibit other mycorrhizal fungi, and this fungus could be a crucial survival link in conditions of water stress. One could speculate that the diversity of fungi belowground in aspen stands enhances aspen's ability to survive a variety of conditions.

The percentage of mycorrhizal roots was not directly correlated with increases in aspen biomass, stem diameter, and height. The biomass of aspen increased substantially with addition of some fungi, but in most cases only a low percentage of roots were colonized in the given time period. This could be a result of high efficiency nutrient transfer through a small number of individual mycorrhizae or due to pre-mycorrhizal effects such as release of IAA. *Boletus piperatus* doubled the number of roots and increased the biomass of aspen seedlings without forming mycorrhizae, again suggesting a pre-mycorrhizal event such as hormone production by the fungus. *Pisolithus tinctorius* (PT) formed mycorrhizae quickly and extensively, covering the roots system in a few weeks and producing dark green healthy plants. PT is sold as a commercial inoculant, but is not native in Montana and Idaho and has failed in field trials in Oregon (Castellano and Trappe 1991). Inoculation with *Inocybe lacera* killed all the aspen seedlings, which could be due to an associated yeast or the high nutrient conditions that might increase its pathogenicity. *Inocybe lacera* typically occurs in sandy, nutrient-poor soil. The morphology of each type of mycorrhiza is unique and recognizable for each fungal species (Cripps and Miller 1995; Cripps 1997).

Nursery conditions can preclude or slow fungal colonization, since fertilizers are usually antagonistic to mycorrhizal formation. Mycorrhizae were slow to form in our study, and methods to speed up the process are necessary for commercial production. Some of the mycorrhizal inoculum tested produced aspen with discolored leaves, spotted black, red, and yellow. This is not a desirable quality for commercial plants, unless outplanting success can be proven to outweigh undesirable cosmetic problems. Another possibility is selecting a proper soil inoculum that could circumvent these problems (Helm and Carling 1990).

Native ectomycorrhizal fungi that are likely candidates for use in reforestation and reclamation with aspen are: *Paxillus vernalis, Tricholoma scalpturatum, Cenococcum graniforme* Fr., and some yet to be tested (*Laccaria* spp., *Hebeloma mesophaem, H. populinum,* and *Thelephora terrestris)*. Care must also be taken in the nursery because *Pisolithus tinctorius* (Pers.) Coker & Couch and *Thelephora terrestris* have been known to adversely affect young plants, and proper timing for inoculation may be essential. It is also advantageous to know the soil type for outplantings. *Hebeloma* species are more likely to associate with young aspen under high fertility conditions such as lawns. Other fungi such as *Thelephora, Paxillus,* and *Cenococcum* may be more useful in heavy metal soils of low fertility.

Summary

Each aspen stand hosts a diverse community of mycorrhizal fungi as determined by soil type, age of the aspen stand, geographic region, and other edaphic and historical factors. Young aspen in pioneering situations, such as post-fire and smelter sites and previously unforested land, depend on "early stage" mycorrhizal fungi such as *Inocybe, Laccaria, Hebeloma, Thelephora,* and *Paxillus* for establishment and health. Their occurrence on the Butte-Anaconda smelter site also suggests a tolerance for heavy metals in some strains. Many of these "weedy" species of fungi also occur with young conifers. These are the fungi most likely to be of use in mined-land reclamation, and our results suggest they increase aspen biomass, height, and stem diameter in vitro. Further tests of outplantings are necessary to determine whether these mycorrhizal fungi enhance establishment of aspen on actual mine sites. In older aspen stands, "late stage" mycorrhizal fungi make up a large part of the mycoflora, and these are species more closely allied with aspen than other tree species.

Soil type and other factors can affect the "succession" of mycorrhizal fungi. The impacts of various management strategies such as clear-cutting and fire on the mycorrhizal communities of aspen are not known. However, this should be given consideration, since management practices could apply selective pressures that promote certain species of mycorrhizal fungi, possibly to the exclusion of others, with long-term unintended consequences.

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Aspen Ecosystems: Objectives for Sustaining Biodiversity

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Abstract—*Recognizing the historical abundance of major vegetation cover types is the foundation for estimating the magnitude and significance of conversion from one cover type to another and the proportion of existing cover types that are in properly functioning condition. Techniques to determine desired conditions are discussed. Existing situations for the need to treat ecosystems where aspen (*Populus tremuloides *Michx.) occur are prioritized: highest—mixed-conifer with aspen but where conifers comprise greater than 50% of the canopy; high—aspen/sagebrush transition; and moderate—aspen dominated landscapes. Though aspen stands are evaluated, aspen landscapes are discussed in the context of aggregations of many stands. Within aspen dominated landscapes, five risk factors help determine the need for action: (1) conifer understory and overstory cover is greater than 25%; (2) aspen regeneration (5–15 feet tall) is less than 500 stems/acre; (3) aspen canopy cover is less than 40%; (4) dominant aspen trees are greater than 100 years old; and (5) sagebrush cover is greater than 10%. Management recommendations for treatments, as well as examples of successes and failures of efforts to restore aspen ecosystems, are summarized. Actions to restore aspen ecosystems must not be taken before excessive browsing by livestock and wildlife is addressed.*

Introduction

Quaking aspen is the most widely distributed tree species in North America and as such has tremendous ecological amplitude. On a local scale, this ecological amplitude is manifested by the species' ability to occupy sites over great elevational ranges, differing aspects, and contrasting soils from deep mollisols to steep talus and scree slopes.

Aspen Clones

The clonal habit of quaking aspen adds to its uniqueness among tree species. It is possible for a clone with as many as 50,000 stems, all genetically identical, to occupy more than 200 acres and trace their common heritage to the germination of a single aspen seedling perhaps millennia ago (Barnes 1975; Kemperman and Barnes 1976). Such a clone has weathered the test of time on that site. Even the most decadent clones should be recognized as superior genotypes that have survived the process of natural selection and are most likely some of the best suited genetic material for that site.

Aspen clones exhibit high genetic diversity. Clones on similar sites may respond differently to treatments or environmental stresses. Such differences may be manifest in the number of suckers produced, browsing impacts, susceptibility to certain diseases, frost damage, and so on. Always keep the clonal concept in mind when comparing the responses of different aspen stands.

The preceding information gives insights about aspen, the species itself. However, for the remainder of this discussion, we shift the focus from a single tree species to the unique ecosystems that occur and are sustained when aspen

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dominates stands and provides a mosaic of compositionally and structurally diverse patches on the landscape. Aspen dominated landscapes are an aggregation of many aspen dominated stands and perhaps other stands where aspen remains a component of the canopy.

A Keystone Species

Wilson (1992) explained the concept of keystone species with the following passage:

> In communities there are little players and big players, and the biggest players of all are the keystone species. As the name implies, the removal of a keystone species causes a substantial part of the community to change drastically.

He defined a keystone species as:

> A species that affects the survival and abundance of many other species in the community in which it lives. Its removal or addition results in a relatively significant shift in the composition of the community and sometimes even in the physical structure of the environment.

Aspen is a keystone species. With the exception of riparian areas, aspen communities are considered the most biologically diverse ecosystems in the Intermountain West (Kay 1997). However, as aspen dominated landscapes convert to other cover types, tremendous biodiversity is lost (Bartos and Amacher 1998; Bartos and Campbell 1998a,b). These losses include not only vascular plants and vertebrate animals but also nonvascular and invertebrate organisms. Thus, measures taken to sustain aspen ecosystems will also meet coarse-filter objectives for sustaining biodiversity.

Properly Functioning Condition

In 1996, the Intermountain Region of the USDA Forest Service began a process that expanded the concept of proper functioning condition introduced by the Bureau of Land Management (Barrett et. al. 1993) and originally applied only to riparian communities. This new concept of properly functioning condition applied to the major upland vegetation cover types and provided an ecological basis for a rapid assessment of general conditions of sustainability on large landscapes. Properly functioning condition is defined with this statement (USDA Forest Service 1997):

> Ecosystems at any temporal or spatial scale are in properly functioning condition when they are dynamic and resilient to perturbations to structure, composition, and processes of their biological or physical components.

That definition is often too technical to use with general audiences (e.g., school classes or public meetings). This alternate definition attempts to convey the same meaning:

> Properly functioning condition exists when soil and water are conserved, and plants and animals can grow and reproduce and respond favorably to periodic disturbance.

Properly functioning condition is not a single state in time or space. Indeed, properly functioning condition includes a range of conditions and situations that allow for the full variation of composition (numbers and kinds of species) and structure (size and age classes) within the processes of functioning ecosystems for that specific cover type.

Properly functioning condition is intended to be a rapid assessment, a triage, to prioritize general conditions on large landscapes. Assessments were made at multiple scales. Some assessments were made for the entire Intermountain Region. Then a more detailed assessment was made for the Utah High Plateaus and Mountains section in south-central Utah. The concept of properly functioning condition used in this paper ties to all of these assessments. The ideas presented in this paper are applicable, at a minimum, throughout the Intermountain West.

Historical Conditions

Baker (1925) wrote about aspen in the central Rocky Mountains and included a fire history case study from Ephraim Canyon on the Wasatch Plateau in central Utah:

> …These results indicate that small, light fires occurred at intervals of 7 to 10 years in the same general region previous to the settlement of the country. After the logger and stockman invaded the mountains, there was a period of frequent and larger fires, after which fires became fewer and fewer, and now virtually none occur.
>
> …Conifers are, of course, more resistant to fire when past the sapling stage, but once destroyed they seed in slowly. A 50-year fire rotation would probably keep conifers entirely out of all the aspen type, except on north slopes or in moist localities favorable to the rapid development of the coniferous trees, although aspen would flourish under such conditions. But under present conditions, fire is not a factor to be reckoned with in forest management in the aspen zone.

Baker's description from 75 years ago is a valuable assessment from a trained forest examiner.

We assume that if aspen are present, even a single aspen, then the area has had an aspen cover type at some time during the past 200 to 400 years. The areas where aspen occur typically had fire return intervals of 20 to 60 years. Aspen are not considered capable of establishing true seedlings under a conifer canopy. True aspen seedlings in the Great Basin and central and southern Rocky Mountains would be extremely rare to nonexistent, but aspen do regenerate profusely following a fire. In these situations, the aspen cover type might be considered a fire induced disclimax rather than an early seral stage. Some feel that it is "normal succession" for aspen to be replaced by a conifer cover type. Based on Baker's (1925) observations and these assumptions, we affirm that it is not "normal" for conifers to completely replace the aspen cover type. However, historical aspen cover types are replaced by conifers or sagebrush with the absence of frequent fires and the presence of heavy browsing by livestock and wildlife.

Repeat photos or historical photos (Rogers et. al. 1984; Kay, in press), fire histories (Chappell et. al. 1997), and landscape assessments (Jackson et. al. 1998) combine to provide an indication of the abundance, historically, of the major cover types on the Fishlake National Forest.

Soils inventories can also be used to provide a better understanding of the historical cover types for certain landscapes. The Fishlake National Forest is fortunate to have the soils mapped and GIS layers created at a scale of 1:24,000 largely through the efforts of soil scientist Michael D. Smith. We displayed this information for the Monroe Mountain subsection and reported that the historical (during the past 200 to 400 years) abundance of the aspen cover type was nearly 71,000 acres (Bartos and Campbell 1998a). Of that amount, currently about 17,000 acres remain in the aspen cover type. Almost 42,000 acres is dominated by mixed-conifers [largely subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with some Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)] scattered throughout. Also, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*

(Rydb.) Beetle) replaced the aspen cover type on nearly 12,000 acres. Fire history data, soils survey data, presence of old aspen logs in a sea of sagebrush, and abundance of heavily browsed aspen suckers at the sagebrush/aspen ecotones all indicate that fewer fires and heavier ungulate pressure contributed to this cover type conversion. Aspen decline occurs when landscapes with aspen are outside of properly functioning condition.

The desired condition should not be identical to the historical condition. Much has changed on these landscapes. Changes include new socioeconomic factors that preclude the landscapes from returning to presettlement conditions.

Social Assessments

We talk about properly functioning condition and desired conditions. Some might say, “Properly functioning condition, how pompous!” Others may question, “Properly functioning to whom? Desired to whom?” The answers to these questions are really social assessments. The techniques necessary to determine desired conditions are those that promote and encourage healthy interpersonal relations. Use of the following 4 C’s in the planning and management phases helps determine the desired condition for a landscape (Mrowka and Campbell 1997):

- Commitment: devote the time and resources to allow the process to occur and mature.
- Communication: talk and interact willingly and openly with each other.
- Collaborative sharing: promote intense and enthusiastic sharing of information.
- Cooperation: work together; walk the talk; make it happen!

Without consistent application of these key concepts, support for efforts to move these landscapes toward the desired condition within the range of properly functioning condition will not mature. And most landscapes with aspen present will not be sustained into the next century or even decades in some cases.

Characteristics of Aspen Stands in Properly Functioning Condition

Aspen stands in properly functioning condition will often have the following characteristics: multi-aged stems in the stand, adequate regeneration to perpetuate the stand, age classes mostly less than 100 years old, and good undergrowth beneath the canopy. Both compositional and structural diversity are important.

An argument could be made for any acre of land to be in properly functioning condition as long as that acre does not have compositional and structural characteristics similar to most of the surrounding area. Comparing and contrasting a smaller area (e.g., the stand) in the context of a larger landscape is critical to recognizing the diversity of a landscape in properly functioning condition. Landscapes (aggregations of stands) that are compositionally and structurally homogeneous are not in properly functioning condition.

Risk Factors for Stands With Aspen

We prioritized situations where actions are needed to sustain landscapes with aspen. The highest priority is the mixed-conifer/aspen cover type (particularly where subalpine fir dominates). High priority exists for the aspen/sagebrush transition. Also, action is needed on aspen dominated landscapes where the risk factors are present (Bartos and Campbell 1998a). The five risk factors for aspen dominated stands are:

- conifer cover (understory and overstory) greater than 25%;
- aspen canopy cover less than 40%;
- dominant aspen trees greater than 100 years old;
- aspen regeneration less than 500 stems per acre (5 to 15 feet tall); and
- sagebrush cover greater than 10%.

Prioritized Key to Risk Factors for Landscapes With Aspen

The risk factors described above are considered in the prioritized key to risk factors associated with stands where aspen is present in the Intermountain West (table 1). We feel that the ecological underpinnings of this key have application to areas beyond the Intermountain West. However, we recognize that within the extensive range of quaking aspen distribution, there might be situations where this key is not applicable.

Three different categories of cover are referred to in this key. Canopy cover is the percent of the ground surface that is covered from directly overhead by the crowns of dominant and codominant trees. Overstory cover would be that cover that is provided by trees, including the subcanopy, that are greater than 5 feet tall. Understory cover is the percent of ground covered by individual plants that are less than 5 feet tall.

In the key, couplet 1 refers to relative cover; couplets 2 through 5 use absolute cover. Therefore, elements 1b and 2a are not inconsistent. In couplet 1, for example, even though total conifer canopy cover might be 60%, if total aspen canopy cover is 70%, then 1b is the appropriate choice. Also, for element 2a to be selected, the actual aspen canopy cover could be 35% while the conifer canopy cover might be 25%, but sagebrush would exceed 15% cover.

Clearly, situations that have the greatest risk and the highest priority are those where canopy cover from conifer species combined exceed the canopy coverage from aspen. These are mixed-conifer rather than aspen cover types.

Table 1—Key to the risk factors used to prioritize areas with aspen for restoration and conservation actions in the Intermountain West. Assumption: Aspen are present with a density of at least 20 mature trees per acre. Note: Couplet 1 refers to relative cover; couplets 2 to 5 use absolute cover.

1.	a. Conifer species comprise at least half of the canopy cover.	Highest priority
	b. Aspen comprises more than half of the total canopy cover.	2
2.	a. Aspen canopy cover is less than 40%; *and* sagebrush, usually a dominant understory species, exceeds 15% cover.	High priority
	b. Not as above.	3
3.	a. Conifer cover (including overstory and understory) exceeds 25%.	Moderate to high priority
	b. Conifer cover is less than 25%.	4
4.	a. Aspen regeneration (5 to 15 feet tall) is less than 500 stems per acre.	Moderate priority
	b. Aspen regeneration exceeds 500 stems per acre.	5
5.	a. Any two of the following three risk factors are represented: 1—Aspen canopy cover is less than 40%. 2—Dominant aspen trees are greater than 100 years old. 3—Sagebrush cover exceeds 10%.	Low to moderate priority
	b. Two of the three risk factors in 5a are not represented.	6
6.	a. One of the three risk factors in 5a is represented.	Low priority
	b. None of the risk factors above are represented.	Candidate for properly functioning condition

However, with proper treatments the aspen cover type can usually be restored and sustained. The literature is sparse with reference to stocking or the minimum number of mature aspen that are necessary to expect adequate regeneration of the aspen stand. Peterson and Peterson (1992) provided some guidelines applicable to Ontario and suggested stands need at least 16 parent aspen stems per acre to produce the minimal acceptable stocking and about 50 parent aspen stems per acre to fully stock a stand. Thus, for the key, we assume that at least 20 mature trees per acre are present. There might not be sufficient aspen roots to restock a stand if fewer than 20 trees per acre are on site. Also, areas with aspen canopies less than 40% and sagebrush greater than 15% have a high risk and high priority for aspen restoration treatments. As the risk factor key indicates, stands dominated by aspen have a lower risk and lower priority for treatments to sustain the aspen ecosystems. However, if some situations are not addressed, even these stands might not be sustained into the 22nd Century.

Rules of Thumb to Identify Aspen Stands at Risk

1. If the profile of the aspen stand is rounded or sloping to the ground with foliage extending to the ground, the stand is probably not seriously at risk. If the white boles of mature trees can be seen from a distance, then the stand is most likely at risk. However, if the edge of a stand also marked the boundary of a clearcut, then the stand may not be at risk and young aspen will grow up in the clearcut to eventually mask the white boles at the edge of the stand.

2. Often we can observe aspen stands on distant ridges from the valley or other areas below the stand. Conditions are not right in the stand if sky can be seen between the canopy of the stand and the ground or understory in the stand.

3. Where aspen occurs at the sagebrush transition, if careful inspection of individual sagebrush plants adjacent to (within 25 to 100 feet) an aspen stand reveals young aspen suckers that have been hedged or browsed for several years and yet are still trying to grow, then the stand might be considered at risk of loosing the aspen component. Hedging and browsing of the aspen regeneration is likely occurring also within the aspen stand to the point that most if not all of the regeneration is gone. These individual sagebrush plants become tiny exclosures that offer some protection to the aspen suckers. Such an observation confirms that the aspen stand is still capable of regeneration but not in the presence of heavy ungulate use.

Possible Actions or Treatments for Landscapes With Aspen

Several possible actions or treatments are available for managers to use in treating landscapes where aspen ecosystems are declining and not in properly functioning condition. These actions include:

- rest from use by domestic animals;
- use protection fencing to keep out wildlife and/or domestic animals;
- harvest (remove or cut and leave on site);
- burn (prescribed fires, wildland fire use, and/or wildfires);
- tip over mature trees (use bulldozers to chain or push over trees); and
- sever roots (use single-toothed ripper or similar equipment).

Detailed discussion of these treatments is beyond the scope of this paper. (For further information, see Bartos and Mueggler 1981, Bartos and Mueggler 1982, Bartos et. al. 1991; Kay and Bartos 2000; Mueggler and Bartos 1977; Shepperd 1993; Shepperd 1996.) However, characteristics of the clones, abundance of aspen in acres occupied, potential for utilization by ungulates, fuel loading, available funding, and site conditions are all factors to consider when planning the types of actions used to implement a treatment.

Relief From Excessive Browsing Is Essential

Unwanted utilization of aspen suckers by livestock and wildlife in treated areas is a major reason why many actions fail to rejuvenate and sustain aspen stands. The following statement underscores this situation:

> Heavy browsing of the suckers can deplete aspen root reserves, jeopardize successful regeneration, and threaten the very survival of the aspen stand. Coordinated and difficult decisions are needed before suckering will be successful. *Actions to induce suckering must not be initiated before relief from excessive browsing is obtained* [italics added] (USDA Forest Service 1994).

Examples of both successful aspen regeneration and failures following treatments (e.g., burns and harvests) in areas with aspen present are plentiful. Exclosures and fenceline contrasts provide ample evidence that success (or failure) is often keyed to the absence (or presence) of domestic and/or wild ungulates.

Recommendations

Recommendations for managing landscapes with aspen will require managers to be creative and use the 4 C's (commitment, communication, collaborative sharing, and cooperation) as they endeavor to restore and sustain aspen ecosystem in properly functioning condition. We challenge managers to be bold.

First, take action now! Do not let another decade or two slip by without substantial treatments on the landscape. Gullion (1985) gave a passionate plea for action:

> Some sites that have lost aspen might still be stocked, had a regeneration program started 10 or 20 years ago. Due to their decadence now, it will be difficult to obtain quality regeneration of many stands today, and each year more stands will move into that category. In 30 years, it will be too late to rejuvenate many of the mature stands that are such an important part of Colorado's wildlife habitat and visual resources today.

Fifteen years have now passed since Gullion's call for action. Have sufficient acres been treated in the past 15 years to restore and sustain the diversity of composition and structure?

Second, make actions large. Where landscapes with aspen present are sufficiently large, treat 500 to 1,000+ acres at a time. These acres need not be contiguous but could be several smaller treatments in the same expanded project area. This will help to restore the structural mosaic to the landscape. Also, the larger areas treated will help disperse ungulate pressures, domestic and/or wild.

Third, take action often. Persistence over time is important. A program of successive actions will help to restore structural diversity to these landscapes.

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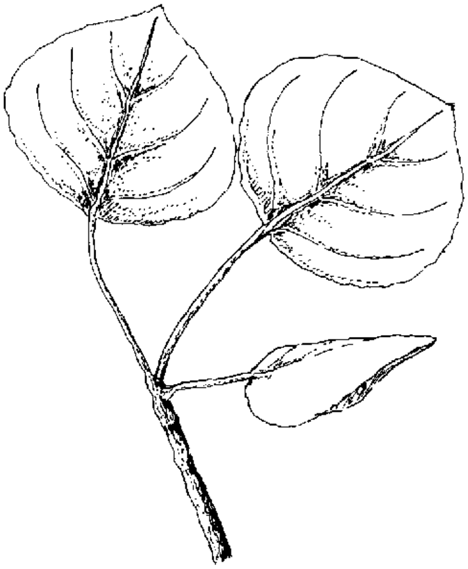

Physiology and Production Ecology

Is the Wide Distribution of Aspen a Result of Its Stress Tolerance?

V. J. Lieffers[1], S. M. Landhäusser[1], and E. H. Hogg[2]

Abstract—Populus tremuloides *is distributed from drought-prone fringes of the Great Plains to extremely cold sites at arctic treeline. To occupy these conditions aspen appears to be more tolerant of stress than the other North American species of the genus* Populus. *Cold winters, cold soil conditions during the growing season, periodic drought, insect defoliation, and competition from conifers are typical stresses faced by aspen. Aspen is capable of high photosynthetic rates but has conservative use of water during high vapor pressure deficits. This paper examines photosynthesis, water relations, morphological characteristics and root growth, and carbon allocation strategies in relation to the above stresses.*

Introduction

By most accounts, poplars are considered to be competitors (Grime 1979) that are adapted for rapid growth in high resource environments (Stettler et al. 1996). Poplars grow most successfully in fertile and moist sites; indeed, high-resource, short-rotation forest plantations have used poplars to achieve very high rates of productivity (Heilman et al. 1996). Poplars are well known for their rapid juvenile growth rates, rapid expansion of leaf area, and high productivity (Heilman et al. 1996). They are generally considered to be fast growing colonizers and intolerant of stresses such as low moisture conditions or shaded environments. In contrast, stress-tolerating species often have slower growth rates but are able to withstand environments that are deficient in nutrients, water, or light (Grime 1979). Slower growth rates are often correlated with greater tolerance to stress (Lambers et al. 1998).

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed poplar in North America ranging from Alaska, to scattered locations in Mexico, and east to New Brunswick (Perala 1990). It is most abundant in the boreal forest zone but it can survive at both the arctic treeline and at the drought-prone fringes of the Great Plains. A large proportion of the genus *Populus* grows almost exclusively on riparian and moist sites (Braatne et al. 1996). Trembling aspen, however, is very widespread and can form extensive stands in upland sites, as indicated by its dominance of the well to imperfectly drained sites in the boreal forests (Peterson and Peterson 1992) To occupy this wide geographic range of harsh climatic conditions, trembling aspen has to be able to tolerate a wide range of stresses, from extreme cold to drought. Aspen, therefore, seems to be different from most other poplars in that it is able to withstand significant stresses. While it may not have the drought tolerance of some of the conifers such as jack pine or the tolerance to the stresses of alpine treeline such as lodgepole pine or subalpine fir, it seems to be well adapted to tolerate stress, especially compared to other poplars.

The objectives of this paper are to examine some of the morphological and physiological characteristics of aspen compared to other species, particularly the other poplars.

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Clonal Root System

Trembling aspen is noted for its extensive clonal root system (Kemperman and Barnes 1976) with many shallow, widely spreading horizontal roots with occasional sinker roots (Strong and LaRoi 1983). When the aboveground trees die following a stand-replacing disturbance, these shallow roots are the main source of suckers that re-establish the next stand. The section of large roots originating near the stump of this dead tree usually die within a few years. Distal ends, however, remain alive if they sucker (figure 1). Thus, each of the major branches of the parent root becomes separated. There is some controversy in the literature regarding the persistence of root connections between suckers on these major branches. They may break down early (from Colorado, Shepperd and Smith 1993), live as long as 40–50 years (from Michigan, Debyle 1964), or remain as persistent connections between mature trees (from Alberta, DesRochers and Lieffers 2000), even if some intermediate ramets on the parent root system died (figure 2). The different observations recorded above may relate to the degree of root damage sustained from burrowing animals during the life of the stand (Shepperd, personal communication). With the next disturbance event, however, the original connecting roots between trees will likely die as these roots are usually untapered and greater than 5 cm in diameter, which makes them very unlikely to sucker (DesRochers 2000). Root grafting may occur near or under the stumps of trees (figure 3). Thus, even though there is partial loss of the original connectivity of root of the parent generation at the time of each disturbance, the roots systems of the clone may reconnect physiologically by grafts. Separated individual trees could, therefore, potentially share resources and hormones with their neighbors both within, and perhaps between clones. The degree of interconnectivity is difficult to assess without extensive physiological testing or excavation. Connectivity of the clone, however, may have ecological significance as discussed below. Other poplars are capable of stump sprouting and sucker regeneration (Pregitzer and Friend 1996) but it appears that aspen relies upon suckering for regeneration more than the rest of the poplars.

The root systems of mature trembling aspen stands in Alberta were recorded at 23 t/ha (Peterson and Peterson 1992) with the highest values ranging up to 41 t/ha. A significant percentage of this root system could potentially be passed on to the next generation of trees after stand-replacing disturbance. This could be from both incorporation of the parent roots into the structural roots of the suckers and transfer of nonstructural carbohydrates (TNC) to sucker development; TNC of coarse roots from maturing aspen stands are about 15% of dry weight (DesRochers 2000). DesRochers (2000) recorded an average of 8.7 t/ha of roots from 12 regenerating stands in Alberta (values ranged up to 18 t/ha). Given the initially small biomass of the regenerating suckers, regenerating stands have a high root:shoot ratio (Shepperd 1993; Shepperd and Smith 1993). If the suckers can eventually meet the respiration costs of a large root system (summer

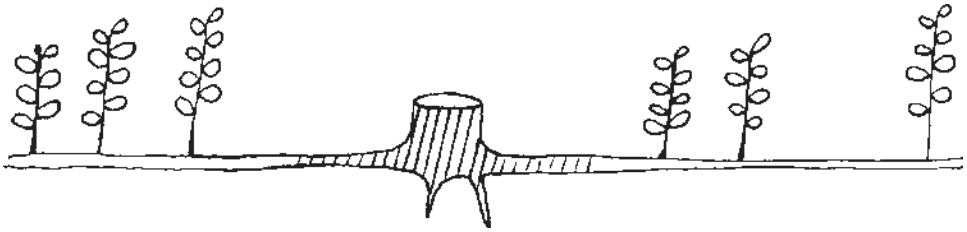

Figure 1—Parental root and suckers. Large roots and original stump of the parent tree (shaded) die shortly after logging or disturbance. Thus, lines of suckers are connected on a root but not necessarily connected to other parent roots.

Figure 2—Root system of aspen in a declining stand. The two trees in the foreground are dead trees with portions of their root system still alive (part of the study by DesRochers and Lieffers 2000).

Figure 3—Grafting of aspen roots. The root in the bottom center, remains alive through a root graft.

rates for coarse roots were recorded at 181 mmol CO2 m^{-3} s^{-1}, at 15 °C [DesRochers 2000]), they should be in a good position to capture water and nutrients from the site. The legacy of the root biomass from the previous stand and the resulting high root:shoot ratio of juvenile stands might allow them to survive a stress (especially drought stress) that might have killed the parent trees or a seedling. Along the dry, northern fringe of the Canadian prairies, aspen stands that die off above ground following drought and/or repeated insect defoliation can simply resucker and reestablish (Peterson and Peterson 1992; Hogg 1994). Regeneration from an established root system seems to be a much more reliable means of reproduction in water stressed environments than from seed. In riparian cottonwoods, Rood et al. (1994) found that 52% of the regeneration of *P. angustifolia*, *P. balsamifera*, and *P. deltoides* was from seedlings, 30% through root suckers, and 18% as resprouts. Seedlings occupied microsites closer to the river while suckers were generally produced in areas away from the river.

Photosynthesis

Photosynthesis rates for trembling aspen range up to 22 µmol m^{-2} s^{-1} (Ceulemans and Isebrand 1996; Landhäusser, unpublished data). These rates are in the same range as most of the high yield poplar clones used in plantations (Ceulmans and Isebrand 1996). Like the hybrid poplars (Ceulmans and Isebrand 1996), aspen produces shade leaves in low light environments (Landhäusser, unpublished data) with a light compensation point of about 25 µmol m^{-2} s^{-1} (figure 4). Leaf dark respiration rates were 1.0 in the understory environment and 2.2 µmol m^{-2} s^{-1} in the open. These values were within the range of other poplars (Ceulemans and Isebrands 1996). Indeed, aspen foliage must have relatively good capability for photosynthesis at low light conditions, as lower foliage in dense stands with high leaf area index would rarely be exposed to high light. Aspen doubles its photosynthetic rates from 5 to 25 °C (Lawrence and Oechel 1983) and photosynthesis declines at temperatures greater than 25 °C. Aspen bark is capable of sufficient photosynthesis to offset the respiration losses from the stem (Foote and Schaedle 1976). While some other poplars have photosynthetic bark in juvenile stages, the fact that aspen bark is usually green and nonthickened even late in life may offer it an advantage over species with thickened bark.

Water Relations

Given trembling aspen's ability to survive on the edge of the drought-prone Great Plains of North America, aspen must have significant abilities to withstand water stress. Aspen appears to react conservatively to both the low soil moisture and high vapor pressure deficit (VPD) typical of drought-prone areas. Stomatal

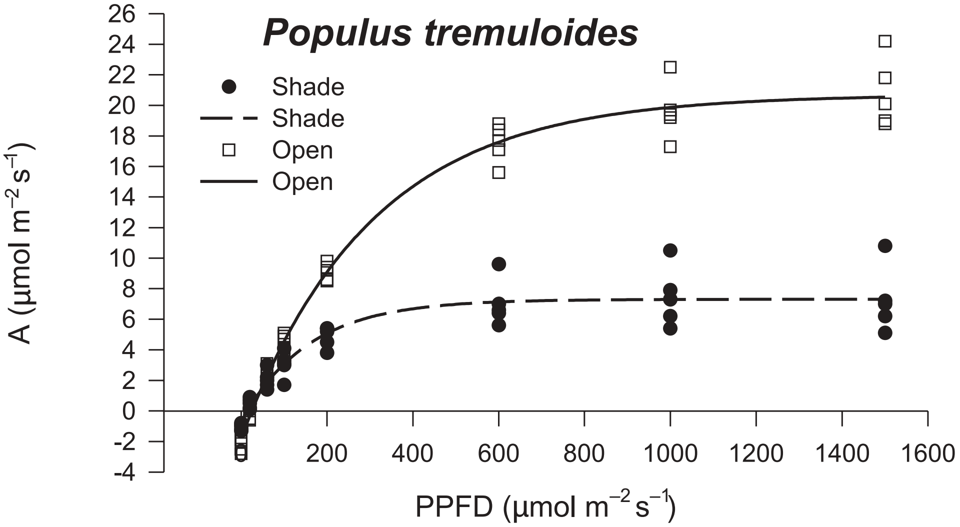

Figure 4—Photosynthetic light response of 2-year-old aspen from seedlings grown in open and understory environments (trembling aspen-balsam poplar stand). Photosynthesis was measured at 20 °C and 40% RH (Landhäusser, unpublished data).

conductance tends to decrease with soil drying (Iacobelli and McCaughey 1993) but also varies inversely with VPD. This leads to reduced photosynthesis on hot days with low humidity (Dang et al. 1997), even when soils are moist (Hogg et al. 2000). An intriguing result of aspen stomatal responses is that daytime transpiration rates remain remarkably constant over a wide range of VPD, from 1.0 to 4.8 kPa (Hogg and Hurdle 1997), thus demonstrating the ability of this species to conserve moisture during periods of high atmospheric demand. At the same time, aspen withstands leaf water potentials of –2 to –3 MPa on most summer days without any apparent impact on photosynthesis rates (Hogg et al. 2000).

In contrast, some of the hybrid poplars have little change in stomatal conductance until there is a large change in leaf water potential (Blake et al. 1984) and there are some clones where stomata are insensitive to VPD, soil moisture, and light levels (Schulte and Hinkley 1987; Ceulemans et al. 1988; Furukawa et al. 1990). Aspen stomatal responses to soil moisture and VPD stresses appear to be operating to maintain water potential above a critical level in an environment where water is frequently limiting, compared to most other poplars that evolved in riparian areas where water supply is usually plentiful and heavy water loss through transpiration is not a critical factor. Given the strongly clonal nature of aspen (Kemperman and Barnes 1976), conservation of soil water may be a critical component of the clone's survival and might have been an evolutionary selection force. With increasing clone size, we speculate that a single aspen clone would exert greater control over stand hydrology so that the rate of soil water depletion might become more strongly coupled with clone-specific transpiration rates. Thus, it could be postulated that during drought, a large clone with high stomatal conductance would deplete its own soil water reserves more rapidly, therefore increasing the risk of mortality of the entire clone.

Under extreme water stress, xylem cavitation may result in vaporization of water, which causes embolism within the conducting elements of the xylem. This prevents water uptake (Tyree and Sperry 1988). Measurements on stem sections of various species show that aspen is far less vulnerable to xylem cavitation than most of the other native poplars in western North America (*Populus balsamifera*, *P. fremontii*, *P. deltoides*, and *P. angustifolia*), which are usually restricted to river floodplains or moist sites (Tyree et al. 1994; Blake et al. 1996). *Populus trichocarpa* is similar to aspen in terms of cavitation resistance, but at least some populations and hybrids of this species are nevertheless vulnerable to cavitation because stomata do not respond to decreases in leaf water potential (Bassman and Zwier 1991), even at values of –4 MPa (Ceulemans et al. 1988).

A few poplar species, including trembling aspen, have strongly flattened petioles, which cause leaves to flutter even in a slight breeze. Fluttering reduces boundary layer resistance to heat transfer, which can cause a cooling of leaf temperature up to 2–4 °C, thus promoting CO_2 uptake on hot days (Roden and Pearcy 1993). Such an adaptation, coupled with the small size of aspen leaves relative to other poplars, might be especially important in preventing overheating of leaves as stomata close to avoid water stress during periods of drought. In boreal forests, aspen is usually confined to the warmest positions on the landscape (Van Cleve et al. 1983). There is virtually no root growth of aspen until soil temperatures are greater than 6 °C while large amounts of roots are produced at 20 °C (Landhäusser and Lieffers 1998). As lignified roots have minimal water uptake and hydraulic conductivity compared to when new non-lignified roots develop (Wan et al. 1999), cold soils will limit water relations.

Cold soils also limit water uptake of roots by reduced activity of water channel (aquaporin) proteins in the membranes (Wan and Zwiazek 1999). Since these proteins require energy to function and cold soils limit respiration, there appears to be insufficient ATP available to allow them to function properly in cold soils (Wan and Zwiazek 1999). These proteins may also be limited by anaerobic conditions, but this needs more work to verify this hypothesis. In contrast, Lawrence and Oechel (1983) found relatively little difference in photosynthetic rates between warm and cold soils; however, in this case, the aspen seedlings were grown in warm conditions and moved to cold soils.

Carbon Allocation

There is developing evidence that differences in photosynthetic rates and water relations among plant species from different ecological niches may often be relatively small. (Reich et al. 1998). Other factors such as C allocation to leaves versus other organs are often the important components for determining growth rates among species or genotypes (Landhäusser, unpublished data). Differences in foliar morphology may also be important in this context (e.g., Niinemets et al. 1998). Leaf area development in aspen is driven by both leaf size and leaf number. Both preformed leaves (flushed from an overwintered bud) and neoformed (initiated during the growing season) are smaller when aspen is grown in cold soils (Landhäusser and Lieffers 1998). Cold soils also result in early bud set on long shoots, greatly inhibiting the production of neoformed leaves (Landhäusser and Lieffers 1998). Thus, in the second half of the growing season, aspen in cold soils appears to horde C in reserves instead of attempting to capture more C by building more leaves. This switch to C storage instead of shoot growth appears to be analogous to the switch that occurs in hybrid poplars in the fall, away from shoot growth to C storage in preparation for winter (Isebrands and Nelson 1983). In other poplars species, smaller leaves are also characteristic of drought and flooding stress (Van Volkenburgh and Taylor 1996). It is likely that cold soils, drought, and flooding all produce water stress and inhibit the leaf expansion rates. Thus, while there may be clonal differences in leaf size, size can be a good indicator of site conditions and the ability of the tree to take up water.

Aspen stands typically develop maximum leaf area at a very early age (Johnstone and Peterson 1980). Leaf area indices (LAI) of 2-year-old stands may be 2 and climb to 4 or 5 by 14–20 years of age (Shepperd 1993; B. Pinno, unpublished data). Based upon light transmission values (Constabel and Lieffers 1996) and litter fall estimations (DeLong et al. 1996), LAI of older stands decline, sometimes to less than 2. It is not clear why LAI declines with age but may relate to increased hydraulic resistance from tall stems, crown abrasion, and/or decreased nutrient supply (Ryan et al. 1997). As older stands have greater biomass to sustain with a smaller leaf area, they are likely more vulnerable to sustained stress. On a stand basis, the LAI of aspen is relatively low compared to hybrid poplars, where values of up to 10 or more have been reported (Heilman et al. 1996). Because these leaves may be positioned more vertically, however, they tend to transmit more light to lower layers than aspen with its more random leaf distribution (Stadt and Lieffers 2000).

Landhäusser (unpublished data) found that in low light conditions, aspen and balsam poplar carbon allocation was opposite to what one would anticipate in a plant growing in an understory. Seedlings of both species grown in shade produced less leaf area, while root:shoot ratio (RSR) was higher compared to open grown conditions. An increase in allocation to roots at the expense of leaf growth is not likely to be adaptive in a light-limited environment. Decreased RSR as a result of increases in leaf area ratio (LAR, $cm^2_{leaf}\,g^{-1}_{plant}$) and leaf mass ratio (LMR, $g_{leaf}\,g^{-1}_{plant}$) are thought to be advantageous to a life in an understory environment (Givnish 1988; Lambers et al. 1998; Reich et al. 1998).

Response of Aspen to Various Stressful Environments

Growth in Extremely Cold Air and Soil Temperatures

Aspen appears to be able to withstand severely cold air temperatures, unlike many other hardwood species that have a cold hardiness limit near –40 °C, corresponding to the freezing point of supercooled water within ray parenchyma (Waring and Schlesinger 1985). In aspen and other boreal species, ray parenchyma cells allow water movement out of cells during cooling, which prevents ice crystal development (Burke et al. 1976), so that dormant twigs can even survive immersion in liquid nitrogen with a temperature of –196 °C (Sakai and Weisner 1973). During the growing season, aspen is relatively frost-tolerant, although foliage does not survive experimental exposure to severe summer frost (–6 °C) (Lamontagne et al. 1998).

Aspen is capable of photosynthesis at relatively low air temperatures of 5 °C or less (Lawrence and Oechel 1983). In contrast, aspen does not perform well under cool soil temperatures (Landhäusser and Lieffers 1998, and see above). Most regeneration of aspen stands in boreal forest regions would have occurred naturally after fire (Rowe and Scotter 1973). Fires reduce insulating litter layers and blackened the soil surface increasing soil temperatures. Hungerford (1988) and Maini (1967) suggest a threshold soil temperature of 15 °C is necessary for successful aspen sucker regeneration. Currently minimal soil disturbance is recommended on northern boreal forest sites after clear-cutting to promote aspen suckering (Navratil and Bella 1990; Bates et al. 1993); however, there have been numerous examples in Northern Alberta where this technique has resulted in sparse and sporadic sucker initiation (Darrah 1991; Landhäusser and Lieffers, personal observation).

Competition From Growth With Other Trees (Notably Spruce)

As noted above, aspen leaves are capable of photosynthesis in low light. This concept is reenforced by the fact that young aspen stands are capable of carrying a large leaf area and the leaves on the lowest parts of the canopy are presumably contributing positively to the carbon balance. In low light conditions, however, aspen allocates resources to root growth at the expense of leaves (Landhäusser, unpublished data). This appears to be an inappropriate strategy for growth in understories. Aspen, like the other species classed as shade-intolerant northern species, has a higher probability of mortality when its growth rates decline than species considered shade tolerant (Wright et al. 1998). In boreal mixed-wood forests, aspen is an early colonizer but usually it is eventually replaced by white spruce (*Picea glauca* [Moench] Voss) (Lieffers et al. 1996). As aspen stands age, there is a gradual decline in aspen leaf area (Lieffers and Stadt 1994), increase in stem decay (Peterson and Peterson 1992), and gradual or episodic mortality of stems (Hogg and Schwarz 1999). In mixed-wood stands this is usually accompanied by development of spruce. As spruce is more shade tolerant and capable of growth in cold soils (Van Cleve et al. 1983), the gradual buildup of insulating forest floor litter with aging of the stand and the shift from warm soils with ample nutrients to colder soils with lower mineralization rates could be important in understanding the decline of aspen with concurrent development of spruce.

Drought and Insect Defoliation

One of the responses of aspen to dry soil conditions is reduced height growth and reduced maximum height growth. This may be seen by a striking reduction in maximum height moving from boreal forest where precipitation is greater than evaporation to the drought-prone parklands of the Canadian prairie provinces (Maini 1972; Hogg and Hurdle 1995). In the extreme examples of this phenomenon, especially in windy areas, krummholz-type forests of aspen develop (figure 5). These stunted forests are subject to widespread dieback following years with severe prairie drought (Bailey and Wroe 1974; Hogg and Lieffers , personal observation).

In the boreal forest, moisture is a significant factor affecting interannual variation in aspen radial growth (Hogg and Schwarz 1999), but under the present climate at least, drought is rarely severe enough to cause aspen dieback except in combination with other stresses. One of the major stresses on aspen is defoliation by insects such as the forest tent caterpillar (*Malacosoma disstria* Hbn.), which can affect vast areas of the landscape (>500 x 300 km) during major outbreak years such as in 1988 (Emond and Cerezke 1989). Severe defoliation causes dramatic reductions in stem growth (figure 6), but its impact on stem mortality is often not evident until several years following major outbreaks (Churchill et al. 1964). Thus, the causes of dieback can be difficult to determine.

Figure 5—Stunted aspen growing in windy open sites in the West Castle Valley, Alberta.

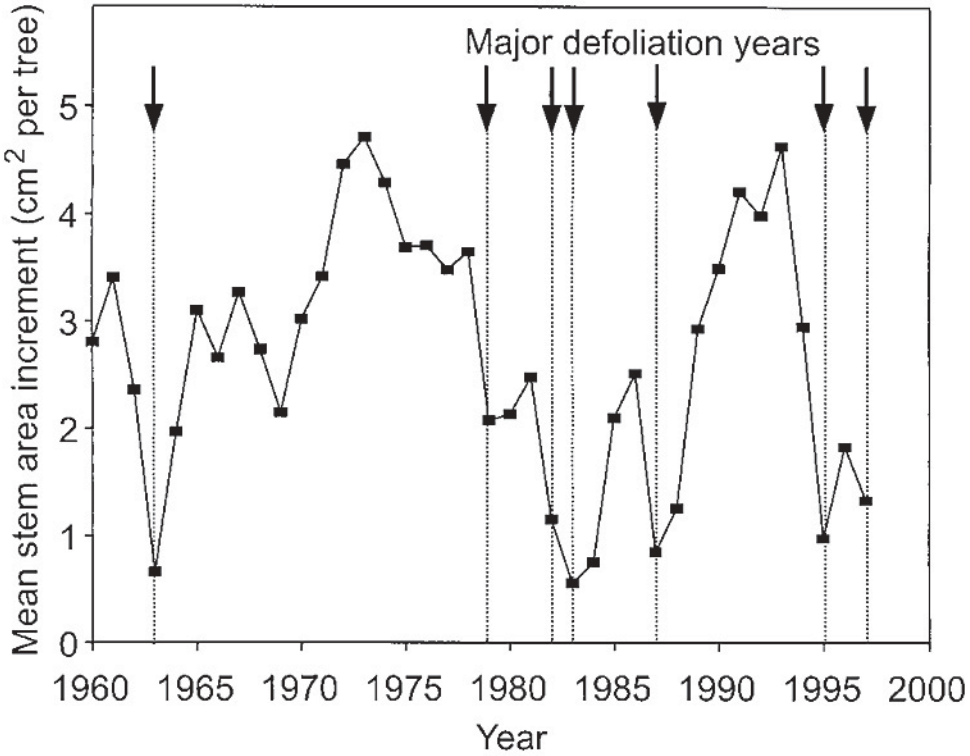

Figure 6—Growth of aspen in relation to defoliation by forest tent caterpillar in a 53-year-old stand in northwestern Alberta, Canada (55° 28′N, 118°23′W). Growth is expressed as mean stem area increment of 10 trees, based on tree rings in disks collected at 1.3 m height). Major defoliation years are shown (1963, 1979, 1982, 1983, 1987, 1995, and 1997). The stand showed significant crown dieback and was affected by three fungal pathogens (*Armillaria, Venturia,* and *Phellinus*) when sampling was conducted in 1997 (part of study by E.H. Hogg, J.P. Brandt, and B. Kochtubajda, unpublished).

Since the early 1990s, extensive dieback of aspen stands has been noted in some areas of the western Canadian boreal forest and adjacent parkland. A recent retrospective analysis using dendrochronology indicated that the dieback was caused primarily by insect defoliation during several consecutive years throughout the 1980s, in combination with drought (Hogg and Schwarz 1999). However, aspen stands showing dieback also usually exhibit symptoms of subsequent damage by fungal pathogens and wood-boring insects (Churchill et al. 1964; Hiratsuka 1987; Ives and Wong 1988). Thaw-freeze events during winter and spring can also lead to crown dieback (Cayford et al. 1959; Cox and Malcolm 1997); such events are especially common near the Rocky Mountains where chinook winds are most intense. Thus, there is a wide variety of stresses, both biotic and abiotic, that aspen, through its continued persistence over much of North America, has demonstrated that it can withstand.

Conclusions and Needs for Further Research

Because of its clonal nature and persistent interconnections through retention of parent roots or reestablishment of connections through root grafts, many aspects of the physiology of natural stands of aspen are extremely difficult to study, particularly C allocation strategies. Aspen clones occupy large areas in drought-prone upland sites. Because of the increased occurrence of drought, aspen appears to have more conservative water use during periods of high VPD. This response may have developed to maintain soil water reserves during periods of extended drought.

Relative to white spruce and other boreal forest conifers, aspen does not grow well in cold soils. This appears to be driven by reduced respiration slowing the activity of root water channel proteins. As aspen is more tolerant to extremely cold air temperatures than other poplars, however, it is likely that it also has better adaptations to cold soils than other poplars (except perhaps for *Populus balsamifera*), but this would need to be studied further by comparative studies.

Understanding aspen's response to competition from conifers is complex. Aspen has high photosynthetic rates in strong light and low VPD. Aspen is capable of producing shade leaves that have a low light compensation point, but saplings may actually decrease their leaf area in shaded conditions, which negates the benefits of a low compensation point. As stands age and the coniferous component increases, there is a buildup of forest floor litter and more interception of solar radiation, especially in winter and early spring. This likely causes a net cooling of soils and decreases in root activity or mineralization rates, which may in turn inhibit the aspen growth. These components need more study.

There is a vast literature on hybrid poplars and a large literature on aspen, but there has not been a comprehensive comparison of aspen with other poplars in responding to the wide variety of stresses mentioned above. While it would be useful to compare aspen with other poplars, particularly hybrids, it is possible that comparisons in block plantings may give unrealistic results because the benefits of conserving moisture may not be apparent when many clones are drawing from the same limited water resource.

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Modeling Aspen Responses to Climatic Warming and Insect Defoliation in Western Canada

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Abstract*—Effects of climate change at three aspen sites in Saskatchewan were explored using a climate-driven model that includes insect defoliation. A simulated warming of 4–5 °C caused complete mortality due to drought at all three sites. A simulated warming of 2–2.5 °C caused complete mortality of aspen at the parkland site, while aspen growth at two boreal sites showed little change from the present climate until after insect defoliation, when dieback was more severe under the warmer climate. The results suggest that future impacts of climate change on boreal aspen forests may not become evident until after major insect outbreaks have occurred.*

Introduction

Populus tremuloides Michx., commonly known as trembling aspen by Canadian researchers, is the most important deciduous tree species in the North American boreal forest. It is especially abundant as pure and mixed wood stands in the southern boreal forest of western Canada, where it has become a major commercial species for forestry over the past 10–15 years (Peterson and Peterson 1992). Trembling aspen is also the primary native tree species in the aspen parkland, a predominantly agricultural zone located between the boreal forest to the north and the prairies to the south. Under the climatically dry conditions in the parkland, aspen forms stunted patches of forest that are prone to crown dieback following periods of drought (Zoltai et al. 1991).

The western Canadian interior is projected to experience relatively rapid warming in response to continued increases in atmospheric concentrations of CO_2 and other greenhouse gases (e.g., Watson et al. 1996). Indeed, the climate record indicates that this region has already warmed by between 0.9 and 1.7 °C between 1895 and 1992 (Environment Canada 1995). Although much uncertainty remains, most General Circulation Model (GCM) projections suggest that precipitation will not increase sufficiently to offset the higher rates of evapotranspiration expected under the expected future warming, thus leading to drier soils and potentially more severe drought (Zoltai et al. 1991). If this occurs, the southern boreal forest of western Canada could develop a future climate similar to that presently found in the parkland, which would pose a major concern for the future productivity of aspen forests in the region (Hogg and Hurdle 1995).

Since the early 1990s, crown dieback and increased stem mortality has been noted in some areas of the southern boreal forest and adjacent parkland in the Canadian provinces of Saskatchewan and Alberta. A recent study of aspen tree rings in the Bronson Forest of western Saskatchewan (Hogg and Schwarz 1999) indicated that repeated defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.) during the 1980s was the major cause of reduced growth and dieback, but that drought was also a significant contributing factor. Forest tent caterpillar and other insects are an important component of the natural functioning of boreal

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aspen ecosystems, because during major outbreaks, they periodically severely defoliate several million ha of forested landscapes across distances of >1,000 km (e.g., Brandt 1995). Thus, the impacts of these insect defoliators needs to be considered when projecting future climate change effects on the forests of this region.

As a first step toward understanding how climate and insect defoliation affects productivity and dieback, a computer model was developed and tested against the results of tree-ring analysis at two aspen-dominated sites in Saskatchewan. These sites included the Bronson Forest (Hogg and Schwarz 1999), located at the southern edge of the boreal forest, and Batoche, a stressed aspen forest in the dry parkland zone (Hogg and Hurdle 1995). The model (Hogg 1999) is carbon-based and driven by daily climate data, with a structure similar to FOREST-BGC (Running and Coughlan 1988), but includes insect defoliation and additional features relevant to a deciduous forest canopy. Sensitivity analysis of the model indicated that simulated aspen biomass would be strongly affected by small changes in air temperature and defoliation severity; however, the combined impacts of climate change and insect defoliation were not examined.

The objective of the present study was to examine modeled aspen responses under a generalized, 2X CO_2 scenario of climate change (Hogg and Hurdle 1995) based on the Canadian Climate Centre GCM2 (Boer et al. 1992). Specifically, I examined how the presence or absence of insect defoliation may affect aspen sensitivity to this climate change scenario, in terms of aspen stem productivity, biomass accumulation, and severity of dieback. Simulations were conducted at three aspen sites located in climatically sensitive areas of Saskatchewan. These sites included the two aspen sites modeled previously (Hogg 1999), as well as a boreal aspen site. This boreal site was used for intensive measurements in BOREAS, a large, international study of forest-atmosphere interactions (Sellers et al. 1997), and is currently one of the tower sites for a longer term, subsequent study called BERMS (Boreal Ecosystem Research and Monitoring sites).

Methods

Study Sites

The three sites used for model simulations are all pure aspen stands, situated along a climatic moisture gradient from the dry parkland (Batoche site) to the southern boreal forest (BERMS site) of Saskatchewan. The Bronson Forest site, situated in the transition zone between parkland and boreal forest (Zoltai 1975), has a climate that is intermediate between the Batoche and BERMS sites (table 1). At Batoche, the aspen has a stunted growth form and stems are frequently forked, crooked or leaning (Hogg and Hurdle 1995). Stands often include two or three age classes, probably due to stand opening during previous dieback events. In the Bronson Forest, stands are taller (table 1) and generally even-aged but many clones show evidence of severe crown dieback and decline (Hogg and Schwarz 1999). At the BERMS site (Hogg et al. 1997), the aspen forest is even-aged, with straight, healthy stems and shows little evidence of crown dieback. Soil texture is sandy at Batoche and varies from sandy loam to clay loam in the Bronson Forest and BERMS sites.

Tree-Ring Analysis and Past Insect Defoliation

Tree-ring analysis was conducted on two radii per tree from increment cores or disks collected from aspen stems at 1.3 m height. Ring width measurements

Table 1—Summary of site characteristics for aspen stands used in simulations.

	Batoche[a]	**Bronson**[b]	**BERMS**[c]
Vegetation zone	parkland	boreal transition	boreal
Latitude	52° 44' N	53° 48' N	53° 38' N
Longitude	106° 09' W	109° 08' W	106° 12' W
Elevation (m)	500	600	600
Mean temperature[d] (°C)	1.2	0.6	–0.2
Mean July temperature[d] (°C)	18.3	16.6	16.3
Mean precipitation[d] (mm y^{-1})	375	400	463
Climate Moisture Index[e]	–13	0	+8
Stand age in 1995 (y)	<30–80	46–66	70–76
Height (m)	<5–14	11–21	18–22
Stem diameter (cm)	<6–23	12–31	17–27
Leaf Area Index (m^2 m^{-2})			
Observed (average)	1.4	2.1	2.3
Observed (range)	—	1.1–2.7	—
Modeled	1.3	1.8	2.7
Stem biomass (kg C m^{-2})			
Observed (average)	1.0	3.2	4.2
Observed (range)	0.9–1.2	1.4–5.7	3.5–5.2
Modeled	1.3	2.2	3.8

[a] Stand measurements in 1994 (Hogg and Hurdle 1997).
[b] Stand measurements in 1994 (Blanken et al. 1997; Halliwell and Apps 1997).
[c] Stand measurements in 1995 (Hogg and Schwarz 1999).
[d] From 1951–1980 climate normals for adjacent stations (Environment Canada 1982).
[e] Based on mean annual precipitation (cm) minus estimated potential evapotranspiration (Hogg 1994).

on finely polished material were made manually using an ocular micrometer under 20X magnification, and results were expressed as annual increment in cross-sectional area (details described by Hogg and Schwarz 1999). For the model comparisons at the Bronson Forest and Batoche sites, I used the results presented earlier (Hogg 1999; Hogg and Schwarz 1999) but included 17 additional trees sampled at Batoche in 1998–99. Model simulations for the BERMS site were compared with tree-ring analysis of increment cores collected from 30 aspen at this site (two stands about 1 km apart) during 1994–1998.

Years with defoliation by insects were first determined at each site from annual insect surveys by the Canadian Forest Service (e.g., Brandt et al. 1995). However, recent studies have shown that aspen forms abnormally pale, low-density growth rings during years when severe defoliation occurs (Hogg and Schwarz 1999; Hogg et al., unpublished). These rings have been referred to as white rings and can be a good indicator of past defoliation of aspen at the stand level. Thus, I determined the year to year occurrence of white rings in the aspen cores and disks that were collected and then used the annual percentage incidence of white rings at each site as an index of defoliation severity for input to model simulations (Hogg 1999).

The Model

Simulations of aspen growth and dieback were conducted using a climate-driven model (Hogg 1999) that operates on a daily time step and has six primary state variables. These include three variables representing the stand-based carbon pools in structural components of leaves, stems, and roots; one variable representing total nonstructural carbohydrate (regardless of location); and two variables describing soil conditions in the rooting zone (temperature and moisture). There are also several derived variables, notably leaf area index of the aspen canopy (LAI), and variables that keep account of cumulative growth, mortality, and transfers of carbohydrate and water on a daily, monthly, and annual basis.

The model is designed to simulate productivity, dieback, and mortality of pure aspen stands over periods of several decades, including stands in remote areas of the Canadian boreal forest where detailed meteorological data are not available. Thus, the model requires only inputs of daily maximum and minimum temperature, daily precipitation, mean monthly solar radiation, latitude (for day length calculations), and elevation (for mean atmospheric pressure). Vapor pressure deficit is estimated by assuming a dew point that is 2.5 °C cooler than daily minimum temperature (Hogg 1997). Simulations are normally initiated with estimated values of carbon pools expected in a young, regenerating aspen stand 5 to 10 years after a stand-replacing disturbance such as fire (Hogg 1999).

The daily sequence of processes simulated by the model is summarized in table 2 and the model parameters are listed in table 3. The specific equations and details of model structure are presented by Hogg (1999). Spring development of leaf area is simulated through the transfer of carbon from the carbohydrate storage pool to the leaf carbon pool. Spring leafing is initiated on the first date when the cumulative number of growing degree days (daily mean air temperature >5 °C) has reached a certain threshold (GDD_{start}) and is completed on the date when a second, higher threshold is reached (GDD_{end}). Insect defoliation is simulated by removing leaf carbon during spring leafing; the proportion removed is calculated from the parameter *wDEFOL* multiplied by the defoliation severity, as estimated from the proportion of white tree rings in a given year. Leaf carbon and leaf area decrease gradually over the growing season according to a minimum rate of turnover expected in healthy stands (e.g., losses from minor insect herbivory and fungi, or breakage of stems and twigs by wind and falling trees). Additional losses of leaves are simulated during frost events, and

Table 2—Summary of aspen model (Hogg 1999) showing sequence of calculations.

Input model parameters **and initialize** state variables.
Input **latitude**, **elevation**, and **defoliation history** at site, and start and end years of simulation.
Calculate **daylength** and mean **solar radiation** for each day of the year at site.

Start daily loop (for 1 January of first simulation year to 31 December of last simulation year).

Input **daily weather** (maximum and minimum temperature, precipitation).
If **climate change scenario**, then apply changes to inputs of temperature and precipitation.
Calculate mean, daytime, nighttime air temperature, and soil temperature.
Calculate growing degree days (GDD).
If **spring** (based on cumulative GDD since 1 January) then **grow leaves** from stored carbohydrate, if year with **insect defoliation**, then remove leaf carbon.
If **frost** then kill leaves.
If autumn based on photoperiod, then start **leaf fall.**
Calculate **Leaf Area Index** (LAI) from leaf carbon and specific leaf area.
Calculate **light interception** by trees and understory (based on LAI and solar radiation).
Calculate **vapor pressure deficit** (VPD) based on maximum and minimum air temperature.
Calculate **canopy conductance** (based on VPD and LAI with reductions for dry soils and frost).
Calculate **transpiration** (based on canopy conductance, VPD and daylength).
Calculate **interception** of rainfall, **evaporation**, **soil moisture** and **runoff**.
Calculate **light** levels on leaves based on solar radiation and LAI.
Calculate **mesophyll conductance** to CO_2 (based on light and temperature).
Calculate **photosynthesis** (based on LAI, daylength and overall conductance to CO_2).
Calculate **respiration** of leaves, stems and roots.
Calculate net photosynthesis and allocate to **carbohydrate storage** versus growth.
Grow stems and roots.
Calculate carbohydrate status.
Kill stems, roots, and leaves: normal turnover plus additional mortality if carbohydrates are low.
Translocate recoverable carbohydrate from dead stems to living stems.
If year end, then **output** annual summary.

End daily loop.

Table 3—Parameters used in model simulations. Values in bold have been modified from those used in the simulations reported by Hogg (1999).

Parameter	Value	Description (units)
GDD_{start}	120	Cumulative growing degree days at start of spring leafing (°C)
GDD_{end}	**200**	Cumulative growing degree days at end of spring leafing (°C)
$DAYL_{min}$	12	Day length inducing autumn leaf fall (h d^{-1})
$wFALL$	0.15	Daily rate of autumn leaf fall (g g^{-1} d^{-1})
$wDEFOL$	0.7	Proportional leaf loss from insect defoliation
k	0.5	Canopy light extinction coefficient
SLA	0.0225	Specific leaf area (m^2 g^{-1} carbon)
$CO2grad$	11.7	CO_2 diffusion gradient (mmol m^{-3})
gM_{max}	**2.5**	Maximum mesophyll conductance, gM (mm s^{-1})
T_{opt}	20	Daytime temperature optimum for gM (°C)
B	4	Coefficient for temperature response of mesophyll conductance (°C)
RAD_{half}	250	Coefficient for radiation response of mesophyll conductance (W m^{-2})
$wMResp_{leaf}$	0.01	Leaf maintenance respiration rate, 10°C (g g^{-1} d^{-1})
$wMResp_{stem}$	0.0002	Stem maintenance respiration rate, 10°C (g g^{-1} d^{-1})
$wMResp_{root}$	0.002	Root maintenance respiration rate, 10°C (g g^{-1} d^{-1})
$Q10$	2.3	$Q10$ for temperature response of maintenance respiration
$wGResp$	0.3	Growth respiration (g g^{-1})
wC_{leaf}	0.5	Proportion of stored carbohydrate (C_{TNC}) used for leaf growth
wC_{stem}	**0.7**	Stem growth as proportion of total growth
$wTNCloss$	0.5	Proportional loss of C_{TNC} during senescence
$wTNCuse$	50	Coefficient for use of C_{TNC} during growth
$wTurn_{leaf}$	0.6	Minimum rate of leaf turnover (g g^{-1} y^{-1})
$wTurn_{stem}$	**0.01**	Minimum rate of stem turnover (g g^{-1} y^{-1})
$wTurn_{root}$	**0.1**	Minimum rate of root turnover (g g^{-1} y^{-1})
$FROST_{max}$	400	Coefficient for frost damage to leaves (°C)^2
$pTNC_{min}$	0.05	C_{TNC} threshold for increased mortality (g g^{-1})
$wKILL$	0.5	Coefficient for mortality during low C_{TNC}
$SOILCAP$	**150**[a]	Soil water holding capacity, rooting zone (mm)
$SOILDRY$	**75**[a]	Minimum soil water before canopy conductance is reduced (mm)
gW_{max}	10	Maximum canopy conductance (mm s^{-1})
VPD_{crit}	1	Maximum VPD before canopy conductance is reduced (kPa)
$wVPD_{min}$	0.333	Coefficient of canopy conductance response to VPD
$wICEPT$	0.2	Coefficient of canopy interception of precipitation

[a] Parameter values for loam soils used in simulations of Bronson forest and BERMS site. For simulations of Batoche site, *SOILCAP* and *SOILDRY* were set at 100 mm and 50 mm, respectively, for sandy soils (De Jong et al. 1992).

in autumn, the loss of remaining leaves is driven by the seasonal decrease in photoperiod. Changes in soil moisture are simulated from the daily inputs of precipitation (less that intercepted and evaporated by the canopy) and daily losses by transpiration and runoff. Simulated photosynthesis of the aspen canopy is determined as a function of leaf area, solar radiation and temperature, and is reduced by dry soils and high vapor pressure deficit. Daily net production of photosynthate is allocated either to the structural growth of stems and roots, or to storage as nonstructural carbohydrate; the proportion used for growth increases as a function of the ratio between net daily photosynthesis and root biomass (Hogg 1999).

Simulated aspen mortality includes two components: (a) a minimum rate of ongoing stem and root turnover that reflects natural processes in the development of healthy stands, e.g., competition and self thinning; and (b) additional mortality and dieback resulting from climatic or biotic stressors such as frost, drought, and insect defoliation. In the model, stem and root mortality normally proceeds at the minimum rates of turnover, and mortality increases only when the level of nonstructural carbohydrate (expressed as a proportion of total stem and root biomass) falls below a certain threshold ($pTNC_{min}$). Thus, stress-induced increases in mortality are simulated as being largely an indirect consequence of reduced net photosynthesis (e.g., following defoliation or drought), which can eventually lead to exhaustion of the carbohydrate reserves necessary to the tree's survival.

The values of parameters used in the present study (table 3) were mostly the same as those used previously (Hogg 1999). However, a subsequent evaluation suggested that the earlier version of the model underestimates the growth of aspen biomass under optimal conditions. This was addressed by increasing the rate of maximum mesophyll conductance, and reducing the values for minimum rate of stem and root turnover; the latter change also necessitated an increase in the proportion of carbon allocated to stem growth to achieve model stability. The cumulative number of growing degree days associated with the end of spring leafing was also increased to more closely correspond with observations at the BERMS site (A. Barr, personal communication). Finally, parameters describing soil water holding capacity were modified (table 3) to correspond more closely to the observed differences in soil texture at each site.

Weather Data and Climate Change Scenarios

Records of daily maximum and minimum temperature and daily precipitation were assembled from climate stations adjacent to each site for the periods 1930–1995 (Batoche), 1940–1995 (Bronson), and 1930–1996 (BERMS). The start of these periods corresponds to when the main (or oldest) age class of aspen in these stands would have been about 5 to 10 years old (table 1). The climate data for simulations at Batoche and Bronson are the same as those used by Hogg (1999), while the climate record for the BERMS site was estimated using weather data from Waskesui Lake and Prince Albert, Saskatchewan, respectively located about 30 km N and 60 km SE of the site.

For simulations of aspen sensitivity to climate change impacts, the inputs of the observed daily weather record were modified according to the projected changes for the western Canadian interior under a doubling of atmospheric CO_2 levels. In this preliminary investigation, I applied a generalized climate change projection for the region based on mean regional differences between the 2X and 1X CO_2 scenarios of the Canadian Climate Centre GCM2 (Boer et al. 1992), which gives a 4.2 °C increase in daily maximum temperature, a 4.9 °C in daily minimum temperature, and an 11% increase in daily precipitation. This is the same scenario used by Hogg and Hurdle (1995) in an earlier analysis of possible impacts of climate change on vegetation zonation in this region.

Results and Discussion

Observed and Modeled Aspen Growth (Current Climate)

The occurrence of white tree-rings at the three sites showed a good correspondence with the years when major defoliation events were recorded during past insect surveys, considering that these surveys were conducted over a large geographic area with limited spatial resolution (Hogg 1999; table 4). In terms of percentage incidence of white rings, 1980 was the year with the most severe defoliation by forest tent caterpillars at all three sites. Severe defoliation also occurred at the Bronson and BERMS sites in the early 1960s, especially 1964. These major defoliation events were accompanied by severe reductions in aspen growth, based on the results of tree-ring analysis (figure 1). However, it should also be noted that 1964 was also a major drought year at all three sites,

Table 4—Percentage of radii with light-colored (white) tree rings during years with insect defoliation, as recorded in aspen stems (1.3 m height). Numbers in bold denote years with records of extensive defoliation by forest tent caterpillar based on surveys by the Canadian Forest Service (excludes records of sporadic outbreaks or defoliation in areas adjacent to each site).

	Site		
	Batoche (47 trees)	**Bronson (102 trees)**	**BERMS (30 trees)**
1953	35	0	0
1956	0	9[a]	0
1962	0	**19**	0
1963	0	**52**	**32**
1964	0	**87**	**96**
1965	0	2	0
1979	**81**	8	**65**
1980	**85**	**97**	**99**
1981	0	1	0
1982	0	1	0
1983	0	12	0
1985	0	37	0
1986	0	69	0
1987	0	**82**	0
1988	0	**64**	0
1989		6	0
1990	0	8	0
1992	0	0	72[a]

[a] Defoliation by large aspen tortrix (*Choristoneura conflictana*).

and 1980 was a major drought year at the Batoche and Bronson sites (climate data not shown). Situations like this, when drought and defoliation occur during the same year, can pose challenges when attempting to separate the impacts of these factors on aspen growth and dieback.

Aspen growth at the Bronson forest was severely reduced by forest tent caterpillar defoliation during several successive years in the mid and late 1980s, and this also appears to be the major cause of the observed crown dieback at this site (Hogg and Schwarz 1999). The other two sites have been apparently free of defoliation since 1980, except for an outbreak by large aspen tortrix (*Choristoneura conflictana* [Walker]) in 1992, which caused a transient reduction in growth at the BERMS site.

The results of the simulations for the three sites showed a good correspondence between the year-to-year pattern of modeled stem biomass increment and the observed stem area increment based on tree-ring analysis (figure 1). The values of r^2 were 0.522 and 0.682 for the Batoche and Bronson sites, similar to those reported from previous simulations for these sites (Hogg 1999), while a much lower r^2 of 0.185 was obtained at the BERMS site. However, such comparisons are of limited value because the expression of annual stem growth differs between the modeled (stand-based biomass) and observed (tree-based area increment) growth. A more appropriate basis of comparison is to express both series in terms of relative interannual changes, so that the influence of longer-term stand dynamics (height growth, recruitment, and mortality) are minimized in the pattern obtained from tree-ring analysis. With both series detrended in this way by differencing of log-transformed growth (Hogg 1999), the revised values of r^2 were slightly less for the Batoche and Bronson sites (0.491 and 0.591, respectively) but increased substantially for the BERMS site ($r^2 = 0.376$).

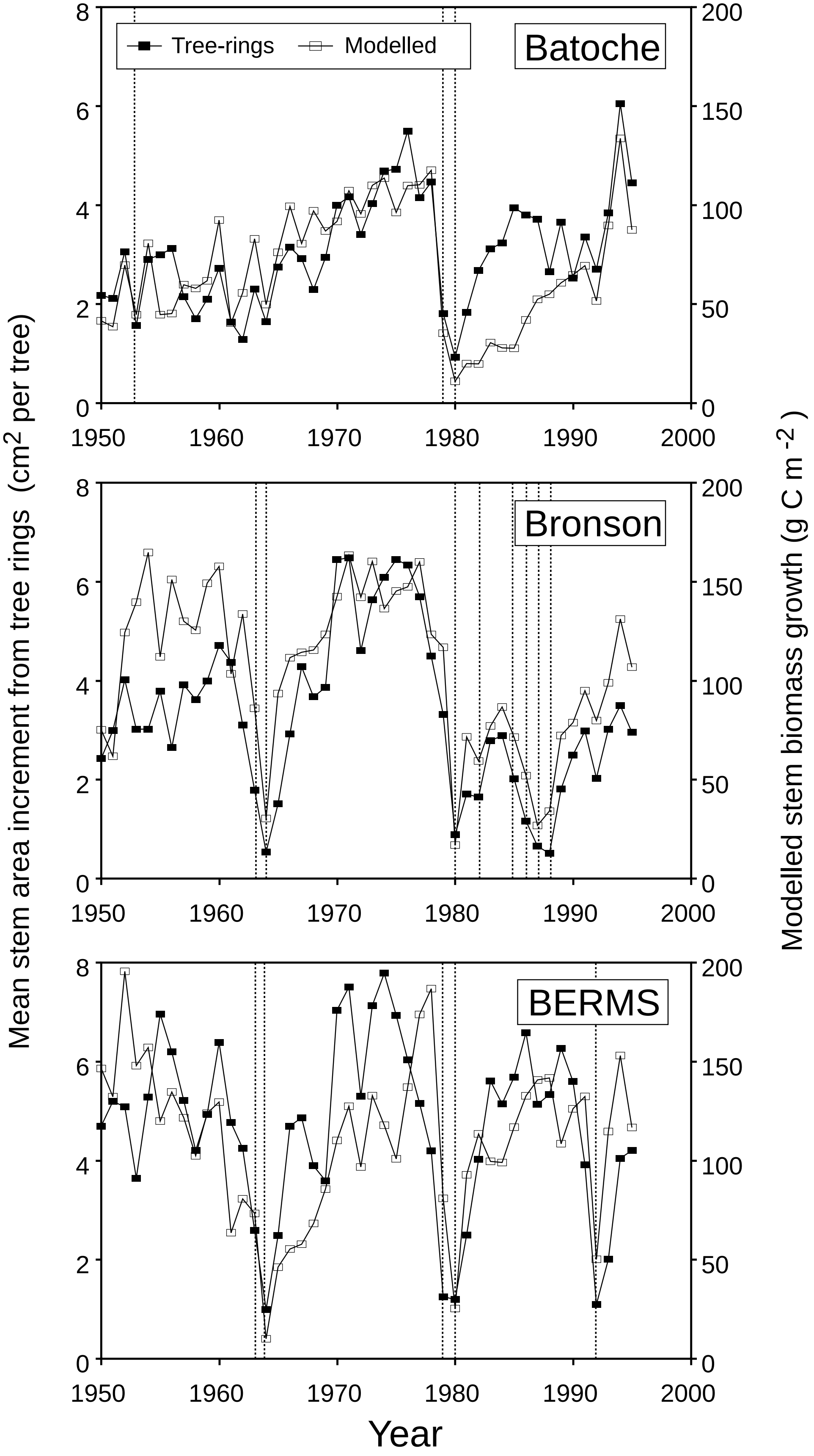


Figure 1—Interannual variation in stem growth at three aspen sites in Saskatchewan, Canada, based on (a) radial growth from tree-rings, expressed as mean stem area increment from cores or disks collected at 1.3 m height, and (b) modeled growth in stem biomass carbon at the stand level. Major defoliation events at each site (table 4) are indicated by dotted vertical lines.

Long-term, permanent sample plot data are not available from any of the three sites. However, a comparison of measured versus simulated aspen biomass and leaf area index in 1994–1995 (table 1) indicates that the model performed reasonably well, considering that it is a very simple model that does not include site-specific factors such as soil nutrient status.

Climate Change Scenarios of Aspen Responses

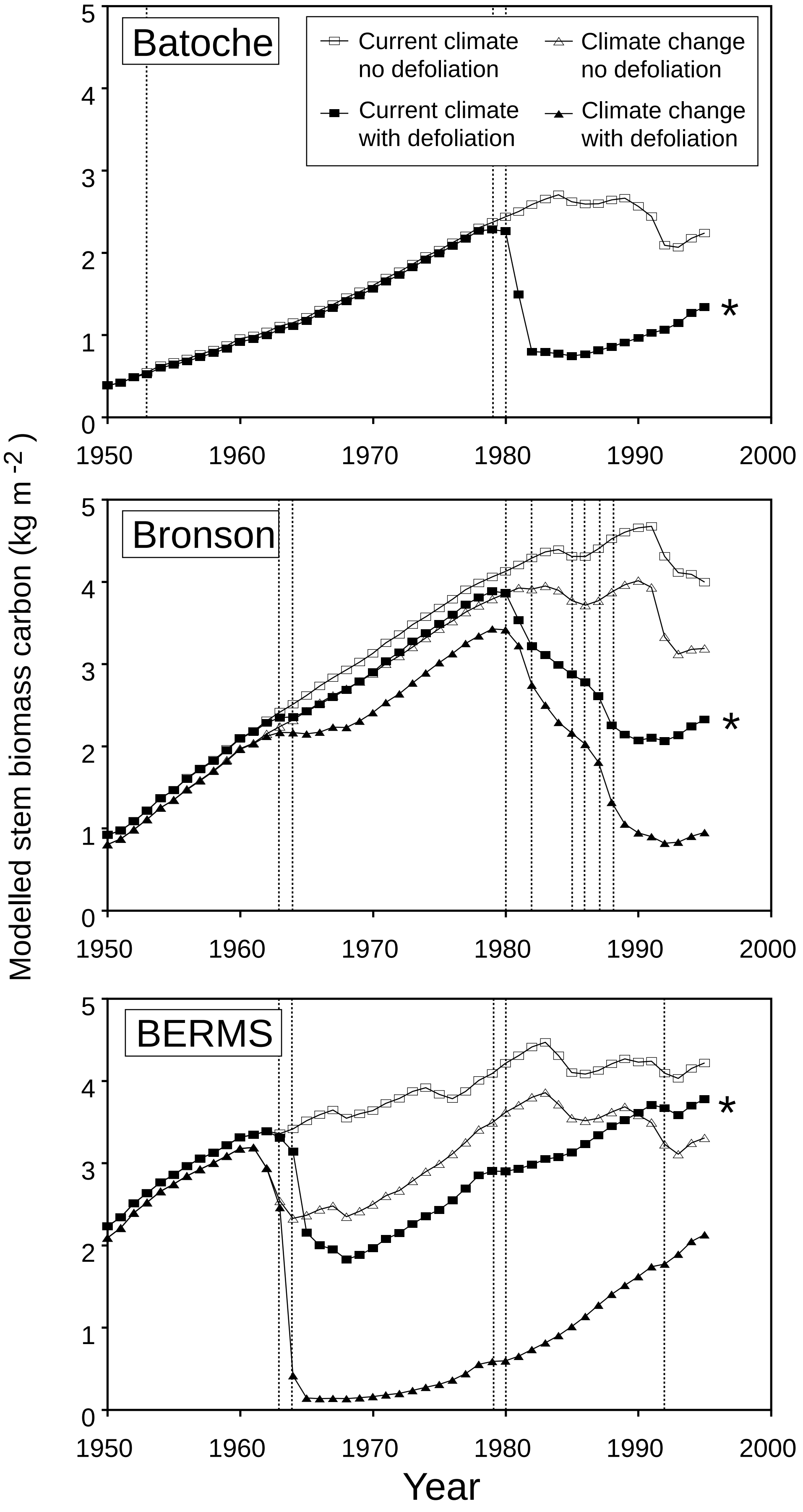
Simulated changes in aspen stem biomass carbon under the observed conditions of climate and defoliation history (indicated by an asterisk for each site in figure 2) show that modeled dieback occurred during and following major insect outbreaks. The most severe dieback occurred following the 1979–1980 outbreak at Batoche and following the 1963–1964 outbreak at the BERMS site, while at the Bronson site, repeated defoliation during the 1980s caused a more gradual but sustained decline in stem biomass during this period. A major contributing factor to the modeled dieback was drought, which accompanied the severe defoliation events at the Bronson and BERMS sites in 1964, and at the Batoche and Bronson sites in 1980. However, when insect defoliation was "turned off" in the simulations (figure 2), dieback was minimal following these drought events. This suggests that under the current climate, drought is not a major cause of aspen mortality except in combination with insect defoliation and other stresses, at least in the boreal forest.

Under the 2X CO_2 climate change scenario (4–5 °C warming), the modeled aspen at all three sites died during the first decade of simulations, despite the 11% increase in precipitation. In the model, stem and root mortality can only increase when nonstructural carbohydrates fall below a critical minimum. Because there was no defoliation during this initial period of the simulation, the modeled stand death can be attributed to (1) a combination of reduced photosynthesis under the drier conditions (high VPD and low soil moisture) and (2) depletion of carbohydrates through temperature-induced increases in respiration rates.

Simulations were repeated by reducing the simulated magnitude of climate change by 50%, i.e., a 2.1 and 2.45 °C increase, respectively, in daily maximum and minimum daily temperatures, and a 5.5% increase in precipitation. Such a scenario might thus correspond approximately to climate change expected under a 50% increase in atmospheric CO_2 levels, which at the current rate of increase would occur by the middle of the 21^{st} century. Even with this modest warming scenario, the modeled aspen at Batoche did not survive. This result is consistent with the observation that aspen is absent from the prairies near the Montana-Saskatchewan border, where the climate is about 2 °C warmer, with up to 15% more precipitation, compared to Batoche (e.g., Estevan, Saskatchewan, with mean annual temperature of 3.4 °C and annual precipitation of 434 mm).

At the two boreal sites, the modest warming scenario had very little effect on aspen productivity during the early part of the simulations (i.e., prior to the early 1960s). However, dieback increased following drought and defoliation in 1964, especially at the BERMS site where almost all of the stem biomass had died by the following year (figure 2). At the Bronson forest, the warming led to increased dieback during the 1980s compared to that under the current climate. As a result of these dieback events, the simulated climate change caused about a 50% decrease in the modeled, final biomass of aspen at both boreal sites. When insect defoliation was "turned off" in the climate change simulations, dieback severity was reduced but it was still sufficient to cause a decrease of about 20% in the final, modeled biomass at these sites.

Figure 2— Simulated changes in stem biomass carbon at three aspen sites under the observed climate, and also under a future climate change scenario with a modest warming of about 2–2.5 °C that results in drier soils (details in text). These two climate scenarios were each applied in combination with the observed insect defoliation at each site (“with defoliation”) or with insect defoliation “turned off” in the model (“no defoliation”). Major defoliation events are indicated by dotted vertical lines. The simulations corresponding to the estimated stem growth at each stand for the period 1950–1996 (figure 1) are denoted by an asterisk.



Carbon Dioxide Fertilization

One of the major factors that was not included in these preliminary simulations is the effect of elevated CO_2 on photosynthesis, which might reduce—or even reverse—the negative impacts on aspen productivity that would otherwise be expected under a warmer and drier future climate. For example, photosynthesis of *Betula pendula* was enhanced by 33% after four years of field exposure to doubled CO_2 levels (Rey and Jarvis 1998). However, ecosystem responses under elevated CO_2 levels are complex, so that the long-term benefits of CO_2 on plant productivity are often much less than would be predicted from simple physiological models (e.g., Ward and Strain 1999). Interactions with other human-induced changes in air quality could also be significant in this respect. For example, preliminary results from a free carbon dioxide enrichment (FACE) experiment in Wisconsin indicate that artificially elevated concentrations of ground level ozone completely eliminated the benefits of CO_2 fertilization on aspen growth (J. G. Isebrands, personal communication).

As a preliminary means of exploring how CO_2 fertilization might affect aspen responses to climatic warming, the simulations (with defoliation) were repeated under the same climate change scenarios using various percentage increases in modeled photosynthesis rates. Under the modest (2–2.5 °C) warming scenario, corresponding to a roughly 50% increase in atmospheric CO_2, photosynthesis rates had to be increased by 31% to achieve the same final stem biomass at Batoche as that simulated under the current climate. The corresponding figures for the Bronson and BERMS sites were 9 and 12%, which indicates that if photosynthesis rates increase by more than these percentages, aspen biomass would increase. However, with the original scenario for 2X CO_2 (4–5 °C warming), much greater increases in photosynthesis would be needed to offset the modeled climate change impacts: the Batoche site would require an unrealistic tripling of photosynthesis rates to achieve the same final biomass, whereas photosynthesis would need to increase by 30 and 47% at the Bronson and BERMS sites. The latter percentage increases in photosynthesis might reasonably be expected under CO_2 fertilization, so that biomass of boreal aspen forests may show little change under a warmer climate; but it appears that aspen biomass in the parkland would be reduced, even under the most optimistic assumptions.

Model Limitations and Knowledge Gaps

Although the model performed reasonably well in simulating interannual changes in aspen stem growth based on tree-ring analysis, the model projections under climate change should be interpreted with caution for several reasons. First, the model outputs of growth, dieback, and mortality need to be more rigorously validated at the stand level, preferably through model comparisons with annual measurements and health assessments in aspen stands exposed to various stresses. Second, other than drought and defoliation, the model does not include many of the factors that can reduce aspen productivity and biomass—e.g., fungal pathogens and wood-boring insects, spring thaw-freeze events, competition with conifers in mixed wood stands, and cold soils (Lieffers et al., this proceedings). Another limitation is that for some of the key physiological processes being simulated, there is little published information available for developing functionally realistic algorithms with reliable estimates of model parameters. These processes include, for example, the allocation of carbohydrate to growth versus storage, and the relationship between whole-tree carbohydrate levels and mortality.

Given the importance of defoliation to aspen stand dynamics, another critical knowledge gap for the future is to understand how forest tent caterpillar and other insects may respond to future climate change. Forest tent caterpillar is favored by warm, dry summers (Ives 1981). For the first time in 1995, a major outbreak was recorded at a latitude >60° N in the Canadian Northwest Territories (Brandt et al.1996), suggesting that the climatic warming observed to date may be facilitating the northward expansion of this species. Thus, be expected to increase—leading to even greater impacts on the growth and dieback of aspen in the region.

Another important consideration is the reliability of future climate projections based on General Circulation Models such as the one used in this study. These models have a very coarse spatial resolution, and until recently, they were very poor at characterizing feedbacks of terrestrial vegetation on regional climate. Indeed, a recent study indicates that seasonal leafing of aspen and other deciduous vegetation may exert a significant influence on the climate patterns of the western Canadian interior (Hogg et al., in press). Thus, even the projections of future climate change could ultimately be improved through a greater understanding of aspen ecosystem processes and their interactions with the atmosphere and regional climate.

Conclusions

The results from the model simulations indicate that future climate change impacts on boreal aspen forests in western Canada may not become apparent until after major defoliation events occur. However, it is not currently possible to predict with any confidence how aspen productivity will be affected, if the climate of this region becomes warmer and drier as projected by most General Circulation Models. Under a warmer and drier future climate, drought and defoliation are expected to increase, leading to reduced growth and dieback of aspen; however, these impacts may be reduced or even reversed in some areas by the benefits of CO_2 fertilization and warmer soils. There are also many knowledge gaps, including limitations of understanding of a large variety of interacting factors that operate over a wide range of spatial and temporal scales. Nevertheless, climate change poses a serious risk for the future productivity and health of aspen forests in western Canada, especially in the drier climate zones that include much of the southern boreal forest. Given the importance of aspen forests, both ecologically and commercially, there is a need for regional-scale monitoring as an “early warning” indicator of how these forests may be responding to the warming trend that is already apparent in the western Canadian interior.

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Establishment of White Spruce Growth Trial in an Aspen Understory

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Abstract—*A conifer release trial was established in a 45-year-old aspen overstory stand in Northeast British Columbia, Canada. Thinning occurred from 0 to 100% in increments of approximately 10% to yield a total of ten units. Treatment consisted of physically cutting aspen stems at the root collar or girdling at breast height (d.b.h.) for trees <10 cm d.b.h., and >10 cm d.b.h., respectively. The thinning treatment was conducted following standard brushing and weeding contracts common to the British Columbia Ministry of Forests. At this time no significant difference in diameter growth can be found between treatments. All girdled trees were flushed the following year after treatment. The result of flushing may have limited the response of the coniferous understory. Continued monitoring of the site may provide valuable information to the operational applicability of thinning aspen stands of this age to release understory spruce.*

Introduction

Many studies have looked at the relationship between total thinning of overstory species and growth (diameter) response of the understory spruce (Lees 1966, 1970; Steneker 1967; Yang 1989, 1991; Yang and Bella 1994). Thinning the stand encourages two important environmental changes: (1) it increases the amount of solar radiation transmitted through the forest canopy; and (2) it alters the quality and quantity of litter accumulating on the forest floor. Man and Lieffers (1999) reported that overstory aspen canopies influence light levels, and air and soil temperatures, and may possibly influence soil nutrient availability and soil moisture.

Aspen overstories can serve as a nurse crop, reducing frost, insect damage, and competition from understory vegetation (Man and Lieffers 1999). At a time when diversity (Anonymous 1995) is a major component of our forest practices, maintaining an aspen component may enhance or maintain structural and species diversity in our boreal forests.

For the most part, mixed-wood stands of the boreal forest are initiated following large-scale disturbance by fire (Anonymous 1995). Following such a disturbance, it is not uncommon for forests to be composites of overstory aspen and understory spruce (Rowe 1972). Many of these stands (deciduous and deciduous/coniferous forests) in the Peace Region of British Columbia and Alberta contain a substantial component of regenerating spruce at varying stages of development. Spruce may be in the understory only (<5 meters); it may be in a juvenile or pole stage or vertically stratified in the main canopy. It is not uncommon to find these attributes in 20- to 30-hectare size stands. The location of seed source, forest floor environment, and type of stand initiating disturbance will affect the timing and success of understory regeneration (Kelty 1996).

In the Peace Region, the abundance of mixed woods where understory spruce is present is unknown. However, a great amount of interest has surfaced

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regarding the facilitation and protection of this understory for future harvest as a commercial crop (Brace 1991). This interest has been advanced by the development of oriented stand board and improvements in pulping technology, which has increased the harvest of Boreal mixed wood and deciduous forests (Lieffers and Beck 1994).

By maintaining a partial overstory of aspen in these stands we may see improved growth of both species and increased overall stand yield. In this study, we were interested in observing the relationship of thinning one species (overstory) on the diameter growth of another species (understory).

Conventional theory suggests that over identical time periods, given equivalent growing conditions, with all else held equal, growth rates will be equal. In a natural experimental setting, it is difficult to hold all variables to equal influence. We have attempted to alter one variable (percent overstory) while holding all else static in this study, assuming all other variables that influence growth do so to the same degree throughout the study area.

We expected to establish a relationship between the degree of thinning and growth response; that is, at what thinning percentage maximum growth of spruce could be attained. Logan (1969), Eis (1970), Lieffers and Stadt (1994), and Coates et al. (1994) all reported increased spruce height growth with improving light environment (increased thinning). Lieffers and Stadt (1994) found that 40% of full sunlight was sufficient to attain growth rates nearly equal to that attained at full sunlight. Coates et al. (1994) predicted that optimal height growth for understory spruce could be attained at 50% of full sunlight, while Logan (1969) reported maximum height growth for white spruce at 45% of full sunlight. Eis (1970), Lieffers and Stadt (1994), and Coates et al. (1994) reported their findings after observing light transmittance and growth over one growing season, while Logan (1969) reported results after nine growing seasons.

This paper is being presented as an establishment report for the purpose of these proceedings. The following information describes initial stand structure, treatment, and current findings.

Methods

The experimental site is located in an even-aged aspen stand 100 kilometers (60 miles) northwest of Fort St. John (56°51'30" N, 121°25' W) in Northeast British Columbia, Canada. The site index for spruce (base age @ 50 years) is 18 meters. Soils are classified as orthic gray luvisols characterized by silty clay loam of glacial lacustrine origin (Agriculture Canada 1986). Forest floor vegetation is dominated by *Cornus canadensis* L., *Lathyrus orchroleucuc* Hook., *Rosa acicularus* Lindl., *Viburnum edule* (Michx) Raf., and *Vaccinium vitis idaea* L. (Douglas et al. 1989, 1991). The site is situated in the Boreal White and Black Spruce moist and warm biogeoclimatic zone (Meidinger and Pojar 1991); series has been classified as mesic (01 site series).

In 1955, a forest fire swept through large portions of what is now known as the Fort St. John Forest District. The disturbance created by this fire began the stand initiation process that has resulted in the current stand structure. Reconnaissance of the site was conducted in the summer of 1998. Aspen and spruce stocking composition was determined. Aspen density prior to treatment averaged 3,920 stems per hectare (sph) and spruce understory averaged 1,050 sph.

Aspen crown canopy height was determined to be 18 meters. No other disturbances have taken place in the stand.

Ten research plots were located on the ground in 1998. Each plot is comprised of a 70- x 70-meter (0.49-ha) treatment plot with a 40- x 40-meter (0.16-ha) measurement plot located in the center. Each thinning plot was randomly selected.

Thinning treatments took place following baseline measurement completion. Each plot was located to reduce edge effect and to minimize stocking variability among plots. Plot perimeters were tight chained, flagged, and painted. Gross treatment area was GPSed in the winter of 1998.

Thinning was conducted under a British Columbia Ministry of Forests Brushing and Weeding Standards Agreement (Anonymous 1998). The standards set out in this agreement require the operation to be conducted using the follow conventions. Aspen stems <10 centimeters in diameter at breast height (d.b.h. = 1.3 meters) were physically thinned (cut at root collar). Aspen stems >10 centimeters at breast height were girdled at breast height. Percent treatments ranged from 0 to 100% removal of the baseline stand in increments of approximately 10% for a total of 10 installations (table 1).

In the fall of 1998, baseline measurements of bark on tree diameter at breast height were taken for six trees on each of the 10 thinning plots. This was repeated in year 2 (1999) where all trees except one was measured. Means and standard deviations were calculated for all thinning treatments in each year (table 1).

Discussion and Results

To date no clear results can be attained from our data set. Figure 1 shows the average change in diameter for all thinning treatments between year 1 (1998) and year 2 (1999). The data set is very small—six measured trees per plot. During the late summer and fall of 2000, we will conduct destructive sampling at the site. This will allow us to acquire a larger data set for 1998, 1999, and 2000 (50 trees each of aspen and spruce per plot). At this time we cannot draw any substantive conclusions, and to do so with such a small data set could be misleading.

Helms and Standiford (1985) found the factors responsible for increased growth to be prerelease diameter growth rate, diameter, and prerelease height.

Table 1—Initial group diameters (year 1) and first-year diameters (year 2) with standard deviation, diameter change, and stems measured in each group.

Group	Thin	Year 1 mean d.b.h.	Year 1 standard deviation	Year 2 mean d.b.h.	Year 2 standard deviation	Diameter change	n
	%	- - - - - - - -	- - - - - - - - - *mm*	- - - - - - - -	- - - - - - - -		
1	0	34.7	8.6	38.9	9.7	4.1	6
7	15	33.7	8	35.8	8.5	2.1	6
9	30	24.4	6.3	27.2	5.4	2.8	6
8	40	28.3	5.7	29.8	6.5	1.4	6
2	50	30.7	13.5	32.6	13.5	1.8	6
3	60	31.6	7.7	36.7	7.8	5.1	6
5	70	34.8	15.6	39.3	14.9	4.5	6
6	80	24	8	28.5	9.2	4.4	5
10	90	25.3	10.2	33.1	12.9	7.8	6
4	100	24.2	7.8	28.9	6.8	4.6	6
Grand mean all groups		29.2	9.1	33.1	9.5	3.9	

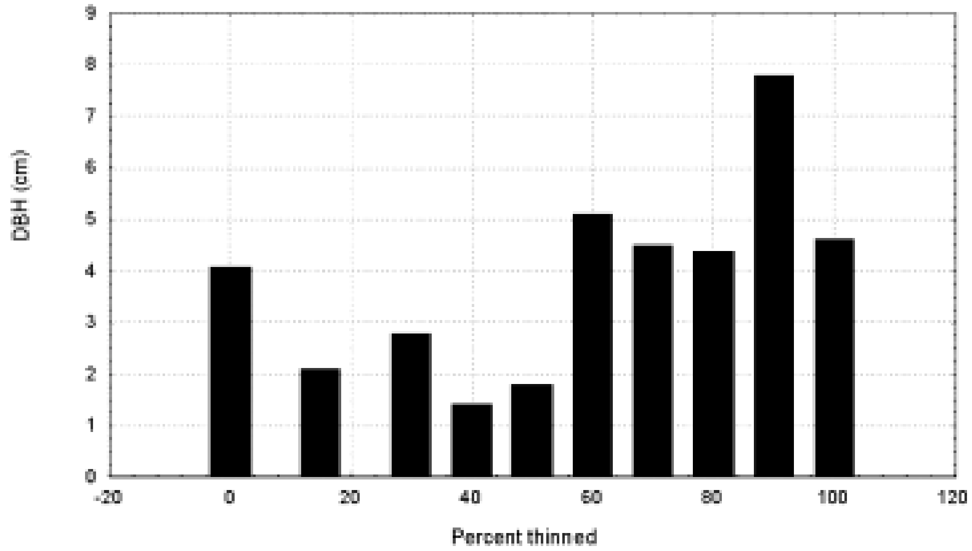

Figure 1—Plot of diameter change versus percent thinning.

In this study the pretreatment light environment may have been sufficient to facilitate near maximum diameter growth, pre and post thinning.

Light environment may be a concern. Girdled aspen trees produced leaves in the summer of 1999. Therefore, the percent thinning (girdling included) does not accurately represent the light environment. This may have resulted in less of a light environment change than anticipated. It is possible that because of the flush in 1999 there was insufficient change in light environment to obtain a significant diameter growth response. Waring and Schlesinger (1985) suggested the allocation priority is first to leaf and root development, and later to stem development. Therefore, stem growth response may not be noticeable until the second or third growing season following treatment.

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Aspen Overstory Recruitment in Northern Yellowstone National Park During the Last 200 Years

Eric J. Larsen[1] **and William J. Ripple**[2]

Abstract—*Using a monograph provided by Warren (1926) and two sets of aspen increment cores collected in 1997 and 1998, we analyzed aspen overstory recruitment in Yellowstone National Park (YNP) over the past 200 years. We found that successful aspen overstory recruitment occurred on the northern range of YNP from the middle to late 1700s until the 1920s, after which it essentially ceased. We hypothesized why the browsing influence of Rocky Mountain elk* (Cervus elaphus) *may be different now than it was historically. At a landscape scale, elk hunting outside YNP may be a significant factor changing elk foraging behavior. At a finer scale, elk foraging patterns and behavior due to predation risk may have been altered with the removal of the gray wolf* (Canis lupus) *from YNP in the early 1900s. Wolves may positively influence aspen overstory recruitment through a trophic cascades effect by reducing elk populations and decreasing herbivory on aspen by modifying elk foraging patterns and behavior.*

Project Description

Quantitative data concerning aspen *(Populus tremuloides)* overstory recruitment in Yellowstone National Park (YNP) prior to park establishment (1872) is scarce or nonexistent. In 1921 and 1922, Edward R. Warren (1926) conducted one of the few early quantitative studies of YNP aspen during the course of his investigations into the habits of the beaver *(Castor canadensis)* inhabiting the Park's northern range. We used the diameter measurements provided by Warren (1926) to study historic patterns of aspen overstory regeneration in YNP (Ripple and Larsen 2000). In 1997 and 1998 we collected 30 aspen increment cores from riparian aspen stands on YNP's northern range and 19 increment cores from the Eagle Creek drainage in the Gallatin National Forest immediately north of the Park. We restricted our sampling to riparian aspen stands to best approximate the aspen habitat type measured by Warren (1926). Using these 49 riparian aspen cores and a dissecting microscope, we counted the growth rings and developed a linear regression equation using their age/diameter relationship.

To analyze the current age distribution of overstory aspen, we collected a second set of aspen increment cores on YNP's northern range. We collected 98 cores from 57 randomly selected stands located in all aspen habitat types. From these increment cores we developed a current aspen age distribution for the northern range.

Results

Applying the regression equation to Warren's (1926) data, we showed that the overstory aspen occurring on the northern range during the early 1920s originated from approximately the 1750s to 1920.

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Combining the results of our current age distribution and the predicted ages of the trees measured by Warren (1926), we concluded that aspen stands were successful in recruiting new stems into their overstory from the middle to late 1700s to the 1920s, and unsuccessful thereafter. As an exception, it appears a few aspen sprouts are surviving in piles of coarse woody debris from fallen conifers killed in the 1988 fires (Ripple and Larsen, in press).

Discussion

We hypothesized that the lack of aspen recruitment since the 1920s may be partially due to the loss of predator/prey relationships between wolves and elk. For prey species, foraging decisions made under the risk of predation may differ from an optimal foraging strategy based only on maximizing nutrient intake (Lima and Dill 1990). Both moose *(Alces alces)* and caribou *(Rangifer caribou)* have been shown to choose lower quality foraging areas with associated lower predation risks in some instances (Edwards 1983; Ferguson 1988). In YNP, elk may have historically avoided extensive foraging in certain high quality habitats such as aspen stands and riparian areas due to the risk of predation from wolves. We suggest that predation risk effects can have a spatially specific influence on elk herbivory at multiple scales. At a broad landscape scale, hunting north of the YNP boundary may have created differential predation risks for elk and a change in the historic patterns of movement and migration. North of the YNP border, the greater risk of predation may have decreased elk browsing pressure and allowed some recruitment of aspen overstory stems. On the northern range within YNP, wolf predation risks may affect elk foraging behavior in aspen stands at a finer scale. In 1999, we initiated a long-term study of the potential influence of the reintroduced YNP wolves on elk herbivory and aspen overstory regeneration. Our objective is to use permanent plots to compare elk use and aspen regeneration within and outside of three core wolf pack territories on the northern range. Our work with trophic cascades involving aspen, elk, and wolves is part of our ongoing "Aspen Project." The web address for the Aspen Project is www.cof.orst.edu/cof/fr/research/aspen/.

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Basic Tree-Ring Sample Preparation Techniques for Aging Aspen

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Abstract—*Aspen is notoriously difficult to age because of its light-colored wood and faint annual growth rings. Careful preparation and processing of aspen ring samples can overcome these problems, yield accurate age and growth estimates, and concisely date disturbance events present in the tree-ring record. Proper collection of aspen wood is essential in obtaining usable ring data. Mounting of increment cores and sawn disk samples to wood backings holds samples rigid for easy surfacing. Sequential use of planers, belt sanders, and an assortment of sanding material on the surface of aspen core and disk samples can enhance visibility of tree rings. Application of stain on samples will color the late wood a dark brown and enhance the rings' visibility.*

Introduction

Many forest ecosystem research studies rely on accurate tree-ring identification to document age, fire frequencies, climate reconstruction, growth rates, and age of wind-thrown logs (Arnold and Libby 1949; Baisan and Swetnam 1990; Briffa et al. 1991; Brown et al. 1998; Swetnam et al. 1985). Several previous studies have described the methods of identifying quaking aspen (*Populus tremuloides* Michx.) annual rings (Maini and Coupland 1964; Rose 1957; Trujillo 1975). Trujillo (1975) shaved the core surface and treated it with a wood preservative and was able to distinguish the rings even after a year's storage. Others have recommended shaving the core sample to enhance ring visibility (Jones 1966; Maeglin 1979; Campbell 1981). Campbell (1981) used a vise to stabilize the core while shaving one side with a razor blade. Techniques for onsite aging of aspen cores were described by Mower and Shepperd (1987). Fresh cores were shaved, re-wetted, and viewed under a microscope for better ring identification.

In this paper we describe methods for collecting, mounting, and preparing aspen core and disk samples to accurately identify and measure annual rings using dendrochronology techniques.

Methods

Several steps are essential to collect and prepare aspen core and disk samples for use in dendrochronology research. The proper use of tools and materials is essential. Increment borers are the most widely used tools to extract tree cores (Jozsa 1988). Time and frustration of identifying ring samples can be minimized by the proper maintenance and care of increment borers. Some of the more common defects in core samples such as rough, broken, and twisted core surfaces are caused by dull or chipped borers. Improper start and directional change from a free-hand start of the borer can produce corkscrew core samples. Properly

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maintained and sharpened increment borers will save time and expense and greatly improve the effectiveness of collecting aspen tree-ring samples. Improper storage and care of the core samples can produce discoloration and decay. Cores collected in the field should be stored and transported in paper straws with the proper date and location of each sample identified on the straw. If plastic straws must be used, it is important to slit the straws to dry the cores. Unfortunately, core samples are often not collected properly in the field, resulting in difficulties in obtaining accurate ring measurements.

To properly mount the core samples, the tracheids must be mounted vertically. This will ensure maximum ring visibility after sanding. We recommend the use of grooved, wooden core mounts on which to mount the core samples to facilitate handling and sanding. As core samples are being taken, the increment borer scores lines on each side of the core perpendicular to the vertical alignment of the tracheids along the length of the core surface (Stokes and Smiley 1968). Cores should be air dried for a few days and glued into the mount so that the score lines run along the edges of the core mount. Aligning the cores in the core mounts is very important, so that the individual cells and ring boundaries can easily be seen when the cores are properly surfaced. Improperly mounted cores cause much frustration and loss of time when one struggles to identify the tree rings. Figure 1A shows a properly mounted unsurfaced core. The glued samples should be secured to the wooden mount with string wound around the mount and core (figure 2). After the glue is dry, the string is removed and the core is surfaced. A water-soluble white wood glue should be used because the core can be easily removed by steaming the mount over a tea kettle should realignment become necessary. Core samples mounted with white glue can be quickly set in a microwave oven for two minutes when time becomes an issue.

Disk samples obtained from standing or downed aspen trees with a chainsaw should be mounted on plywood backing to prevent breakage. Some disk samples

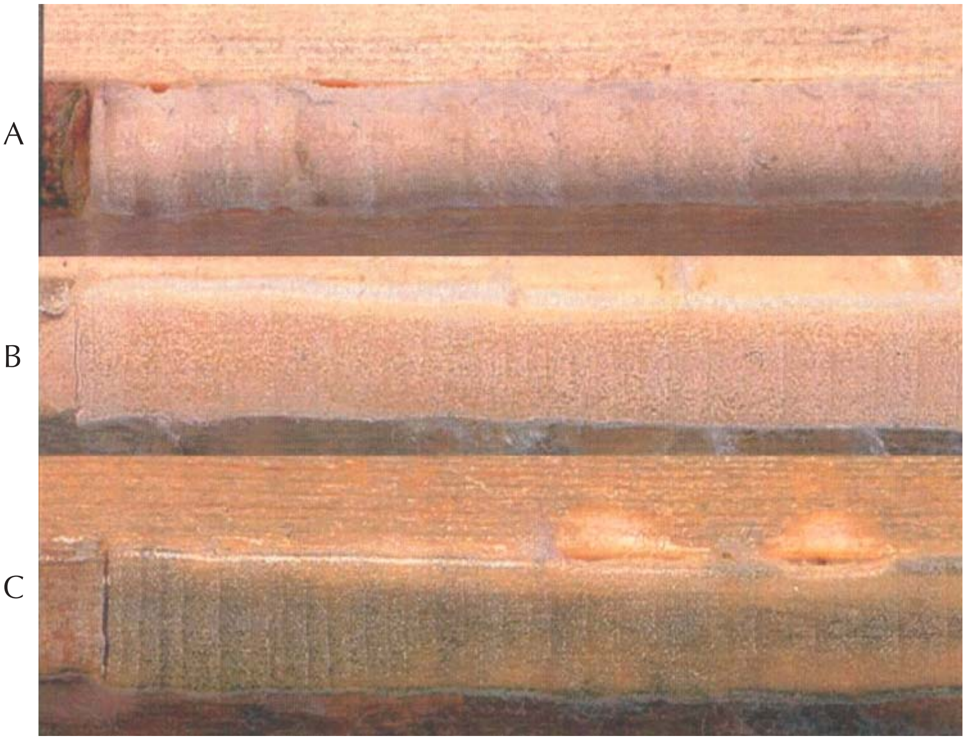

Figure 1—(A) Unsurfaced aspen core glued to wood mount, (B) surfaced and glued to wood mount, and (C) surfaced, stained, and glued to wood mount.

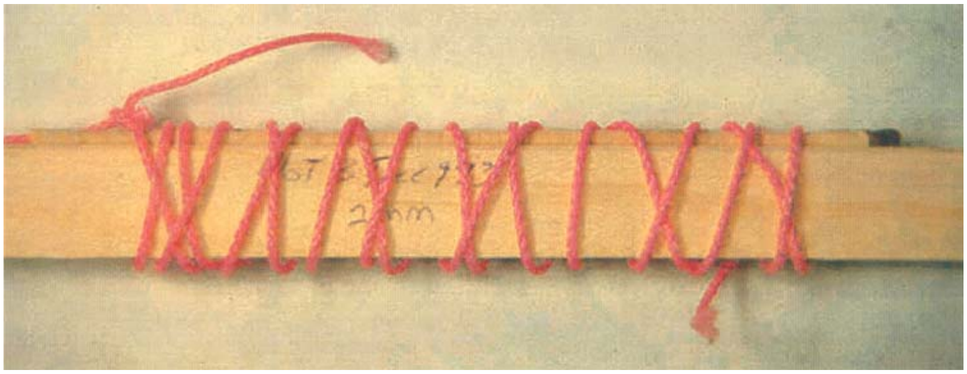

Figure 2—Aspen core glued and secured to wooden mount with string.

may be in an advanced stage of deterioration and break into small pieces. Transporting these samples intact is accomplished by drawing a series of lines with felt tip pens across each breakage point, then using plastic wrap to hold the samples together for transport. Each sample should be documented with the date, location, and sample number. Upon arrival at the laboratory, samples should be left to dry for several days. Then they should be reassembled by matching the marker lines and gluing the samples to a wood backing with construction glue (figure 3). Construction glue will secure the disk sample to the wood backing and make it rigid enough to use power equipment to prepare a ring surface.

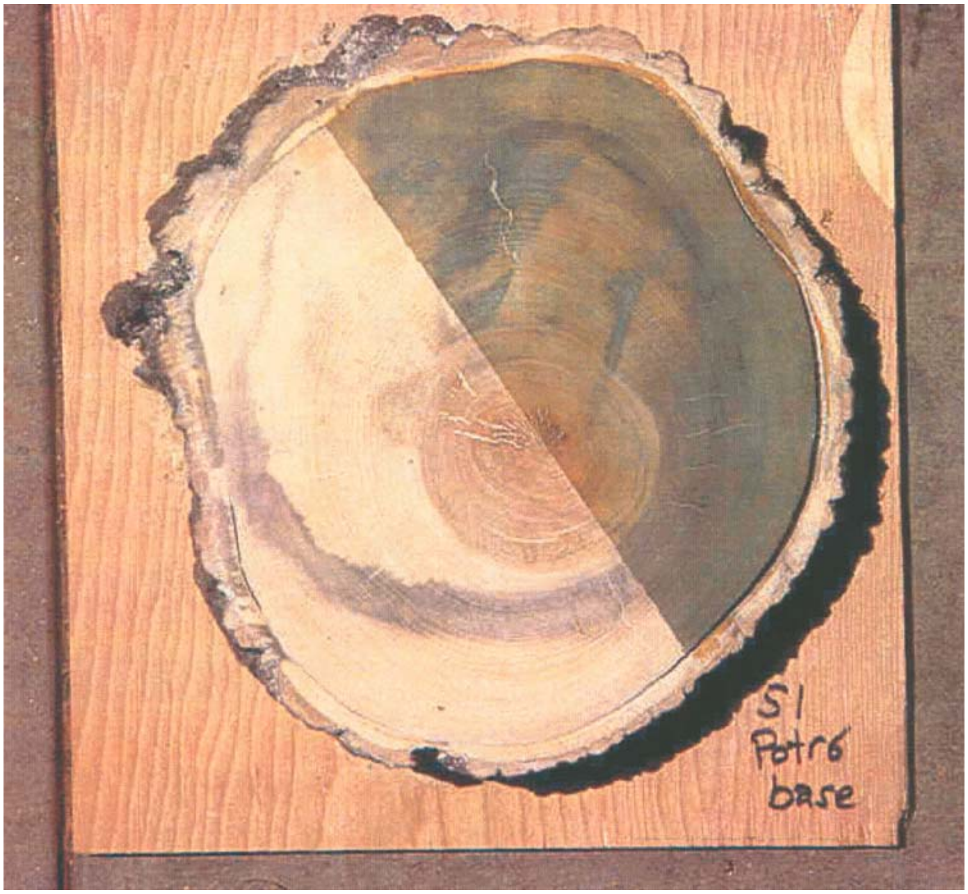

Figure 3—Surfaced aspen disk half stained and glued to wooden backing.

Equipment needed to prepare tree-ring samples includes electric hand planers, belt sanders, stains, and an assortment of different grits of sand paper and sanding belts. Mounted aspen core and disk samples should be sanded with a belt sander, using progressively finer grits of belts from 150, 240, and 320. Then they should be sanded by hand using a 400 grit sheet and finally a micro-finishing film sheet of 15 m grade. Disk surfaces should first be leveled off using an electric hand planer. Then a belt sander with progressively finer grits from 150 to 400 should be used to prepare surfaces for ring analysis.

If the thorough sanding of aspen samples is completed and the tree rings are still difficult to distinguish (figure 1B), a stain should be applied. Fehling's Solution (Forest Products Laboratory 1962) works well to distinguish sapwood from heartwood in aspen. It stains the latewood portion of the tree rings a dark brown and thus makes ring identification easier (figure 1C). The mix contains 3.5 g copper sulphate ($CuSO_4 \cdot 5H_2O$), 17.3 g potassium sodium tartrate, 6.0 g sodium hydroxide, and 100.0 ml water.

A good source for obtaining sample preparation material can be found on the web at www.valdosta.edu/~grissino/supplies.htm.

Conclusion

Aspen annual growth rings are much easier to see when samples have been prepared using these techniques. The extra effort needed to collect and prepare samples in this manner will result in more accurate age and growth determinations and facilitate the identification and measurement of tree-ring growth patterns for dating disturbance events in aspen forests.

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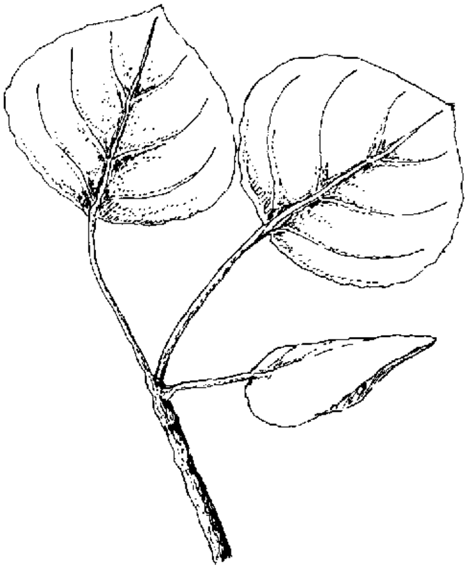

Manipulating Aspen Ecosystems

Manipulations to Regenerate Aspen Ecosystems

Wayne D. Shepperd[1]

Abstract*—Vegetative regeneration of aspen can be initiated through manipulations that provide hormonal stimulation, proper growth environment, and sucker protection—the three elements of the aspen regeneration triangle. The correct course of action depends upon a careful evaluation of the size, vigor, age, and successional status of the existing clone. Soils and site productivity, competition from other plants, and the potential impact of browsing animals upon new regeneration should also be considered. Treatments may include doing nothing, commercial harvest, prescribed fire, mechanical root stimulation, removal of competing vegetation, protection of regeneration from herbivory, and in limited circumstances, regenerating aspen from seed.*

Introduction

Aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Little 1971) (figure 1). It occurs in a wide variety of ecosystems and climatic regimes and is a crucial component of many landscapes. Aspen is a disturbance-dependent species that adapted well to the frequent fire regimes that existed in western landscapes prior to European settlement. Several silvical and ecologic characteristics of aspen allow it to fit this role well. Aspen is very intolerant of shade, requiring full sunlight to thrive. Because of this, it is very sensitive to competition from shade tolerant species like spruce (*Picea* sp.) and fir (*Abies* sp.). Aspen can grow on a variety of soils (Peterson and Peterson 1996), but it thrives on deep heavy (clay) organic soils that are often Mollisols (U.S. Department of Agriculture 1975). Although aspen does produce abundant crops of viable seed (McDonough 1979), it reproduces primarily by root suckering throughout most of its western range.

Vegetative regeneration of aspen requires a stimulation to initiate the sucker response. This can be any disturbance that interrupts the auxin/cytokynin balance between roots and shoots, and it stimulates root buds to begin growing. The hormonal imbalance can result from a disturbance that kills the parent trees outright, such as a fire, disease, and timber harvest, or one that only temporarily defoliates the parent, such as a late frost or defoliating insects. This process has been referred to as interruption of apical dominance (Schier and others 1985). In either case, the initiation of bud growth must also be accompanied by sufficient sunlight and warmer temperatures at the forest floor to allow the new suckers to thrive (Navratil 1991, Doucet 1989). Full sunlight to the forest floor best meets these requirements. Even so, young aspen suckers are susceptible to competition from other understory plants and herbivory from browsing ungulates, especially when conditions exist where less than optimal numbers of suckers are produced.

The interaction and co-dependency of these features can be summarized into a model similar to the regeneration triangle used for other species (Roe et al.

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Figure 1—Distribution of aspen (*Populus tremuloides* Michx.) redrawn from Little (1971).

1970; Shepperd and Alexander 1983). Successful vegetative regeneration of aspen is dependent upon three key components: hormonal stimulation, growth environment, and protection of the resulting suckers (figure 2). Each of these factors involves one or more of the silvical characteristics of aspen discussed above. Any manipulation of aspen ecosystems has to satisfy all of these requirements to successfully regenerate the species.

Manipulation Techniques

Manipulation techniques that are potentially available to perpetuate aspen forests include:

Doing nothing
Commercial harvest
Prescribed fire
Mechanical root stimulation
Removal of vegetative competition
Protection of regeneration from herbivory
Regenerating from seed

Choosing the appropriate technique for a given aspen stand depends upon its age, vigor, stocking, associated vegetation, accessibility, the abundance of other aspen in the landscape, and the importance ascribed to maintaining aspen at a particular location. None of the above techniques can be used in all situations.

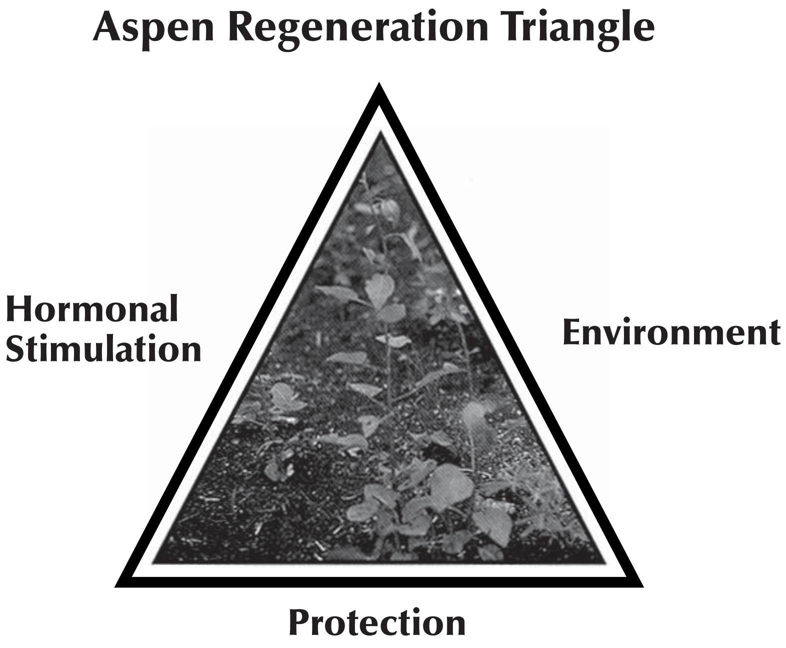

Figure 2—The aspen regeneration triangle illustrates the interdependence of factors that are crucial to aspen regeneration success.

To be successful, a manipulation technique must meet the three requirements of the aspen regeneration triangle, be cost effective, and be technically feasible.

Doing Nothing

Surprisingly, this alternative is often overlooked but appropriate in many situations. Decisions about manipulating individual aspen clones should be based on their health, vigor, and role in the surrounding ecosystem. If a clone is showing little sign of decline, disease, or distress from competition, contains multiple age classes, or is successfully suckering, it is unlikely that any immediate management intervention is necessary to preserve its existence in the landscape. Even clones that are declining may not require active intervention if they are successfully regenerating.

Identifying clones that need to be treated is crucial. Mueggler (1989) presents a general decision model that can be used to prioritize aspen stands for treatment. Aspen stands that are dominated by conifers, or those that are breaking up and not naturally reproducing, are likely to need treatment to rejuvenate the aspen clone. Mueggler further recommends protecting regeneration that is heavily grazed or browsed until it can grow beyond reach of animals.

Although developed for Intermountain aspen stands, these guidelines are generally applicable throughout the West. However, site capability, local conditions, and management objectives will all influence the decision to regenerate aspen. For example, it may be wise to harvest healthy aspen clones to establish new age classes in large single-aged landscapes. Conversely, a declining clone might provide better wildlife habitat than a healthy one in some situations. It is important to remember that what constitutes a desirable condition for aspen in one ecosystem may not be acceptable in another. Each situation needs to be judged in its own context and appropriate action be selected accordingly.

Commercial Harvest

Harvesting aspen for commercial products is a viable means of regenerating aspen forests on operable terrain where an aspen wood market is available and a transportation system exists to remove it. Clearcutting, or (more specifically) clearfell-coppice cutting, is the harvest method of choice in most situations. Removing all aspen at once (including understory stems, if present) best meets all three requirements of the aspen regeneration triangle and will stimulate dense suckering (figure 3). Soil compaction (Shepperd 1993; Alban 1991; Navritil 1991) and nutrient recycling may be problems with some harvesting systems that concentrate tops and limbs at centralized landings.

Partial cutting may be sufficient to stimulate suckering in some clones, but it often does not work well. It is extremely difficult to avoid damage to residual trees while logging a partial cut. Rot and canker disease organisms may be introduced through even the smallest bark wounds and thus, affect the future value of stems that are left. Stems left after a partial cut are also susceptible to breakage, windthrow, and sunscald when exposed to the elements (Jones and Shepperd 1985). Growth of subsequent suckers will be reduced under a partial overstory (Doucet 1989; Perala 1983).

Group selection is an uneven-aged option that may be applicable to managing aspen. The suckering response is usually adequate if group openings are sufficiently large to allow full sunlight to reach the ground throughout most of the area. Harvesting in smaller units partially shades the openings but creates a greater amount of edge between uncut and regenerating aspen than an equivalent area of large harvest units. Smaller openings provide easier access to browsing animals (Timmermann 1991). In one documented case on the Fraser Experimental Forest in central Colorado, cutting small 0.1 ha openings resulted in numerous disease-infected suckers (Jacobi and Shepperd 1991).

Fire

Fire meets all the requirements of the aspen regeneration triangle. It stimulates suckering by killing overstory stems and by killing near-surface root segments and thereby interrupting the flow of auxin to surviving downstream root segments. Fire removes competing understory vegetation and conifer seedlings, and it allows sunlight to reach the forest floor. The vegetation consumed by the fire provides a nutrient pulse for new suckers and the blackened

Figure 3—Aspen successfully regenerated using a commercial clearfell coppice harvest. Uncompahgre Plateau, Colorado.

surface warms soil in the root zone, further stimulating sucker growth (Hungerford 1988). Dense suckering over large burned areas can act as a deterrent to browsing animals (see protection discussion below).

Using fire as a primary regeneration tool in aspen forests requires the availability of fuels and acceptance of the risk that accompanies the uncertainty of applying treatment. It is usually difficult to get a fire to carry through a pure aspen stand, even in the understory. Because of this, aspen stands are often used as living fire breaks. Elevated crowns and green understories restrict prescribed burning in pure aspen stands to narrow time periods in the spring and fall when vegetation is dry, but not covered with snow. Wildfires in aspen are most likely to occur in early spring before green-up. Thin-barked aspen stems are extremely sensitive to heat damage, so fire can be highly effective in stimulating aspen regeneration, if a burn of sufficient severity and ground coverage can be obtained (Brown and DeByle 1989).

Burning mixed aspen/conifer stands to regenerate aspen brings risks associated with an overabundance of fuels. Dense conifer understories, heavy loadings of downed logs, and continuous ladder fuels to the upper canopy usually require a prescribed crown fire to meet the requirements of the aspen regeneration triangle. Such fires can be quite effective and very spectacular, but may be damaging to aspen roots if the heat penetrates into the soil (Perala 1991). One means of mitigating this risk is to use prescribed fire as a secondary or site preparation tool in conjunction with harvest or mechanical manipulation to remove excess biomass. Fuels can be manipulated by the initial treatment to allow safe and effective burning later. Combining fire with other manipulation treatments can greatly benefit the aspen regeneration triangle, maximize suckering, and closely mimic natural fire disturbance cycles in mixed aspen/conifer ecosystems. We are currently testing the use of prescribed fire in combination with the harvest of competing overstory conifers in a cooperative study with the Coconino National Forest in Arizona. Fueled by the scattered logging slash, a subsequent prescribed burn stimulated much more suckering than did the removal of competing overstory conifers alone (figures 4, 5).

Mechanical Root Stimulation

Regenerating aspen by mechanical removal of overstory stems can produce successful aspen regeneration (Shepperd 1996; Perala 1991). Severing aspen roots from parent stems is also known to produce aspen suckers (Perala 1991). In a replicated study comparing bulldozing with chainsaw felling, Shepperd (1996) found that portions of clones where aspen was tipped over with a bulldozer produced significantly more sprouts than portions felled with a chainsaw. The difference was attributed the removal of stumps, which isolated lateral roots depriving them of any residual auxin left in the stumps. If true, it should be possible to initiate suckering in clones by mechanically severing some of the lateral roots. We currently are testing this stimulation effect at two sites in Arizona using a single-pass tractor-ripping technique (figure 6). The idea was to cut lateral roots spreading away from existing living stems, thereby interrupting the flow of auxin to bud primordia on the roots allowing the buds to sprout. So far, the two test clones have responded well. A map of sprout densities from a small, isolated, clone that was edge-ripped shows that the single ripper pass stimulated suckering about 20 m into the adjoining meadow at a density equivalent to 26,000+ stems/ha (figure 7). This one-time treatment effectively tripled the size of this small aspen clone without sacrificing any existing mature stems. None of the mature trees have died in the 5 years since the ripping treatment.

Pine removal/Slash burn

After pine harvest

After burn

5 years later

Figure 4—Pine removal and slash burn. The pine overstory was commercially harvested and then a light prescribed burn stimulated abundant aspen suckering. Coconino NF, Arizona.

Pine removal/No burn

After harvest of pine

5 years later

Figure 5—Pine removal (a) and no burn (b). When the pine overstory was removed without subsequent slash burning, fewer suckers were produced than in the stand in figure 4.

Figure 6—Severing lateral aspen roots using a dozer-mounted ripper, Coconino NF, Arizona.

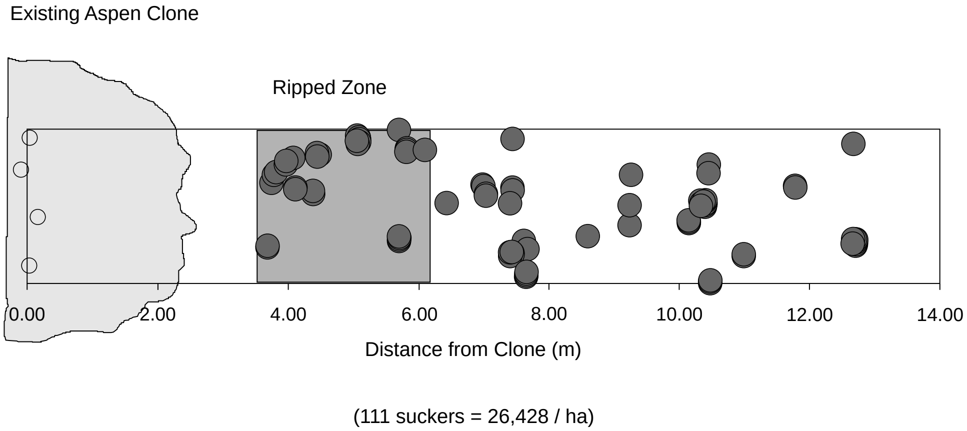

Figure 7—Mapped transect measured into a meadow adjoining an edge-ripped aspen clone. Circles represent locations of individual aspen suckers. Note clustering of suckers at root nodes, thus not all dots are visible.

Mechanical root stimulation may therefore be a cost effective tool useful to expand or rejuvenate small isolated clones where retention of existing mature aspen trees is highly desired. Full sunlight and warmer soil temperatures are still required at the location of the lateral roots being severed, so root stimulation should be limited to clones adjoining meadows, created openings, or in very open deteriorating clones (that are free of root disease). The limited size of most clones that can be treated in this manner will usually require protecting the new suckers from browsing animals until the suckers are established. Disking to stimulate aspen suckering is not recommended, however. The excessive mechanical disturbance to aspen roots can be detrimental to sucker survival and cause internal decay (Basham 1988; Perala 1977). The benefits of combining root stimulation with other treatments, such as clearfelling or burning, have not yet been tested.

Removal of Competing Vegetation

One thing that can be done to help a struggling clone to regenerate is to remove the vegetation that is inhibiting the process by shading or smothering young suckers. Vegetation removal can be done alone or in conjunction with other manipulations to increase initial suckering and slow or set back the rate of vegetative succession in aspen forests. It can include removal of competing overstory or understory vegetation as well as reduction of fuel loadings on the forest floor. Removal of competing vegetation can be accomplished with commercial timber harvest, mechanical treatment, prescribed fire, and chemical treatment via herbicides (Perala 1991). Removing vegetation meets only one of the three aspen regeneration triangle criteria by allowing sunlight to reach the forest floor and improving the growth environment for aspen. It does not directly stimulate sucker production or protect new suckers. However, it can have a dramatic effect, as happened in a small demonstration we installed on the Kaibab NF in Arizona. (figure 8). Removing competing pine from around the only two surviving aspen trees in this clone allowed the surrounding roots to sucker and expanded the clone to 0.1 ha in size. Fencing was required to protect sprouts from browsing animals, but the stimulation effect was readily apparent.

Protection of Regeneration From Herbivory

Protecting new aspen suckers from damage is an important consideration, regardless of the manipulation technique being used. A thorough assessment of the potential for damage should be conducted as part of any aspen management activity (including the do-nothing alternative) to determine whether new

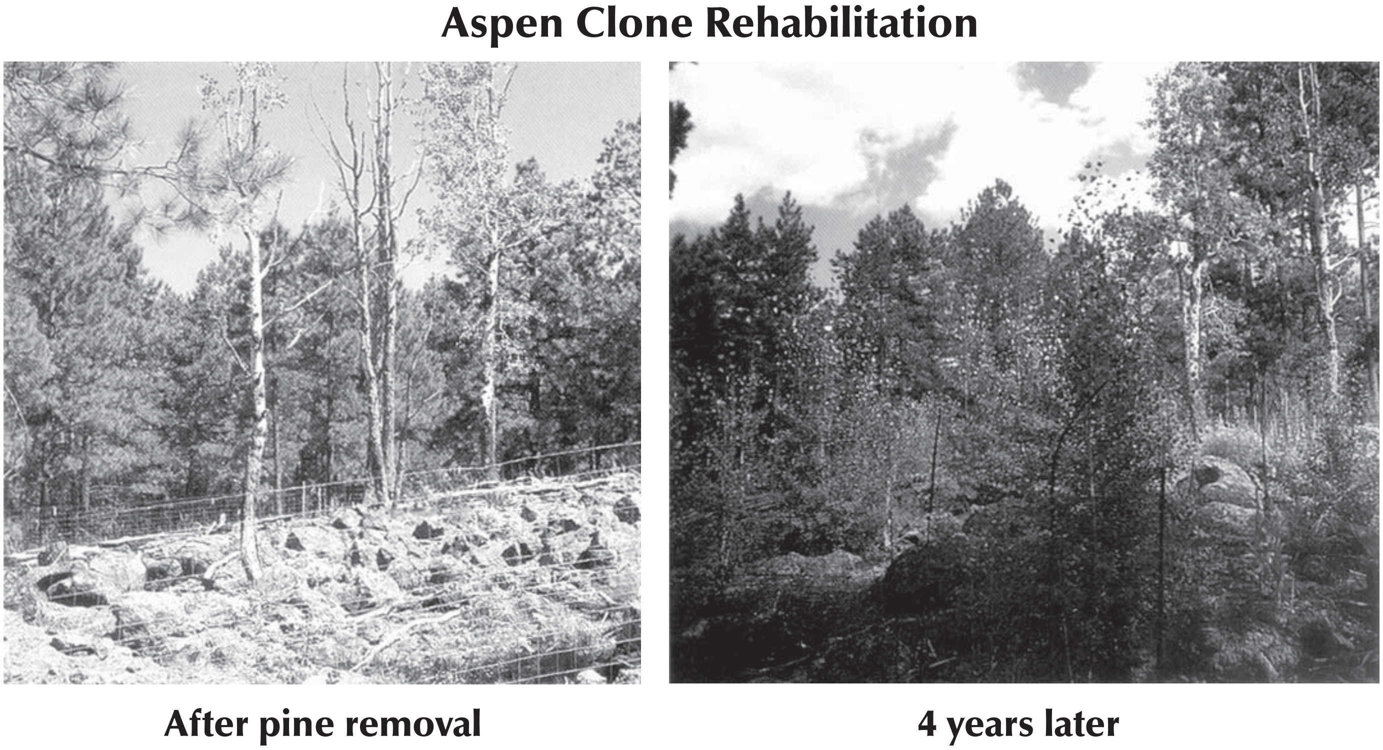

Figure 8—Aspen clone rehabilitation. Removal of a competing pine overstory allowed this two-stem aspen clone to sucker throughout a 0.1 ha area. Fencing assured survival of the new regeneration. Kaibab NF, Arizona.

suckers need to be protected from browsing animals. Getting aspen to sucker usually isn't the problem when manipulating aspen. Even declining aspen clones will sucker if conditions exist or are provided. Keeping sufficient numbers of suckers alive to accommodate natural sucker mortality (Shepperd 1996) and still restock the clone is often the real issue. This can be accomplished by either satiating the demand for sprouts (for example, providing more aspen suckers than all the animals within walking distance can eat), or by directly protecting the new aspen from browsing animals. Satiating the demand is easy if large acreages of aspen are treated. Experience in Colorado has shown that harvesting a number of large (6-8 ha) clearfell units at one time in a landscape will result in successful aspen regeneration without undue browsing damage, even when large numbers of animals were present (Crouch 1983).

Leaving logging slash has been reported to serve as a physical barrier to protect aspen sprouts from browsing (Rumble and others 1996), but slash appeared to inhibit suckering in another study (Shepperd 1996). The reasons for this discrepancy may be the amount and density of material that is left on site, or the inherent ability of some aspen genotypes to sucker in partially shaded conditions.

A recent experiment testing browse repellents on aspen under controlled field conditions demonstrated that elk browsing was significantly reduced under high repellent concentrations (Baker and others 1999). The cost of repeatedly applying repellents would likely be prohibitive under most wildland management situations, but repellents may be useful in deterring browsing in landscape plantings or other intensive cultures of aspen. Further testing of this technique is needed.

Fencing is the only guaranteed means of directly protecting sprouts from browsing animals. Constructing game-proof fences is a costly, labor intensive, time consuming, and long-term activity. Research (Shepperd and Fairweather 1994) and extensive management experience on the Coconino NF (Rolf, this proceedings) have shown that fencing is operationally feasible but must be maintained 8–10 years (or until dominant stems are 3 cm d.b.h.) to effectively protect aspen regeneration from high populations of elk. Wire fences constructed from two widths of 1 m wide field fencing, or one height of 1.4 m wide fencing with one or two high tensile smooth wires strung above, have been found to be effective. Electric fences have not proven effective, because of high maintenance requirements (Rolf, this proceedings).

Regenerating Aspen From Seed

Recent reports (including one in this proceedings) have demonstrated conclusively that aspen can occasionally reproduce naturally from seed in the western United States. However, given the stringent requirements of a bare mineral seedbed and ample supply of moisture needed to establish aspen seedlings (McDonough 1979), it seems unlikely that we can rely upon natural seedling regeneration or planting of artificially produced seedlings in most wildland management situations. We have established a research plantation of containerized aspen in a riparian area on the Arapaho National Forest to test the possibility of restoring aspen to areas with abundant soil moisture. Two-year survival is less than 50%, and seedling growth has been poor. Although not encouraging, these results do indicate that it may be possible to reestablish aspen in an area where it has been lost. Research using larger-sized transplant stock is needed to further test the feasibility of reestablishing aspen in critical areas.

Conclusions

Several options exist to manipulate existing aspen clones to stimulate vegetative regeneration. Success of any manipulation method depends upon taking advantage of aspen's silvical and growth characteristics to provide the correct combination of factors to initiate root suckering and to ensure maximum growth and survival of the new aspen. Manipulation should stimulate roots to sucker, provide optimal growth conditions for the new regeneration, and protect new suckers from browsing animals. The aspen regeneration triangle provides an easy means of visualizing these three key factors.

Choosing the correct course of action to provide these elements depends upon a careful evaluation of existing conditions. Size, vigor, age, and health of the existing aspen clone, soils and site productivity, competition from other tree and understory species, and the potential impact of browsing animals upon new regeneration should all be considered. Success also depends upon careful monitoring of treatment results and adapting future activities to fit local conditions.

Decisions to manipulate aspen also need to be based on the role it plays in the surrounding landscape. Basing management decisions on the current condition of an individual clone may be insufficient to meet ecosystem needs. The need for age class and structural diversity in the overall landscape, as well as the need to maintain desired resource outputs (timber, forage, wildlife habitat, visuals, and so on), should be factored into the decision. No single manipulation prescription can be expected to work under the continent-wide diversity of conditions where aspen is found.

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Dynamics of Aspen Root Biomass and Sucker Production Following Fire[1]

Roy A. Renkin[2] **and Don G. Despain**[3]

Abstract—*Changes in preburn aspen root biomass 8 years following prescribed fire were analyzed for five experimental sites distributed across a moisture gradient. Total root biomass decreased across all sites but was proportionately greater in xeric than mesic sites. Response of post-burn aspen suckers to ungulate browsing varied according to site and treatment. Browsing influenced the age class structure and height growth, but had no influence on stem density, in aspen occurring on more mesic sites. Aspen occurring on the more xeric sites responded differently, with the extreme case being the almost total elimination of one site as a result of burning and browsing. Aspen sucker biomass production of protected plots, measured as the ratio of current annual biomass versus prior year biomass accumulation, revealed wet site aspen to differ from drier sites and suggests production over the long term may be more influenced by site conditions than other extrinsic factors. Aspen suckers 1–4 meters in height and protected for 8 years were quickly reduced to <1 m when exposed to browsers, suggesting height growth alone is not sufficient to guarantee escape from browsing. Eleven years of 100% annual biomass removal via clipping on one of the mesic sites demonstrated that biomass removal alone is not sufficient to eliminate aspen from the site.*

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Quaking Aspen Reproduce From Seed After Wildfire in the Mountains of Southeastern Arizona

Ronald D. Quinn[1] **and Lin Wu**[2]

Abstract*—Quaking aspen regenerated from seed after a stand replacement wildfire in the Chiricahua Mountains of southeastern Arizona. The wildfire had created gaps in the canopy so that aspen were able to establish from seed. Seedlings were found at a mean density of 0.17 m^{-2}, 30 m or more from the nearest potential seed trees. Six clumps of aspen seedlings contained 18–186 trees, occupying areas of 145–500 square meters at densities of 0.09-0.27 m^{-2}. White-tailed deer (*Odocoileus virginianus*) browsed 14.3% of the seedlings. Occasional sexual reproduction of aspen may be a general trait of the species throughout the western portion of its range in North America.*

Introduction

In the Mountain West, quaking aspen trees (*Populus tremuloides*) commonly reproduce by asexual root suckering. After fire or other disturbance that kills overstory stems, suckers sprout from surviving root systems. Reproduction after fire from seed has been reported, but apparently this is exceptional (Kay 1993; Renkin et al. 1994). Aspen seeds require consistently moist soil to germinate and survive, a condition that is rarely met in the climates of the mountains of Western North America. Presumably this is the reason that aspen seedlings are seldom observed in the West. This paper is a preliminary report on a population of aspen established from seed after a wildfire in southeastern Arizona during 1994.

Study Area

The Chiricahua Mountains are located in southeastern Arizona, near the borders of New Mexico and the Republic of Mexico. The range is approximately 65 km long and 32 km wide, with a maximum elevation of 2,975 m. The upper reaches of the range are dominated by a series of ridges and peaks in excess of 2700 m. Common trees at elevations above 2,400 m are Arizona pine (*Pinus ponderosa* var. *arizonica*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), southwestern white pine (*Pinus strobiformis*), and quaking aspen. The primary study area was located at elevations of 2,700 to 2,900 m, immediately north of the Chiricahua Wilderness, within the Coronado National Forest of Cochise County, Arizona. It fell between two meadows named Long Park and Flys Park (Universal Transverse Mercator grid coordinates 3528500N 662100E). Slope in the sampling area varied from 0 to 8%, with an easterly aspect.

Rattlesnake Fire

In June and July of 1994, a fire ignited by lightning burned 11,000 ha of forested land in the Chiricahua Mountains. This fire was the first large fire that had burned through these mountains in about 100 years (Skelecki et al. 1996; Swetnam et al. 1990). The fire burned at various intensities across almost all of

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the upper elevation forests including all areas with aspen. Stands of aspen occurred in scattered clumps through the predominantly coniferous forest in relatively mesic locations above approximately 2,400 m. We estimate that aspen covered less than 10% of the area burned by the fire. The wildfire continued for 3 weeks under burning conditions that were quite variable, propelled by erratic winds, steep terrain, and through various fuel types. It was finally extinguished by the arrival of monsoon rains. Within the fire perimeter the fire burned almost all forested areas; however, the fire intensity was quite variable over the landscape. In some watersheds all trees were killed and the soil structure was destroyed by heat so intense that boulders shattered. At the opposite extreme, some places had light ground fires that burned only the smallest downed fuels. The aboveground parts of most aspen were killed but some canopy aspen, particularly in the more mesic areas, were only lightly scorched at the base. In places many of these large aspen survived, although often the bottom of the tree was partly killed on the side from which the fire approached.

Climate

Maximum precipitation occurs in the monsoonal months of July and August. Nearly one-half of the annual precipitation falls within this period, which is during the growing season for aspen (figure 1). The months of May and June, when aspen seeds are produced and dispersed, are much drier. In some years this period has no precipitation at all. Since aspen seeds require soil that is consistently moist in order to germinate and survive (McDonough 1985), in many years soil moisture conditions would not permit aspen seedlings to become established, even if other physical conditions were optimal. In the Mountain West the lack of soil moisture near the surface during late spring and early summer, even for a very short period, has been presumed to prevent the establishment and survival of aspen seedlings.

Sampling Methods

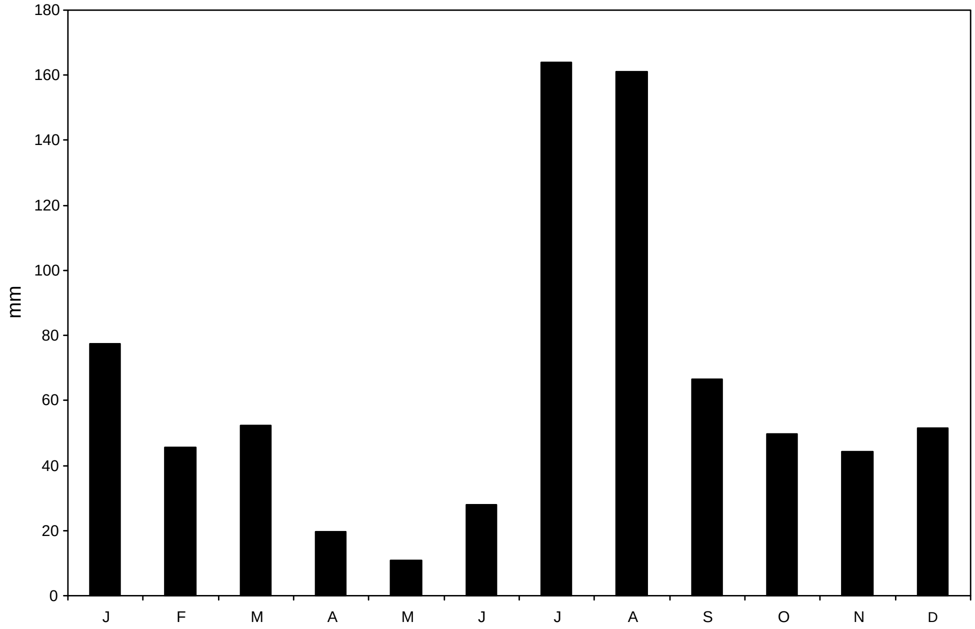

Figure 1—Mean monthly precipitation at Rustler Park, Chiricahua Mountains, Arizona.

In the summer of 1998 a belt transect was established on a gently sloping plateau where most trees had been killed by the 1994 fire. A second belt, perpendicular to the first, was added in 1999. The belts were 4 m wide, with lengths of 225 and 300 m. In 1998 the composition of the prefire forest was measured at points 15 m apart along the center of the 4 x 225 m belt using the point quarter method (Cottam and Curtis 1956). All trees killed by the fire were still standing, and both living and dead stems were included in the tree sample. The cover and species composition of the understory vegetation was measured around the same points using circular plots with a 1-meter radius. In the summer of 1998, tree seedlings of all species within the belt were counted. The height and diameter of each aspen seedling were measured. Seedling measurements were repeated in the summer of 1999 along both belts; all aspen were tagged and mapped; and evidence of browsing on individual aspen was noted.

In the summer of 1998, 11 small aspen, ranging in stem height from 9 to 65 cm, were excavated. The entire root systems were exposed, and the lengths and diameters of all major roots were measured, along with the height and basal diameter of the tallest stem. In 1999, 16 additional aspen were excavated and measured. Plants to be excavated were randomly chosen from the area defined by a 225 x 300 m rectangle that enclosed the perpendicular belt transects, excluding seedlings that fell within the belts. Cross-sections were cut from just above the base of an additional 16 randomly chosen small aspen in the same area. The cross-sections were examined under magnification for growth rings.

Results and Discussion

Forest Composition

Prior to the fire the forest in the study area was comprised of half Arizona pine, mean d.b.h. 27 cm (SD = 12.2), and half Douglas-fir, mean d.b.h. 31 cm (SD = 15.5). Tree density was 700 per hectare. Twenty-six percent of the sampled Arizona pines survived the fire; all of these were growing in an area where the fire did not crown. All Douglas-fir within the study area were killed. The largest diameter tree sampled was a Douglas-fir snag with a d.b.h. of 96 cm. This was the only tree measured that showed a conspicuous scar from fires long before 1994. The estimated height of canopy trees was 16–18 m. Canopy cover from snags in areas where all trees were killed was 53%, and overstory cover was 71% in places with living Arizona pines. Mean understory cover in 1999 was 50%, comprised of a mixture of 45 species of annuals and short-lived perennials from 20 plant families. Asteraceae, with 11 species, was best represented both in terms of number of species and total cover.

Excavated Seedlings

The 11 aspen excavated in 1998, and 16 aspen excavated in 1999, had a mean of 3.3 major roots, with a range of 1–14 (table 1). A major root was defined as one originating from the base of the union between stems and roots, and having a diameter similar to that of the corresponding stem. These roots had a mean diameter of 4.2 mm, as compared to a mean stem diameter of 4.6 mm. Mean root length, measured from the base of the plant to the point where the root divided into two or more secondary roots, was 24 cm as compared to a mean stem height of 26 cm. There was great variation in the length, number, and paths followed by the roots. Some extended to depths greater than 20 cm while others grew

Table 1—Mean characteristics of excavated aspen seedlings (standard deviations in parentheses).

	1998	1999	1998 + 1999
Stem height (cm)	22 (21)	27 (29)	26 (26)
No. stems	2.1 (2.0)	1.7 (1.4)	1.8 (1.6)
Stem diameter (mm)	4.1 (2.7)	4.8 (3.4)	4.6 (3.1)
No. roots	3.1 (2.9)	3.4 (3.2)	3.3 (3.1)
Root diameter (mm)	3.5 (1.5)	4.5 (2.8)	4.2 (2.4)
Root length (cm)	28 (28)	22 (21)	24 (24)
N	11	16	27

laterally only a few cm beneath the surface. Roots grew around and between rocks and other barriers, and some followed very circuitous paths, changing direction several times both horizontally and vertically. Between 1998 and 1999 the seedling population showed development in all variables measured except root length; mean height and diameter of stems increased, and roots became slightly more numerous (table 1). The excavations provided evidence that the small aspen being sampled were in fact seedlings that had originated after the fire and not suckers that had arisen from mature roots. All of the excavated plants had spreading root systems, and neither sinker roots nor feeder roots were observed. For comparison, several suckers approximately the same size as the seedlings were excavated from nearby aspen clones. In every case the feeder root from which the sucker had grown was readily located, and a sinker root provided a direct and obvious connection between the sucker and the feeder. In one case the feeder root had died, but it was still present and the sinker had a markedly different morphology than the roots of the seedlings. No evidence was found in the study area of aspen root systems that predated the 1994 fire. There were no aspen snags or living aspen larger than seedlings within the study area. No evidence of aspen was found close enough to have produced roots to extend inside the study area.

Cross-sections collected from the 16 aspen in 1998, the fourth growing season after the fire, had from one to three growth rings, with a mean of 1.9 (SD = 0.7). Precipitation records from a weather station approximately 4 km from the study site showed that May and June, the critical months for germination and survival of aspen seedlings, were very dry in 1995, the first full growing season after the fire (figure 2). In 1996 there was ample precipitation in June, and in 1997 there was substantial rain in May. There may have been no seedlings with four growth rings because none germinated and survived until 1996, the second year after the fire, when precipitation was adequate. These rainfall and ring patterns support the hypothesis that aspen seeds can germinate in fire areas in the years following fire, provided that moisture is consistently available to them during the first few months of the growing season. Laboratory and field studies have shown that aspen seeds retain viability for only a few months, and after germination even the slightest drying kills them (McDonough 1985). We did not notice aspen seedlings anywhere in the study area or larger fire area before 1997.

Seedling Dispersion

The dispersion pattern of the aspen seedlings along the belts in 1999 was examined using two-term local quadrat variance and paired quadrat variance, dividing up the transects into 4 x 4 m blocks (Krebs 1999). These analyses failed to show a clumped distribution, probably because the scale of sampling was not appropriate to the scale of aspen clumps. A map of the 358 aspen seedlings was

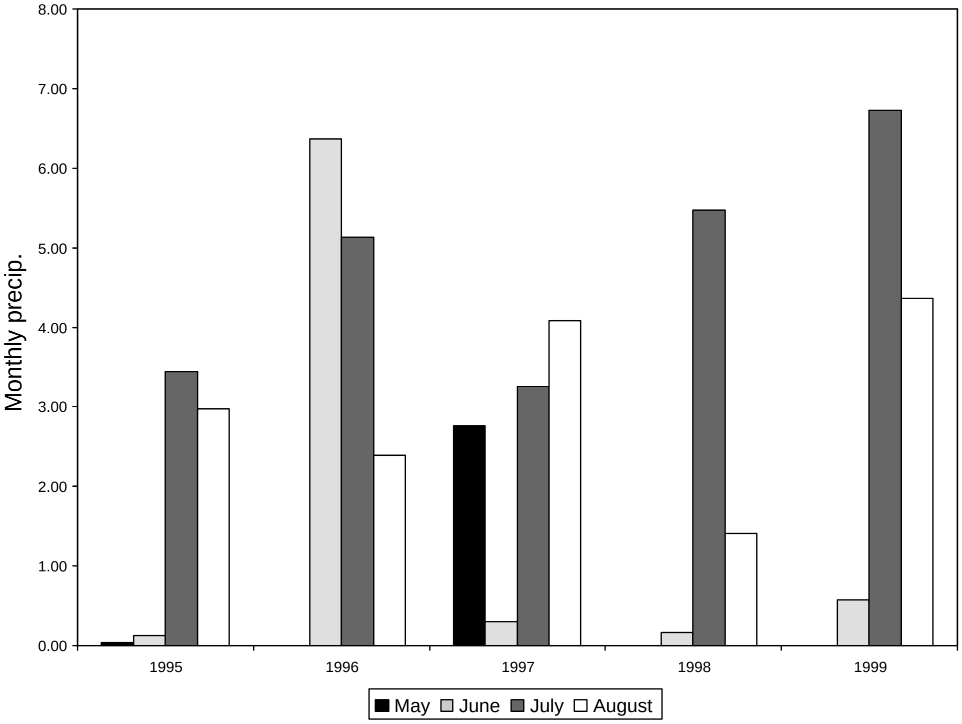

Figure 2—May-August precipitation 1995–1999, Chiricahua Mountains, Arizona.

made from the 1999 data using the GIS software of Arcview. Seedling clumps were identified from this map using a GIS grid interpolation algorithm that divided the belts into an array of 1 x 1 m squares; a circle with a 3.5 m radius was then drawn around the center of each square containing aspen (figure 3). If other aspen were found within that circle, then all trees inside the circle were identified as being members of a clump. The process was then repeated by drawing additional circles around the centers of squares in which aspen had already been encountered. With each iteration more trees might be added to the

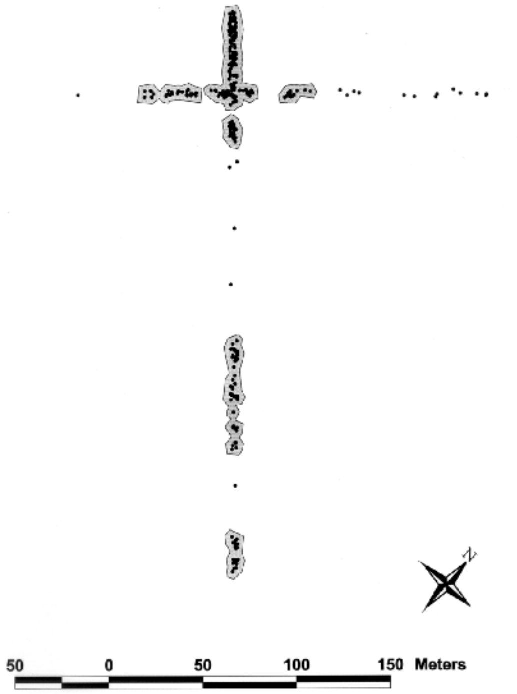

Figure 3—Six aspen seedling clumps. Each dot represents an individual seedling.

clump, and the process was repeated as long as successive circles generated from squares already included continued to capture additional aspen. This analysis identified 16 clumps. Ten of these had fewer than five aspen and these small clumps were excluded from further analysis. Perimeters drawn around the remaining six clumps were defined by a series of overlapping arcs with radii of 3.5 m originating from the center of squares that had captured one or more aspen. These perimeters were confined to within the boundary of the sampling belts. Six clumps of aspen seedlings contained between 18 and 186 trees, occupying areas of 145–500 square meters at densities of 0.09–0.27 per square meter (table 2). Linear regression analysis among the clumps showed no significant relationship between clump density and mean stem elongation (SEL) or between clump density and mean height.

The two clumps with the highest densities of aspen seedlings were at the northwestern end of the sampling belts, 30–75 m from the nearest living canopy aspen that could have been a source of seeds (figure 3). Aspen seeds are dispersed by the wind (McDonough 1985). The prevailing winds in late spring when seeds would be dispersed are from the west and northwest, placing these dense clumps immediately downwind from the nearest potential seed trees. Between aspen clumps there are gaps of as much as 50 m containing few or no aspen seedlings (figure 3). It is probable that wind deposited aspen seed on the ground in a more uniform pattern than that of the seedlings. Aspen clumps probably arose in places where soil moisture and perhaps other variables were most favorable for germination of aspen seed and survival of aspen seedlings.

Herbivory

There is no evidence that herbivory was significant in the observed patterns of aspen regeneration. Only 14.3% of the aspen seedlings on the permanent plots showed evidence of having been browsed in 1999. Between 1998 and 1999 the mean height of seedlings almost doubled, from 0.49 to 0.85 m, and overall seedling density decreased only slightly, from 0.14 to 0.12 m^{-2}. However, the decrease from 2.1 to 1.7 in the mean number of stems of the excavated seedlings between 1998 and 1999 may have been due to stems killed by deer browsing (table 1). In other parts of North America heavy browsing by cattle, elk (*Cervus elaphus*), or deer (*Odocoileus* spp.) sometimes retards or prevents the regeneration of aspen, even in dense stands of suckers (Romme et al. 1995; Suzuki et al. 1999; Kay and Bartos 2000). Cattle were not present in the study area, and elk have been absent from the Chiricahua Mountains for at least 100 years, if they were ever present at all. The only ungulate now present is white-tailed deer (*Odocoileus virginianus*). Deer have been observed near the study area browsing on aspen. But within the study area these animals were seldom observed, and their scats were rare. In 1999 and 2000, direct observa-

Table 2—Characteristics of six clumps of aspen seedlings. Sel = elongation of uppermost stem during 1999.

Area	Den	N	Mean ht	Mean sel
m^2	*m^{-2}*		*m*	*cm*
698	0.27	186	0.63	19.4
500	0.10	52	0.42	16.8
284	0.09	25	0.81	34.4
199	0.11	22	0.18	8.3
147	0.12	18	0.50	16.7
145	0.21	30	0.63	27.6

tions of deer foraging near the study area among abundant aspen suckers showed they spent over half their feeding time eating items other than aspen, even though aspen was the most abundant species of plant. There were no rabbits (*Sylvilagus* spp.) present.

Conclusion

Fires that last for weeks, across variable topography and variable burning conditions, can produce a very heterogeneous burn pattern. Forest patches where all trees are killed by crown fires and the mineral soil laid bare are interspersed with patches that burn as a ground fire, while other places may be missed by fire altogether. This is the fire pattern that occurred in Yellowstone in 1988 and in the upper reaches of the Chiricahua Mountains in 1994. Aspen were produced from seed in both places. Both of these fire episodes were natural in the sense that they were ignited by lightning and were ultimately extinguished by precipitation, with very uneven burning conditions in between. However, the fire in the Chiricahuas was also an artifact of management because the interval between fires was prolonged by a century of active fire suppression (Skelecki et al. 1994). Fires of this nature are becoming increasingly frequent in many other places in the West. Undesirable as these intense and often uncontrollable fires may be in terms of other public objectives, they open up the canopy so that aspen might be established in new places from seed. Fires of lesser intensity or at closer intervals can rejuvenate aspen clones by suckering; however, to the degree that less intense fires fail to create patches where canopy conifers have been killed and bare soil exposed, it is less probable that aspen will subsequently extend their local range by seeding.

It may be that throughout the western portion of aspen range, occasional sexual reproduction is a more general trait than has been recognized. Seedlings that survive in nature may have been rarely observed due to the exacting and unlikely conditions of fire pattern and subsequent precipitation that are prerequisites for the successful germination and survival of aspen seed. Reproduction from seed as documented by this study, and after the 1988 Yellowstone Fire (Kay 1993; Renkin et al. 1994; Romme et al. 1997), may be important for the long-term survival of aspen populations in the forests of the West. Aspen reproduction from seed, although infrequent, could be important as a source of genetic diversity and as a way of establishing clones on sites previously unoccupied by aspen. Over the long run, sexual reproduction of aspen may be necessary for this species to continue to adapt to the variable environment of the Mountain West, where frequent changes in precipitation and fire regimes have affected the character of forests for thousands of years (Bonnicksen 2000). The aspen stands in the Chiricahua Mountains are growing near the southern edge of the natural range of aspen. Such marginal stands of aspen may be relatively close to the limits of physical tolerance for growth and survival. If this is the case in the Chiricahua Mountains, then the genetic and spatial flexibility conferred by reproduction from seed could be especially important for the long-term survival of these particular populations.

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Aspen Regeneration in South-Central Colorado, San Isabel National Forest

Tim Benedict[1]

Abstract—*The potential for aspen regeneration in conifer stands has been underestimated on the Salida Ranger District. Harvest of mature aspen stands on the Salida and San Carlos Districts encouraged regeneration. Following harvest, the Douglas-fir and some Engelmann spruce stands in the Arkansas Hills area regenerated primarily to aspen. Disturbance through aspen harvest, prescribed fire, wildfire, and other approaches is critical to aspen sustainability and health for the San Isabel National Forest. Disturbance must take place to regenerate the aspen component and reduce the conifer invasion.*

Introduction

Quaking aspen (*Populus tremuloides*) covers about 80,450 acres of the San Isabel National Forest's Salida and San Carlos Ranger Districts in south-central Colorado (figure 1). Although aspen is present in many conifer sites throughout the San Isabel National Forest, aspen occupies only about 10% of the two ranger districts. The potential for aspen regeneration in conifer stands (i.e., Douglas-fir) has been underestimated on the Salida Ranger District. Disturbance through aspen harvest, prescribed fire, wildfire, and other approaches is critical to aspen sustainability and health for the San Isabel National Forest. About 13,320 acres of aspen are suitable sites for harvest (figure 2).

In the past, the public and small purchasers on the San Isabel have primarily harvested aspen for fuelwood. Only recently has there been an increased demand for aspen fiber. This is due to a decrease in local supply that results in purchasers having to haul longer distances to meet their current demand. The majority of aspen could be utilized by mills found in Delta and Olathe, Colorado. These mills produce aspen flakeboard and panels.

Aspen is highly valued for its scenic beauty. In south-central Colorado, it is found at elevations ranging from 8,200 to over 10,000 feet (Powell 1988). In the fall, usually mid to late September, many visitors come to view the vibrant colors of yellow, gold, orange, and red. People seek out the aspen to take pictures, stopping along the roadside to view it. Some want to write about it, others want to take in this slice of Colorado and enjoy it. Aspen has many other values such as enhancing wildlife habitat and providing forage for cattle. It also has an ecological value for forest health and diversity.

Aspen is an unusual tree species. On the one hand, aspen stems are among the shortest lived in the area and usually die before their first century. On the other hand, aspen clones are often among the longest-lived individuals in an area, tenaciously holding to a site and living through many regenerating events, to maximum ages of centuries or even millennia (Johnston 1996).

Aspen is one of the most shade-intolerant species in the Rockies (Shepperd 1985). Most stands in the Rockies reproduce by root suckering after a disturbance to existing overstory stands (DeByle and Winokur 1985). This is also true of treated aspen stands throughout the Salida and San Carlos Districts of the San Isabel National Forests.

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Figure 1—Aspen landscape on the San Isabel National Forest.

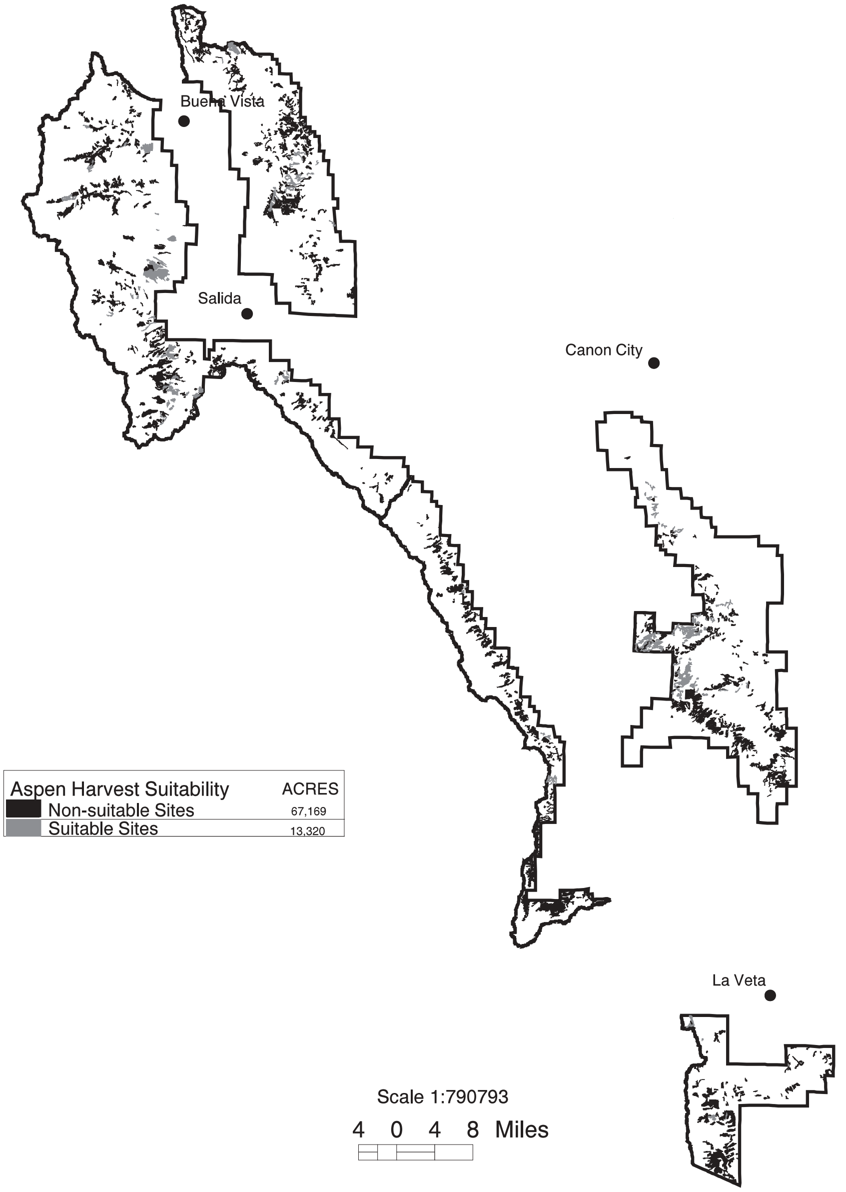

Figure 2—Suitable and nonsuitable sites for aspen harvest on the San Carlos and Salida Ranger Districts, San Isabel National Forest.

Regeneration Data

Treated aspen sites were queried from the Region 2 Resource Information System (R2RIS) and site folders reviewed from 1980 to 1997 for the Salida and San Carlos Districts, as this is where the majority of the aspen sites reside on the San Isabel National Forest. These data and associated information are summarized in appendix 1, which lists the most current regeneration survey, stems per acre, and other key data. The regeneration surveys consisted of walk-throughs that sampled representative regeneration or systematic sampling of the site with fixed plots (1/100th or 1/300th acre), generally 1 plot per acre for the site. For example, if you had a 20-acre site, crews would sample 20 plots of the site in a general grid of three chains by three chains.

Salida Ranger District Aspen

Appendix 1 illustrates 13 aspen clearcuts varying in size from 11 to 45 acres. There were some small patch cuts varying in size from 2 to 5 acres. The aspen cover types greater than 11 acres seemed to regenerate well. The number of stems/acre ranged from 800 to 9,000, generally in the fifth year following harvest (figure 3). The median for stems/acre is 2,400. The small patch cuts appeared to regenerate (on some patch cuts upward to 2,000 stems/acre from earlier regeneration surveys); but over time, due to repetitive big game and cattle damage and other reasons not known, they failed to survive.

The average stocking percentage for the 13 aspen sites clearcut is at 90% of minimum stocking and distribution. The Forest Plan states a minimum stocking of 300 trees/acre and 75% of the plots are stocked. However, one of those sites regenerated mainly into conifer. The elevation ranges are 9,400 to 9,800 feet. Aspect did not limit regeneration. All aspen types that were clearcut averaged 21 acres. The average heights of aspen 3 to 5 years after harvest ranged from 1 to 5 feet with the majority of sites being 3 feet. There was no site preparation on any of these sites indicated in the records.

The treatment or disturbance from cutting encouraged the regeneration of the mature aspen stands that were harvested. When movement of auxin into roots is halted or reduced by cutting, burning, girdling, or defoliation of trees, auxin levels in the roots decline rapidly (Eliasson 1971, 1972). This permits new

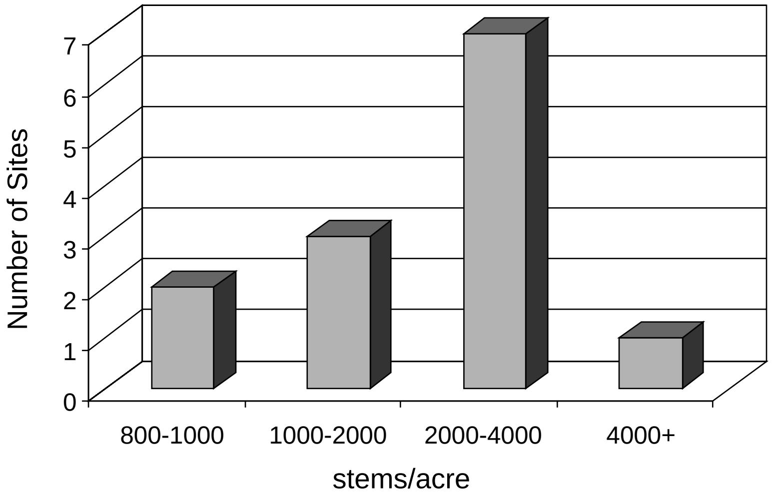

Figure 3—Summarized regenerated stems/acre for 12 aspen sites harvested from 1984 to 1991, Salida Ranger District, San Isabel National Forest. (One stand regenerated to conifer and was not included in the graph.)

suckers to begin; it also allows preexisting primordial, buds, and shoots whose growth had been suppressed by auxin to initiate growth (DeByle and Winokur 1985).

Aspen Regeneration in Conifer Stands

Following harvest, the Douglas-fir and some Engelmann spruce stands in the Arkansas Hills area (East Salida District—Kaufman Ridge, Herring and Bald Mountain) regenerated primarily to aspen (appendix 2). This was found quite unexpectedly in the Herring Timber Sale area when units planted to conifers began sprouting aspen. However, in the original planning this was not apparent. There was an existing aspen root system or remnant aspen scattered throughout these conifer sites that consisted mainly of Douglas-fir in the Kaufman Ridge area. Individual genotypes can cover several hectares and ramet generations may persist over 150 years (Shepperd 1981). The Herring Creek area was primarily Douglas-fir with a lodgepole pine component on three sites. When these conifer stands were harvested, these areas sprouted in aspen. Regeneration surveys showed mainly aspen regeneration with some conifer reproduction (appendix 3). The stems/acre varied from 855 to 2,550 mainly on level ground or northern aspects. This was 4 years after harvest. In the Kaufman Ridge area, aspen stems/acre ranged from 652 to 1,233 with heights of 1 to 3 feet. In 1998, aspen had grown to 6 feet plus.

According to research in Colorado of eight plant species studied, Berndt and Gibbons (1958) found quaking aspen roots to have the greatest lateral extent, up to 48 feet from the tree. Also, several studies of soil water depletion by aspen imply effective rooting depth to be at least 9 feet on deep well-drained soils (Johnston 1970; Johnston et al. 1969). The scattered aboveground aspen and the existing root systems were present for quite some time in the Kaufman Ridge and Herring areas, and the harvest disturbance caused the aspen to sprout.

It is theorized that during past succession cycles, an aspen stand was ultimately replaced by Douglas-fir in these areas. If a coniferous seed source is present, young conifers will soon begin to establish themselves under aspen (Shepperd 1985). The aspen acts as a nurse for the more tolerant conifers (usually spruce, subalpine fir, or Douglas-fir, but in some cases ponderosa pine and lodgepole), resulting in a mixed aspen/conifer stand (Shepperd 1985).

Wildland and Prescribed Fire

Possibly in the 1800s, prolonged drought conditions encouraged wildfire that created sufficient disturbance to conifer stands and as a result aspen sprouted. Perhaps this succession cycle continued for a long period. Another possible source of ignition for fires were human caused (i.e., Native Americans using fire to improve area for big game). Even a mere scattering of aspen in a coniferous stand commonly will restock the area with a new aspen forest after a severe wildfire (DeByle and Winokur 1985).

There were 59 fires recorded from 1970 to 1992 on the east side of the Salida District (figure 4). Thirty-one of these fires were fires less than ¼ acre. These small fires comprised the majority of fires. The policy during this timeframe was to suppress fires as soon as they were reported. Most fires were kept small due to suppression efforts. Typically, unless there is a very dry year associated with

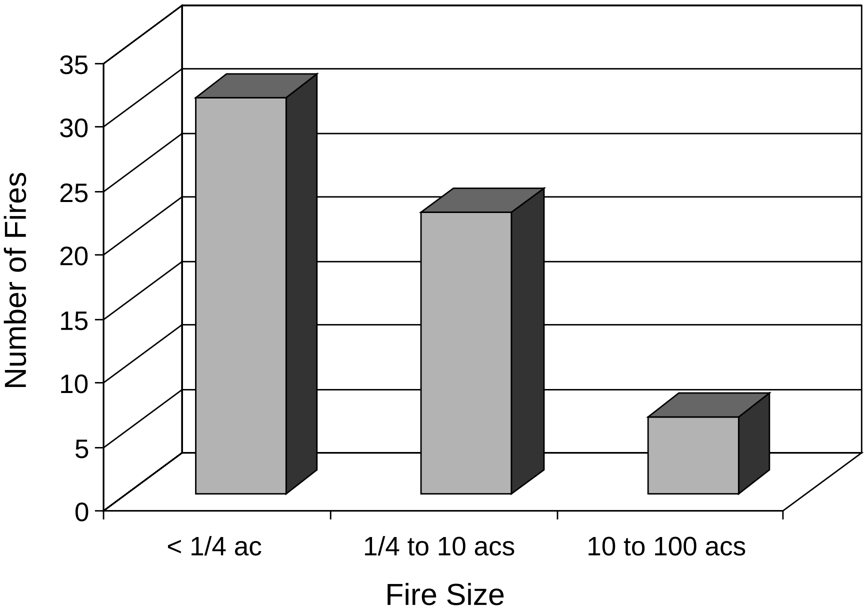

Figure 4—Fire frequency from 1970 to 1992 for the East Side of Salida District, San Isabel National Forest.

high winds, most fires stay small. The typical fire season is from mid-April to early/mid July. Most of the lightning in this time frame is late June to early July followed by monsoon rains around the Fourth of July.

Lightning was the main cause (83%) with the remainder human caused (17%)(table 1). One could surmise that lightning-caused fires in the 1800s (prior to suppression efforts) along with other causes that created disturbance quite possibly regenerated aspen.

There were only six of the 59 fires between 10 and 100 acres. Although this is not a long period, it does indicate that in a 22-year timeframe fires have not grown to large size. This would show a minimal disturbance from wildland fire. This could be attributed to the aggressive program to put out fires, lack of fuel continuity, and green vegetation.

The Bald Mountain Prescribed Burn also regenerated aspen (appendix 2). This was observed 2 to 3 years after treatment in an aspen patch that had sprouted and grown very dense. Most prescribed burns in the aspen type are designed to regenerate declining, overmature clones. To maximize sprouting, at least 80% of the overstory should be killed (Powell 1988). Research indicates that fires with flame lengths of 1.7 to 2.1 feet are required to kill aspen trees. This equates to fireline intensities of 18 to 28 BTU/ft/sec (Brown and Simmerman 1986). To achieve this intensity in aspen community types with undergrowths dominated by shrubs or tall forbs, the herbaceous vegetation should be at least 50% cured (Brown and Simmerman 1986). A good burning window to create a high burning intensity in aspen sites is immediately after leaves have fallen in September and before leaves are compacted.

Table 1—Fire cause summary (1970–1992, east side Salida District).

Cause	Fire occurrence	Percentage
Lightning	48	83
Campfires	8	14
Smoking	2	3

Source: GIS fire history maps.

San Carlos District Aspen

The San Carlos District has aspen intermixed in the conifer stands throughout the district. In one instance a unit in the Little Froze Timber Sale (located in the Wet Mountains) regenerated 500+ stems/acre on a conifer site after being harvested. Aspen sites throughout the district are experiencing a conifer invasion. Generally, there has been a lack of disturbance. From the R2RIS records, only 172 acres of aspen have been treated since 1986. It has been observed that aspen encroachment is occurring in natural meadows as aspen crowd the edge and tiers of different age classes (Mike Smith, personal communication).

The Forest Plan (Land and Resource Management Plan, Pike and San Isabel National Forests, Comanche and Cimarron National Grasslands) states that wildfire has historically been the primary disturbance initiating aspen root sprouting. Control of wildfire has permitted many aspen stands to become overmature with little success in regenerating. In the absence of disturbance, either natural or human caused, much of the aspen will convert to conifer types in 100 to 200 years.

Management Recommendations

It is clear that to sustain healthy aspen on the San Isabel National Forest, disturbance/management must take place to regenerate the aspen component and reduce the conifer invasion. Here are some recommendations:

- Manage aspen sites at a minimum of 8 to 10+ acres. Small patches seem to be vulnerable to big game or cattle damage. Consider treatments scattered over a large landscape.
- In areas where access is limited or does not exist, consider prescribed burning to meet resource goals and objectives. It is critical to burn at an intensity to kill a majority of the overstory to obtain regeneration.
- Explore market opportunities to encourage future aspen treatment.
- Aspen management does not need site preparation to regenerate aspen. This will serve as a reduced cost when considering other conifer species that will require site preparation.
- Consider conifer sites (i.e., Douglas-fir) with an aspen remnant or root system that will sprout/regenerate after disturbance (prescribed fire or cutting). Some indicators of aspen presence are: downed aspen from past years, occasional live standing aspen, and adjacent aspen stands.
- Consider wildland fire use and integrated fire planning through an approved Fire Management Plan. This examines the appropriate management responses to a management area. In some areas “fire breaks” of pure aspen are being considered so that a catastrophic fire could stopped much easier by running into pure aspen.

- Look at boundaryless management through agreements and memorandums of understanding between state and federal agencies to treat the landscape.

Aspen sites throughout the San Isabel National Forest need further management due to lack of disturbance. Treatment and care of this important species is critical to continued scenic beauty, forest health/diversity, wildlife, range and forest management, and sustainability of our forest for future generations.

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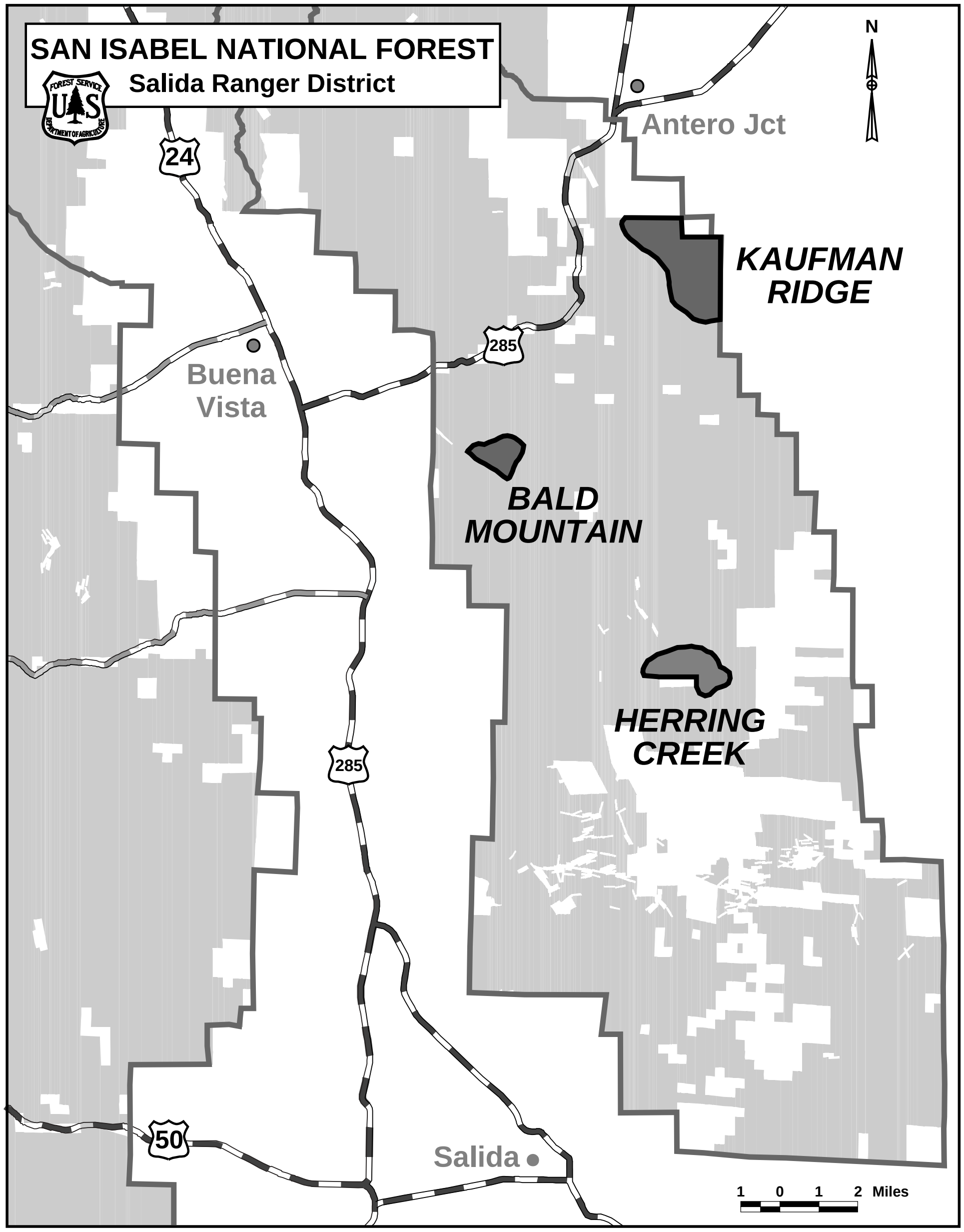
Appendix 1: Regeneration Surveys of Treated Aspen Sites of the Salida District, San Isabel National Forest

Location and site	Acres	Plant assoc.	Elevation	Aspect	Harvest year	Regen. survey type and year[1]	# of stems/acre	% stocked and ave. height
			ft.					
101301- 004	22	—	9,700	NE	1987	1996 P	2,086	100% 3 ft.
101301- 014	45	—	9,900	NE	1984	1989 W	3,000–4,000	95% 4–5 ft.
101301- 036	42	—	9,900	NE	1985–1986	1988 P	2,500+	100% 3–4 ft.
101301- 043	17	—	9,700	NE	1986	1989 W	2,500+	100% 3.5 ft.
1013001- 044	22	—	9,700	NE	1987	1992 W	4,000	90% 3–5 ft.
101405- 0100	16 Thurberi	POTR- Festuca	9,800	N	1988	1992 W	2,400 patchy	50% 5 ft.
101405- 0102	16 Thurberi	POTR- Festuca	9.800	Level	1989	1994 W	9,100	100%
101405- 0105	11 Thurberi	POTR- Festuca	9,800	Level	1990	1993 P	1,782	100% 0.5 to 2 ft.
101405- 0106	19 Thurberi	POTR- Festuca	9,800	Level	1991	1996 P	1,021	100% 3 ft.
101801- 003 (11 acs)	4 (1–5 acre) patch cuts	—	9,400	Level	1978–1980	1992 W on the edge	0 Some aspen regen.	0%*
101806- 008 (13 acs)	5 (1–4 acre) patch cuts	—	9,800	Level	1980–1981 for stocked site	1992 W and P aspen regen. on the edge	0 Some	0%*
101806- 012	4 and 5 acre patch cuts(9)	—	9,600 9,500	Level Level and 1993, 5 acs	Approx. 1980, 4 acs 1996 W	1992 W 1,000 Mainly conifer	0 100%	0%*
102311- 066	14 Thurberi	POTR- Festuca	9,500	Level	1989	1996 P	833	87% 2 ft.
102206- 46	29	—	9,400	S	1983–1984	1989 P	3,300	88%
102206- 047	22	—	9,400	S	1986	1990	800	100%
102206- 048	11	—	9,500	E	1987	1992	1,264	63%

[1] P = Systematic sampling with plots and W = Walk-through.

*Big game and cattle damage, 101801-003 and 101806-008 showed earlier surveys with regeneration.

Appendix 2: General Locations of Aspen Regeneration in Conifer Stands



Appendix 3: Aspen Regeneration in Conifer Stands (Mainly Douglas-fir) of the East Salida Ranger District, San Isabel National Forest

Location and site	Acres	Plant assoc.	Elevation	Aspect	Harvestyear and method[1]	Regen. survey type and year[1]	# of stems/acre[2]	% stocked and ave. height
			ft.					
Herring Creek								
101405-107	9	PSME/ARUV JUCO	9,880	Level to E	1990 CC	1996	855 P	89% 2 ft.
101405-0108	26	PSME/ARUV JUCO	9,880	NE	1990 ST	1996	2,550 P	100% 3 ft.
101405-109	15	PSME/ARUV JUCO	9,880	N-NE	1990 CC	1996	1,353	93%
Kaufman Ridge								
101402-0097	38	PSME/JAAM	9,850	NE	1992 ST	1996	1,137 P	89% 1–3 ft.
101303-0067	23	PSME/JUCO	9,800	NE	1992 ST	1996	652 P	91% 3 ft.
101305-086	28	PSME/ARAD JUCO	9,700	NE	1992 ST	1996	1,233 P	92% 2–3 ft.
Beaver Creek								
102311-069	5	PIPU-PSME JUCO	9,100	NE	1993 CC	1996	350 P	100%
102311-070	43	PIEN/JUCO PICO/JUCO	9,360	NE	1993 ST	1996	440 P	91% 1–3 ft.

Note: The majority of the regeneration is aspen with some conifer intermixed.
[1] ST = Seed tree and CC = Clearcut.
[2] P = Systematic sampling with plots.

Aspen Response to Prescribed Fire and Wild Ungulate Herbivory

Steve Kilpatrick[1] **and Diane Abendroth**[2]

***Abstract**—Land management agencies in northwest Wyoming have implemented an active prescribed fire program to address historically altered fire regimes, regenerate aspen, and improve overall watershed functions. Treated clones are susceptible to extensive browsing from elk concentrated on supplemental feedgrounds and from wintering moose. Previous attempts at fire-induced aspen regeneration in the area indicate various levels of success due to existing herbivory levels. Belt transects were established in fire-treated aspen clones along the Gros Ventre drainage, northeast of Jackson, Wyoming. Sucker heights and densities were compared between northeast and south/southwest exposures to determine fire-induced regeneration success and opportunities for future successful treatments. Overall stem density has not changed ($p < 0.05$) from 1996 to 1999. Mean stem height increased from 0.79 m in 1996 to 1.1 m in 1999. Due to differential snow accumulations affecting browse availability, northeast (NE) and south-southwest (SSW) aspects were compared. Mean stem densities are not different between these aspects ($p < 0.05$). However, mean stem height on NE aspects (1.4 m) was greater ($p < 0.05$) than SSW aspects (0.80 m). Our ability to detect a difference in regenerating aspen height between aspects was probably due to differential browsing levels of ungulates. Such information is important for prioritization of future vegetation treatments.*

Introduction

Aspen (*Populus tremuloides*) communities are recognized for their multiple values, including recreation, scenic vistas, water yield, water quality, wood products, habitat for an array of wildlife species, forage for wild and domestic ungulates, and landscape diversity (Bartos and Campbell 1998; DeByle and Winokur 1985). The role of fire in perpetuating aspen forest has long been recognized, and without it many aspen stands are being replaced by conifers or shrubs and herbaceous vegetation (Jones and DeByle 1985). Many stands in the Intermountain West are mature, overmature, or decadent with a small percentage of the stands less than 60 years of age (Bartos et al. 1994; Mueggler 1989). Mueggler (1989) found that approximately two-thirds of the aspen stands in the Intermountain Region exceed 95 years of age.

Aspen communities must be rejuvenated by a disturbance event such as fire, or they will be lost to successional competition. Krebill (1972) sampled 100 aspen plots within the middle Gros Ventre drainage and concluded that parent tree mortality (3.6% per year) was excessive and that far too few aspen sprouts were escaping browsing and pests for successful replacement of overstory mortality. Adequate replacement was occurring in only three of the 100 sample plots.

Suckering generally increases substantially within the first 2 to 3 years post treatment (Bartos and Mueggler 1981; Bartos et al. 1994; Brown and Debyle 1989). The long-term viability and successful vegetative responses of prescribed burns are less understood. Impacts of wild and domestic herbivory on aspen

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suckers following prescribed burn treatments can be adverse and may quicken the demise of clones (Bartos 1979; Bartos and Mueggler 1979; Bartos et al. 1991, 1994; Krebill 1972).

The Gros Ventre drainage is a historical winter range for 4,000–5,000 elk (*Cervus elaphus*) and 200–300 moose (*Alces alces shirasi*). Wild ungulate herbivory can be significant in localized areas, with 2,500 supplementally fed and 1,500 elk remaining on native winter range. Previous aspen investigators working within the Gros Ventre drainage have expressed concern that regenerating aspen with existing levels of herbivory would be difficult. Aspen monitoring in an adjacent drainage, Dry Cottonwood Creek, indicated typically 75% of the regenerating suckers have one or more of the leaders browsed each year. Approximately 90% of the browsing occurs during the fall/winter season and 10% during the spring (Wyoming Game & Fish Department 1999).

Krebill (1972) concluded that if current browsing and parent tree mortality continued, most of the aspen type in the Gros Ventre would ultimately be eliminated from these winter ranges. Bartos et al. (1994), after monitoring sucker response 12 years post burn in the Breakneck Ridge area, questioned the continued use of fire to regenerate aspen stands that are subject to heavy ungulate use. Such management action could speed the elimination of aspen stands.

Bartos et al. (1994) and Bartos and Mueggler (1981) also evaluated the effects of prescribed fire on decadent aspen stands within the Gros Ventre drainage. The primary purpose of the prescribed burns was to produce more aspen suckers than the local wintering elk population could consume and thus perpetuate aspen stands. Initial suckering response, approximately 20,000 stems per ha, was adequate to regenerate deteriorating aspen stands. Densities 6 years post treatment, 4,300 to 10,300 stems per ha, were approximately the same as pretreatment. Bartos et al. (1994) reported sucker densities 12 years post treatment ranging from 1,500 to 2,400 stems per ha, which was 29 to 38% less than pre-burn densities. The control also had a 39% decrease in production, which was attributed to elk use.

It has been hypothesized, however, that some burned aspen stands are capable of successful regeneration despite heavy elk use (Despain et al. 1986; Gruell and Loope 1974; Houston 1982). Evidence of successful prescribed fire-induced aspen regeneration amid large wild ungulate populations on other sites in the Gros Ventre drainage and elsewhere in northwest Wyoming has encouraged managers to continue treating aspen. An additional 15,000 acres of sagebrush/grassland and aspen have been treated with prescribed and wild fire within the Gros Ventre drainage since the 1974 burn evaluated by Bartos et al. (1994). Managers continue to monitor the effects of fire-induced aspen regeneration and ungulate herbivory to determine site opportunities for successfulness regeneration. Browsing impacts are usually the greatest on trees less than 13 feet (4 m) tall. DeByle and Winokur (1985) recommend 400 well-formed stems per acre (1,000 per ha) at 13 feet (4 m) for clone establishment. This paper reports on density and height of 8- to 11-year-old fire-induced regenerating aspen stands on opposing aspects.

Setting and Methods

Aspen belt transects were monitored from 1996 to 1999 within the Bacon Creek drainage, a tributary of the Gros Ventre River. It is located approximately 50 km northeast of Jackson, Wyoming, and approximately 10 km southeast of the Bartos et al. (1994) study. Elevation is approximately 2,500 m and is located near the upper end of the Gros Ventre drainage. Multiple prescribed burns were conducted in the Bacon Creek drainage from the spring of 1989 through the fall of 1991. General objectives were to recycle sagebrush communities and regenerate decadent aspen stands. Successful clone establishment objectives were: (a) mean stem density >12,355 stems per ha, and (b) mean stem height >3 m.

The closest supplemental feeding site is 3 to 4 km from the monitoring sites and has an attendance of approximately 1,000 elk. Supplemental feeding of elk generally begins around January 1 and continues into April of each year. Supplementally fed elk are not confined to the feeding sites and frequently forage various distances from feeding sites, depending on snow depths. An additional 15 to 30 moose also utilize the Bacon Creek tributary.

Monitored clones were burned during the springs of 1989 and 1990 (n = 4), and fall of 1991 (n = 2). General burning conditions, fuel loads, and fuel moistures varied, resulting in different burn severities and intensities. Post treatment sucker densities appeared adequate for clone reestablishment throughout most treated sites, but herbivory levels appeared to be impacting successful regeneration of some clones, especially those with a southerly exposure. Managers began monitoring clone regeneration on opposing exposures to determine fire-induced regeneration success. Comparing treatment exposures may assist in prioritization of future treatment sites and enhance the odds of successful regeneration.

Six (6) permanent belt transects (0.91 x 30.48 m [3 x 100 ft]) were established during 1996 in previously burned aspen clones and monitored annually (1996 to 1999) for height and density. Sites were located within 300 meters on both sides of Bacon Creek and monitored September or October each year. Four sites were located on the north side (south and southwest aspects) and two sites were located on the south side (northeast aspect) of Bacon Creek. All are within designated winter range for elk and moose. Sucker heights and densities were compared.

Results and Discussion

Mean annual sucker growth rate ranged from –0.03 to 0.21 m and averaged 0.12 m per year. Percentage of stems in lower height classes has decreased while percentages in the upper height classes have increased (figure 1). A 44% reduction of stems in the 0.6–0.9 m (2–3 ft) class occurred from 1996 to 1999. This is the first year (1999) that stems exceeded the 2.7 m (9 ft) height. Bartos et al. (1991) reported sucker growth rates of 0.02 and 0.22 m per year on burned sites in the Breakneck Ridge area of the Gros Ventre drainage.

Mean sucker height 8 to 11 years post fire for all six sites was 1.1 m (3.6 ft) (figure 2). Browsing by elk and/or moose was evident but quite variable, ranging from slight (5–20% use of available leaders) to heavy use (60–80% use of available leaders). Bartos et al. (1994) reported suckers to be only 0.5 m in height 12 growing seasons post burn at the nearby Breakneck Ridge site and attributed the short growth form to repeated browsing by elk. On other sites within the Gros Ventre drainage and Jackson area, Bartos et al. (1991) documented greater mean sucker heights 6 years post burn: Russold Hill—1.0 m, Uhl Draw—0.8 m, and Burro Hill—1.0 m. Browsing level and sucker height responses at the Bacon Creek site appear to be intermediate between the more severely browsed sites at Breakneck Ridge and the less severely browsed sites at Uhl Draw, Russold Hill, and Burro Hill.

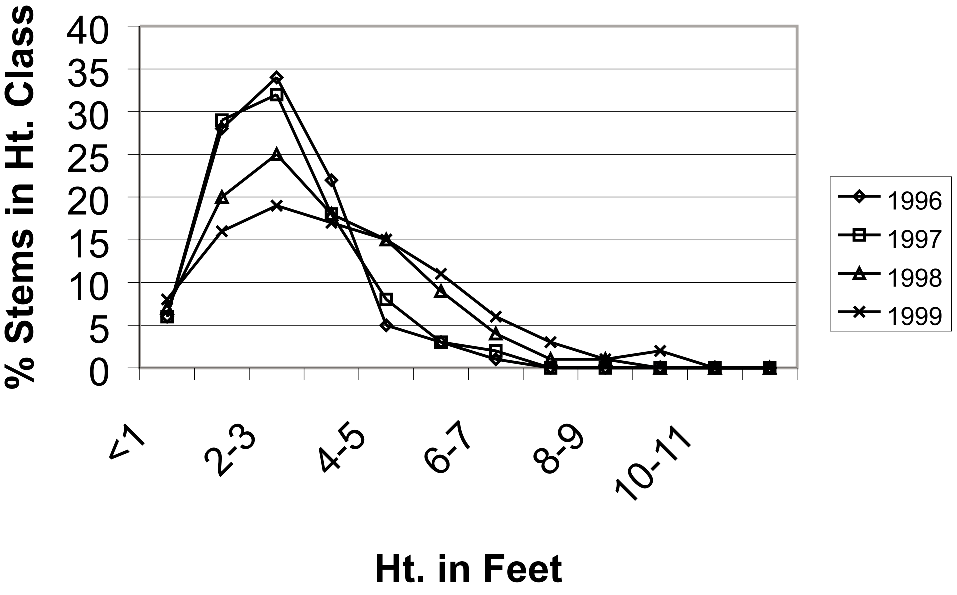

Figure 1—Aspen sucker height classes 8 to 10 growing seasons following prescribed burning. A 44% reduction of stems in the 2 to 3 foot height class occurred from 1996 to 1999.

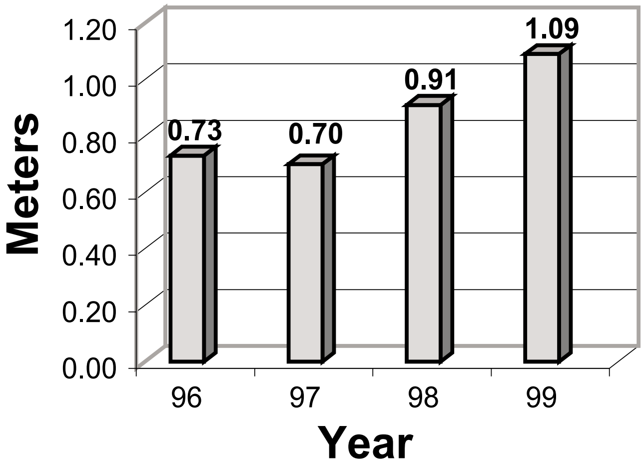

Figure 2—Aspen sucker heights following 8 to 10 growing seasons following prescribed burning.

Height comparisons between suckers on northeast and south/southwest aspects were made. Mean sucker height on south/southwest aspects (0.79 m) was significantly less than mean sucker height on northeast aspects (1.4 m) ($p < 0.05$) (figure 3). Clones on south/southeast aspects receive higher levels of use and are being maintained at shorter growth forms than adjacent clones on northeast aspects. Even though monitoring sites were close to each other (<1 km apart) and were within 300 m of the drainage, herbivory levels were quite different. Differences in sucker heights and herbivory levels were attributed to differences in snow depths and browse availability on opposing aspects.

Sucker heights within the Bacon Creek tributary appear to be slowly approaching the objective height of 3 m. Some suckers on the northerly exposures exceeded 2.7 m (9 ft) and are near the objective of 3 m. They may meet or exceed it within the next year if past growth trends continue. Suckers on southerly exposures are gaining height more slowly. No suckers on southerly exposures exceeded 1.8 m (6 ft). They are more available and are receiving additional herbivory but are slowly gaining height. It may be several more years before they reach the objective.

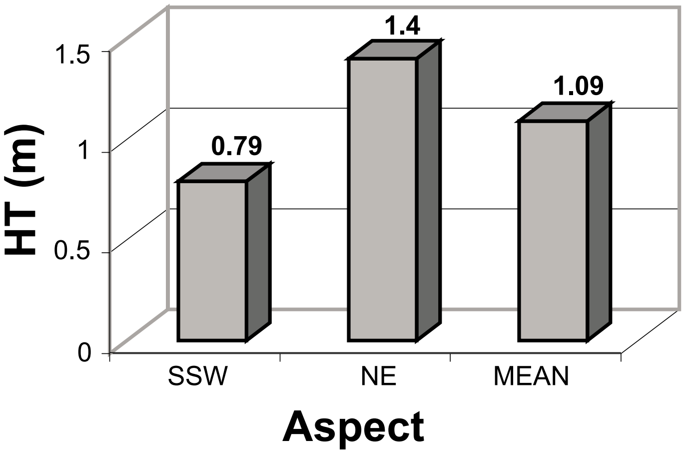

Figure 3—Comparison of aspen sucker heights between aspects (SSW = south/ southwest; NE = northeast). Height differentials between aspects were significantly different (*p* <0.05).

Mean annual sucker densities for all sites ranged from 13,983 to 26,889 stems per ha (5,666 to 10,890 stems per acre) and averaged 19,299 stems per ha (7,816 stems per acre) in 1999. There was no significant decrease in sucker density between 1996 and 1999 (p <0.05) (figure 4). Sucker mortality was noted within clones, but annual production of new suckers appears to be compensating. Sucker mortality is mostly attributed to shepherd's crook while mortality due to herbivory appears minimal to date.

Mean sucker densities on south/southwest aspects (21,160 stems per ha [8,567 stems per acre]) were greater but not significantly different (p <0.05) from those on northeast aspects (15,609 stems per ha [6,317 stems per acre]) (figure 5). Current levels of herbivory apparently are not impacting sucker densities since they have not changed significantly over the past 4 years on either aspect and are actually greater on southerly aspects where herbivory is greatest. This is in contrast to the adjacent Breakneck Ridge study where sucker densities ranged from 1,500 to 2,400 stems per ha 12 years post burn (a 90% reduction in sucker density when comparing year 1 to year 12) (Bartos et al. 1994).

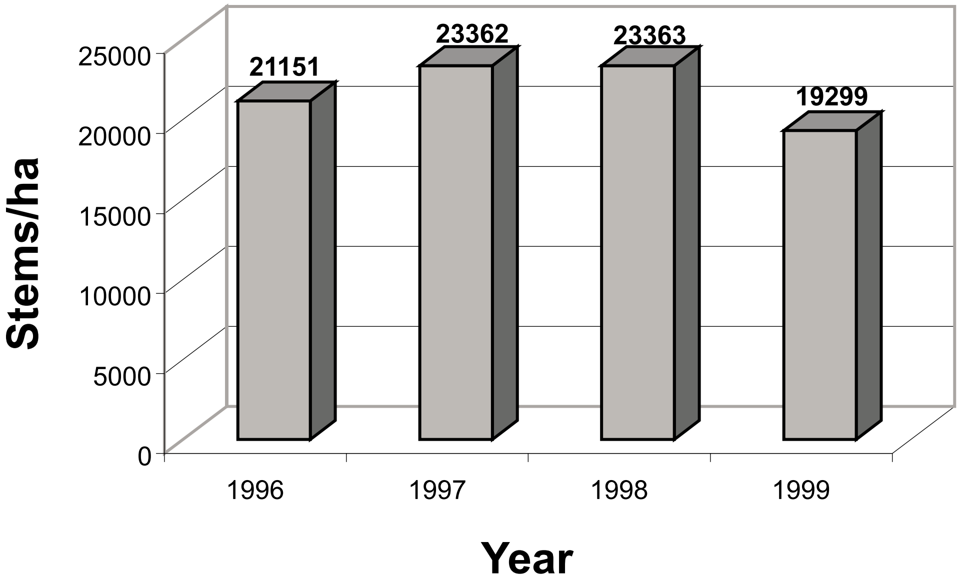

Figure 4—Aspen sucker density 8 to 10 growing seasons following prescribed burning. There was not a significant difference between years (*p* <0.05).

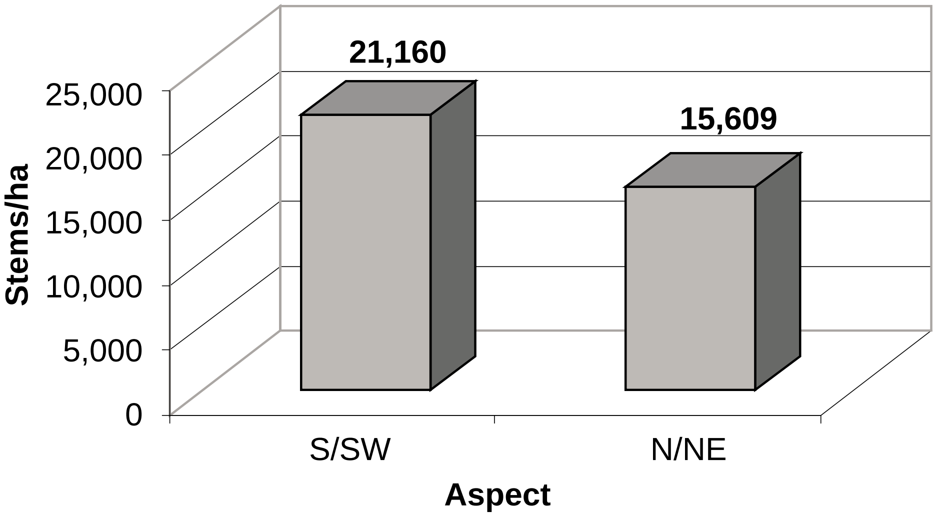

Figure 5—Aspen sucker density 8 to 10 growing seasons following prescribed burning. There was not a significant difference between aspects (*p* <0.05).

Summary and Conclusions

Aspen communities are generally seral to conifer climax communities in northwest Wyoming. Through successional processes, aspen communities along with their many ecological and social values are in decline. With drastically altered fire regimes and fuel conditions, managers must take aggressive management action toward restoring these important communities or potentially lose them for good. Success of fire-induced aspen regeneration appears to be quite variable across the landscape. While there are some apparent failures using fire to regenerate aspen, there are also many definite successes in northwest Wyoming. Many of the successful sites are within areas of high winter ungulate populations and even near supplemental elk feedgrounds.

Many factors such as clone vigor, community type, fire intensity/severity, herbivory by wild and domestic ungulates, aspect, elevation, soil type, moisture regimes, etc., will determine the successfulness of our efforts in maintaining aspen on the landscape. Managers' control over these factors ranges from complete control to no control. Selecting potential aspen treatment sites based on aspect appears to be one of many factors managers can control and should be considered in areas of high wintering ungulate populations. Monitoring results in the Bacon Creek tributary indicate northerly aspects have a better chance of escaping suppressive levels of herbivory. Sucker growth rates, heights, and densities indicate successful clone establishment 8–11 years post treatment. Clones on southerly aspects appear to still have vigor, are maintaining adequate densities, and are slowly gaining height. Southerly aspect will require continued monitoring before drawing conclusions on success/failure.

Detailed knowledge of wintering ungulate distribution and concentrations is also critical to successful aspen regeneration and is something managers can obtain. Although the Breakneck Ridge area and Bacon Creek are close to each other and adjacent to supplemental elk feedgrounds, herbivory levels differ considerably. Historic observations of winter elk use indicate much larger numbers using the Breakneck area for wintering, migration, and loafing. Combining the knowledge gained from Bartos et al. (1994) with what we now know about elk distribution, managers would emphasize the Breakneck Ridge site for potential aspen regeneration. More detailed information on numbers of animals, timing of use, and duration of use will be helpful in selecting potential treatment sites.

The time of initiation of supplemental elk feeding can be managed and may affect aspen herbivory levels. Herbivory appears to be reduced during years when abrupt accumulations of snow trigger earlier supplemental feeding in the Gros Ventre. The potential exists for early initiation of feeding to attract elk away from treatments until stems are more browse resistant.

Locating treatments a certain distance from elk feedgrounds may or may not help to protect suckers from browse pressure. Localized wintering elk and/or moose populations can easily suppress aspen regeneration. Determining seasonal use patterns for wild ungulates is critical. Fire-induced aspen regeneration within summer and transitional ranges appears to be very successful in northwest Wyoming.

Fire-induced aspen regeneration has also been successful in human-impacted areas. Areas receiving higher levels of human use usually preclude wintering wildlife use, thus reducing the probability of suppressing herbivory levels. While winter browse for ungulates is not realized, all other values associated with aspen communities will still be realized.

Other factors such as selection of aspen community type, stand vigor, soil type, and fire intensity/severity can be controlled by managers. We must combine our knowledge of such factors and apply it to future aspen treatments—to increase our odds of success and to increase the efficiency of our limited resources in light of ongoing plant community succession.

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Multiple Factors Affect Aspen Regeneration on the Uncompahgre Plateau, West-Central Colorado

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Abstract—*In 1996, I inventoried over 90 aspen stands in 12 timber sales that had been clearcut >3 years previously. Units that regenerated adequately were larger, had higher slope angles, and had soils with a thick Mollic surface layer. Units that regenerated inadequately often had plant species that indicated high water tables. The factors associated with inadequate regeneration were high water tables, heavy browsing, soils with a thin Mollic surface layer, and logging practices that compact large portions of the unit. One of these factors alone often does not lead to inadequate aspen sprouting. Most often, inadequately regenerated aspen stands have two or more negative factors, so the factors act as cumulative stressors on aspen. It is important for managers to know soils, landforms, history, and behavior of animal populations in the area.*

Introduction

Aspen (*Populus tremuloides* Michaux[2]) grows in clones that form relatively distinct 1–3 ha (2–7 acres) groves of trees, all with the same genotype (Gullion 1985; Shepperd 1993a). Within such a stand, aspen reproduces entirely from root suckers. There is effectively no reproduction from seed, so clonal characteristics are more important than individual stem characteristics. Each stem is considered a ramet of the genet, embodied by the entire clone (Shepperd 1993a). Clones (genotypes) may differ in branching, stem color, phenology, and decay characteristics (Wall 1971).

As many as 50 to 100 stems may be connected by a single root system of as much as 17 m (56 ft) radius (Tew and others 1969; Tew 1970; Schier 1973; Schier and Zasada 1973), and these connections may persist for at least 15 years following a stand-replacing disturbance (Shepperd 1993a). Many complex, interrelated factors influence aspen regeneration. It is often not possible to separate the influences on aspen regeneration or to assign events such as a poor sprout crop to one or a few factors (Hildebrand and Jacobi 1990; Jacobi and others 1998). This paper explores these factors and presents a study conducted on the Uncompahgre Plateau in western Colorado.

Sprouting

Aspen sprouting is stimulated primarily by release from hormonal suppression; clearcutting does this nicely (Patton and Avant 1970; Hungerford 1988). Another primary factor, recently documented, is the thickness of the Mollic surface layer in the soil (Cryer and Murray 1992). In short, a Mollic surface layer is an upper layer (or layers) that is dark and organic-rich. In soil inventory, a Mollic surface layer >18 cm (>7 in) thick is called a *Mollic Epipedon*; in some soils, a thicker layer may be required before this term can be used (Soil Survey

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[2] Plant species names after Weber and Wittmann (1996).

Staff 1998). In the following discussion, I have used the term "Mollic surface layer" generally to apply to a dark, organic-rich surface layer of any thickness.

Many of the small sprouts in the understory of an aspen canopy are suppressed, and some of these will remain suppressed even if part of the canopy is removed. However, other small sprouts will release and grow to reach the new canopy or form another, lower canopy.

Because the implications of clonal growth and vegetative reproduction of aspen were not well understood by past authors, readers must use caution when interpreting older literature. In particular, the small sprouts in the understory of a mature aspen stand were incorrectly termed "reproduction," though they will never reach the overstory. For examples of such errors, see Dayton and others (1937) and Houston (1958).

The number of aspen sprouts decreases exponentially from the time of the disturbance that stimulated sprouting (figure 1; Crouch 1983 and 1986; Johnston and Hendzel 1985; Shepperd 1993a). Injuries to aspen sprouts can be caused by animals browsing the terminal leader, by the weight of snowpack, by trampling, by diseases, or by pocket gophers (Marston and Julander 1961; Smith and others 1972).

Hildebrand and Jacobi (1990) studied aspen regeneration failure after treatment in several sites in the Central and Southern Rocky Mountains. They documented failure of aspen regeneration associated with herbivore browsing pressure, greater than normal site moisture, and smaller cutting unit sizes. They also mentioned weather conditions—especially heavy snowpack and drought—as factors negatively influencing reproduction. They used several plant species as indicators of high water tables, notably cornhusk lily (*Veratrum tenuipetalum* Heller).

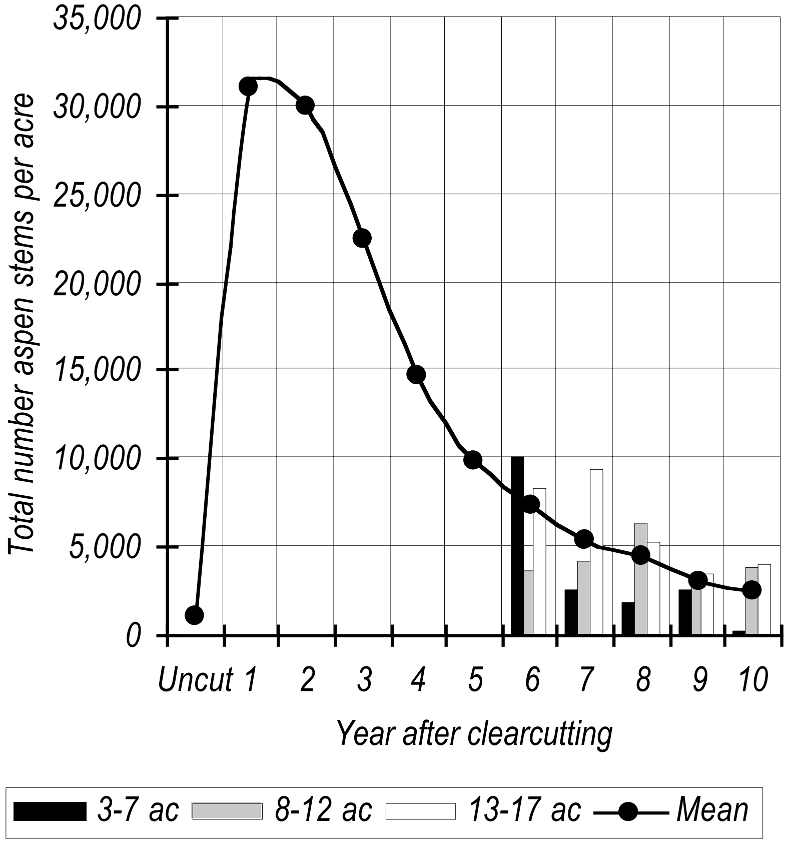

Figure 1—Number of aspen sprouts each year for 10 years following clearcutting in patches of several sizes (data from Crouch 1983 and 1986).

Jacobi and others (1998) focused on aspen regeneration failure on seven sites in western Colorado. They used two scenarios to describe aspen regeneration failure at their sites:

1. On moist sites, aspen root mortality occurs from excess soil moisture after deep, late spring snow packs, followed by summer drought, "predisposing aspen trees to infection by canker pathogens."
2. On dryer sites, drought conditions in spring and the following summer "predisposed aspen to infection by canker pathogens." At two sites, portions of the sites with poor regeneration had poor soil drainage at lower depths; there, shallow aspen rooting contributed to the drought stress.

In Minnesota, unexpectedly few root suckers sometimes develop following summer clearcutting (Bates and others 1998). Part of the absence may be assigned to clearcutting in the summer, when root carbohydrate reserves are low. In their growth chamber study, the authors documented a different contributing factor: reduced soil aeration following logging on poorly drained soils.

Big Game Use

The aspen stands in the study area are commonly used by elk and deer as summer range, providing forage, browse, and cover (Hess and Alexander 1986). Only two of the units inventoried were close to deer and elk winter range; most of the units were summer range.

After a stand is cut or burned, browsing by elk and other big game can eliminate a sprout crop completely, reduce the survival of sprouts to the depth of snow accumulation, or damage all sprouts so that all trees in a clone will have poor form for a long time (Krebill 1972; Komárková and others 1988; Romme and others 1995; White and others 1998; Suzuki and others 1999). Differences in protein content may cause the aspen trees in some clones to be browsed by elk more than others (McNamara 1973).

Elk use aspen stands preferentially and heavily after prescribed fire creates a sprout crop (Basile 1979; Canon and others 1987), but actually elk prefer serviceberry (*Amelanchier alnifolia*) over the aspen (Canon and others 1987). As Sampson (1919) suggested for cattle, when aspen sprouts in openings are destroyed so that a commercial stand cannot form, such destruction is an indicator of too many elk. Elk also eat blue wildrye (*Elymus glaucus*), asters, geranium, and meadow-rue (*Thalictrum fendleri*), common plants in aspen stands (Canon and others 1987).

Mule deer also browse aspen sprouts, but the effects are not as severe, because deer do not concentrate in such large numbers and apparently do not prefer aspen sprouts as much as elk do. However, deer can have significant effects in small areas (Smith and others 1972). Sprout crops disappear quickly if more than one species is browsing, such as cattle and deer together (Smith and others 1972), or if soils are light-colored, or if water tables are high in addition to browsing (Jacobi and others 1998).

Elk often gnaw the bark of mature aspen trees, which is sometimes unsightly but rarely fatal. Mortality or poor form in aspen caused by big-game browsing is usually a combination of browsing with other factors such as pathogenic fungi or injurious insects (Krebill 1972). The severity of browsing effects depends on how many animals use the area and for how long.

Livestock Use

Forage production ranges from moderate to high when stands are undepleted by continual herbivore use. Continued grazing reduces productivity markedly. Live understory vegetation production on aspen range in undepleted condition can range from 2,500 to 3,500 lb/ac/yr; in poor condition, 900 to 1,200 lb/ac/yr; and in depleted condition, 150 to 400 lb/ac/yr (Turner[3], Hess and Alexander 1986).

Cattle will use aspen stands near openings, either natural or human-made, much more than interior aspen stands. Aspen stands <0.3 km (<0.2 mi) from an opening may get used, depending on the quantity of forage left in the opening. Sheep, which can be herded to interior stands, can make more use of them than cattle.

Most of the species in aspen stands that are palatable to livestock are forbs. A few are shrubs, but there are relatively few palatable graminoids. Houston (1954) devised a range condition rating based on six criteria: four groups of plant species, soil cover (vegetation plus litter), and evident indicators of erosion. Another criterion he uses, "presence of aspen reproduction," is inappropriate given what we now know about clonal aspen reproduction processes.

Aspen sprouts are palatable to livestock, which can result in loss of some sprouts in regenerating clearcuts (Larson 1959). Sampson (1919) suggests that on aspen clearcuts in cattle range, if the aspen sprouts have been destroyed so that a commercial stand will not be formed, then the "range has been stocked beyond its normal carrying capacity." I suppose the same would apply to use by elk. In parts of Alberta, where aspen invades rangeland and reduces grazing capacity, "a single late grazing [by cattle] eliminated aspen regeneration" (Fitzgerald and Bailey 1984; also see Jones 1983 and Fitzgerald and others 1986).

Timber management and range management should be coordinated to ensure that aspen regeneration crops are not lost. Livestock damage is mostly (90%) due to browsing but also occurs because of trampling and rubbing (Sampson 1919). Size of treatment blocks (pastures, clearcuts, burned patches) is critical, with the very small blocks usually not surviving because of concentration of animal use (Mueggler and Bartos 1977).

Materials and Methods

In June, 1996, I was asked by the Grand Mesa, Uncompahgre, and Gunnison National Forests to conduct a regeneration survey of aspen stands in selected timber sales on the Uncompahgre Plateau in west-central Colorado (figure 2). The timber sales and stands had been selected because they were not meeting standards for aspen regeneration; the purpose of my work, then, was to determine why these stands were not meeting the standards. As part of my investigation, I noticed many aspen stands (other than the ones reported below) that were obviously meeting the standards. Since this study over-sampled stands that did not meet standards, the results reported below do not represent the true proportion of units and acres not meeting the standards. This study was designed to show those factors that lead to inadequate aspen sprouting.

Most of the aspen stands had not been surveyed for aspen regeneration before. Most of these stands had been cut for harvest 3–6 years previously, although some were as old as 13 years. Mostly they had been clearcut, especially the more recent cuts. The stands I was asked to survey were in 12 timber sales, all but three of which were on the Uncompahgre Plateau, a large northwest-to-southeast plateau in west-central Colorado, on the Ouray and Grand Junction Districts of the Uncompahgre National Forest. The other three sales were on the south slopes of the Grand Mesa, on the Paonia District of the Gunnison National Forest.

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[3] Turner, George T. 1951. Evaluation of range watershed conditions of aspen and mountain grassland types in western Colorado. Unpublished Office Report, Typescript, 19 p.

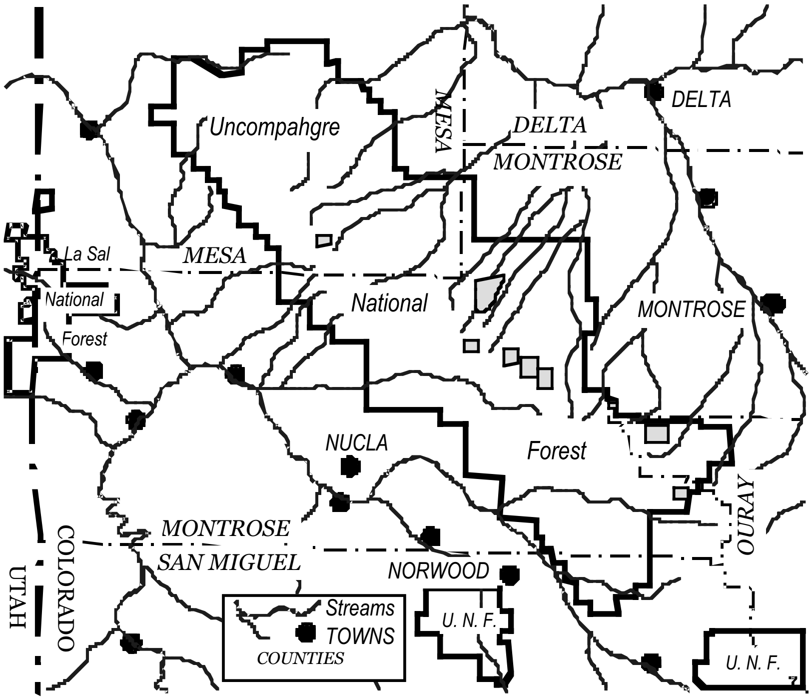

Figure 2—The Uncompahgre Plateau, the Uncompahgre National Forest, and the location of the timber sales studied. Study areas are in gray.

Before inventorying each clearcut, called a *unit* in timber sale terminology, I estimated the acreage of the unit. In each unit, I located three or more points methodically, usually by means of one or more parallel lines of equidistant points. The number of points in a unit was determined by the acreage of the unit: the minimum of three points was used for units of 0–4 acres, and one point was added for each additional 5 acres. The points were spaced at a regular interval from one another in multiples of 80 ft. Centered at each point was a 0.002-acre (0.0008 ha) circular plot. Within the plot, I tallied all tree stems (live or dead) by diameter and condition class.

For each group of trees within a plot with like characteristics, I recorded tree status (growing stock, cull, or dead); species; diameter at breast height (d.b.h., inches); total height (feet); tally; apparent age (years); and apparent damage-causing (or death-causing) agent. I used a form from the most recent appropriate handbook (USDA Forest Service 1993b).

For each unit (cut block) I recorded size (acres), shape, and location by means of a sketch map on which I located the sample points. I located each unit on an appropriate quadrangle map and on the maps for the recent soil survey (Hughes and others 1995). I observed and recorded signs of animal use, such as droppings, tracks, elk wallows, or cattle watering places. Often the animals themselves were observed, and I was able to also observe them eating aspen sprouts.

Calculations and Analysis

I determined whether each sample point was considered to be *stocked* according to the Forest Plan (USDA Forest Service 1993a). The Forest Plan standard that needed to be met was 1,200 stems per acre of growing stock (GS) stems, which are live, noncull stems (figure 3). In order to meet this standard, the plot at each point needed to have three or more live, non-cull stems. A *cull* stem is live but estimated to be incapable of forming an 8-foot log at maturity. Usually, they are more than two-thirds defective (from disease or damage), they

Figure 3—An example of abundantly adequate aspen regeneration in a medium-sized unit at a reasonable slope angle on good soils, with moderate livestock pressure. Harvested by clearcutting in 1988, 8 years before the photo was taken. Unit is 10 acres, on a 17% slope at 9,520 ft. Soil Map Unit 22, good for aspen regeneration. 6,700 growing stock stems/ac, growing 0.73 ft/yr, 100% of points stocked. Picture looking 350° magnetic (NNW), July 24, 1996.

have a dead top, or they are too deformed to compete in the canopy (USDA Forest Service 1993b).

I calculated number of growing stock stems per acre using:

$$G_a = \frac{G \times 500}{P}, \qquad [1]$$

where G_a is growing stock stems per acre, G is the sum of growing stock stems counted, and P is the number of points in the unit.

Additionally, the forest plan requires that 75% or more of the sample points be stocked. There were some units where the whole unit had >1,200 growing stock stems/ac, yet <75% of their points were stocked; in many of these sites, the distribution of aspen was naturally patchy, coinciding with microsite variations in soils, landform, and water. One can easily visualize those sites being fully regenerated in a few years. For these reasons, I feel that it is better to estimate aspen regeneration success against the >1,200 growing stock stems/ac standard than to use the >75% points stocked requirement. In the following discussion, units are rated as having *adequate sprouting* if there are >1,200 growing stock aspen stems/ac. In my estimation, stands will be fully functional aspen stands for wildlife, watershed, and other values if they are adequate by this definition.

For calculation of the average height of aspen sprouts in a unit, I used the height of the tallest layer of growing stock stems in the plots, averaged across all the plots in the unit. Sometimes I used two layers for a plot if there were few stems in the tallest layer. I used the height of the tallest cull layer if there were no growing stock stems in that plot. I then calculated the average (mean) height of the tallest layers, weighted by the number of stems (tally) for each of those layers.

I used time since the clearcut that stimulated the sprouting as an estimate of age of an unit.

To calculate average slope azimuth for a group of units, I used a circular transformation as described in Zar (1984). First, the aspect *x*- and *y*-coordinates for each unit can be calculated:

$$x_i = (\sin[\alpha \times \frac{180}{\pi}] + 1) \times 100,\ x = \frac{1}{n}\sum_{i=1}^{n} x_i \qquad [2]$$

$$y_i = (\cos[\alpha \times \frac{180}{\pi}] + 1) \times 100,\ y = \frac{1}{n}\sum_{i=1}^{n} y_i \qquad [3]$$

where α_i= azimuth angle associated with measurement *i*. Then the average radius (r) and average azimuth angle (β) are calculated:

$$r = \frac{\sqrt{\left(\sum x_i\right)^2 + \left(\sum y_i\right)^2}}{100}, \qquad [4]$$

and

$$\beta = \cos^{-1}\frac{y}{r} \qquad [5]$$

The average radius (r) ranges $0 \leq r \leq 1$; $r = 1$ indicates a very tight clustering of azimuths about the average, and $r = 0$ indicates a very loose clustering.

I included data in the data set from a few units that had been surveyed by Les Choy in 1995 from the same sales. For those units, I visually checked the units to make sure the data were still valid in 1996. For data bases, I used Paradox®, Versions 8 and 9 (Corel 2000). To statistically analyze data, I used Statistix®, Version 2 (Analytical Software 1999).

Results and Discussion

For the 113 units in this study, the average unit sampled had 7,010 live stems per acre, of which 3,963 per acre were growing stock stems (table 1). In the units where sprouting was adequate, average height growth was 1.12 ft/yr; in units where sprouting was inadequate, average height growth was only 0.37 ft/yr, less than one-third (table 2).

Units where sprouting was adequate, but in addition >75% of the points were stocked, were larger, had taller sprouts, were on steeper slopes, and had a deeper Mollic surface layer. Interestingly, if a unit had inadequate sprouting, it invariably also had <75% points stocked, but not vice versa.

Slope Angle

In units with adequate sprouting, average slope was 12.5%; but in units with inadequate sprouting, average slope was only 6.4%, about half (table 2). Slope angle was positively correlated with number of aspen sprouts per acre, their height growth per year, and proportion of points stocked (table 3, figure 4), which indicates that slope angle is indeed an important predictor of aspen sprouting in this area, as indicated by Hildebrand and Jacobi (1990). Slope angle was negatively correlated with aspect y-coordinate; this means that northerly slopes are steeper on the Uncompahgre Plateau.

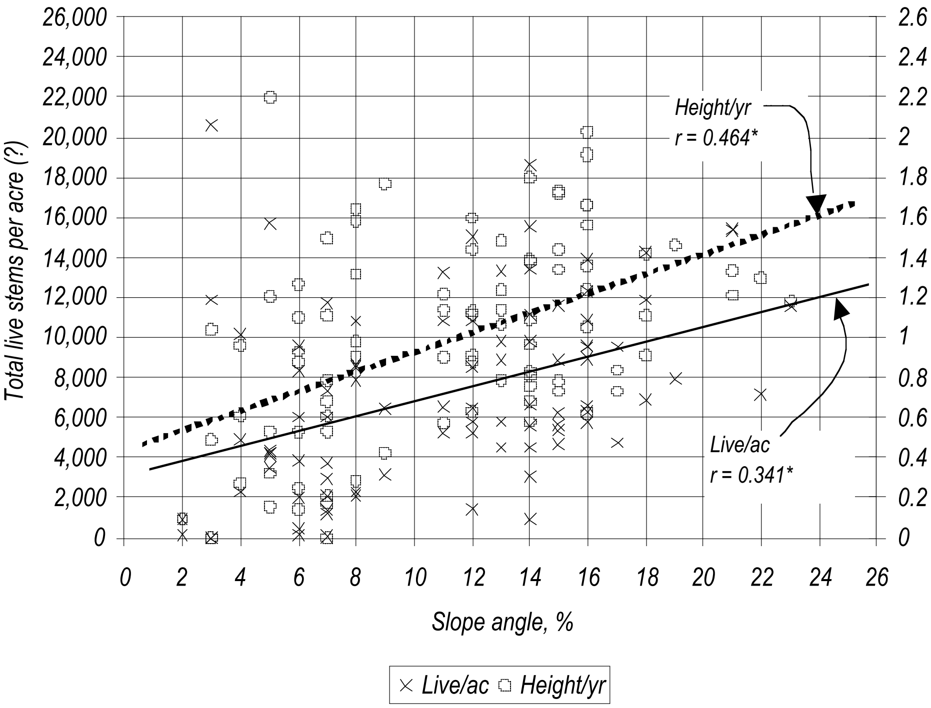

Figure 4—Height growth per year in aspen sprouts and number of live aspen stems per acre, as functions of slope angle. *Significant correlation, *a* <1%.

In all but two of the units with inadequate sprouting, slope angle was <10% (tables 4 and 5). One of these two remains a mystery, and the other was on a wet slope, with evidence of deep snow in winter. Low slope angle indicates that soil water may accumulate seasonally in these sites, in part because many of these sites have plant species indicating seasonally high water tables (table 6). Units with adequate sprouting but where slope was <9% were mostly marginal either in number of growing stock stems or number of points stocked (table 7).

Apparently, high water tables are most detrimental in the first few years following a clearcut, especially in combination with other negative factors such as heavy pressure by browsing animals. I suspect that just one high-water year is sufficient to accomplish complete mortality of an aspen sprout crop, although I saw complete mortality very seldom in this study. Because of natural self-thinning of the aspen sprouts, there is always some aspen sprout mortality, even in the absence of any negative factors. Mortality of all or most of the sprout crop apparently can occur 5 or more years after clearcut, in situations where the stress combination includes both high water table and aspen disease, and both are above some threshold of intensity. The threshold of intensity is probably higher in cases where the sprouts are more than 5 years old than it is in the first few years following the cut.

Browsing and Grazing

Most of the units with inadequate sprouting showed signs of being grazed or browsed heavily or very heavily: nine units by elk and four units by cattle (table 5). If I add units that were grazed moderately heavily by animals, there were 12 units with inadequate sprouting that had been grazed at least moderately heavily by elk, and six units by cattle. There were only two units with inadequate sprouting that were not grazed or browsed at least moderately heavily. This indicates that browsing pressure from animals is an important factor in predicting sprout mortality, but somewhat less important than seasonally high water tables. Both elk and cattle are involved here, but elk were about twice as important as cattle in this area.

Size of Units

Units with adequate sprouting averaged 24.3 acres; but units with inadequate sprouting averaged only 11.8 acres (table 2). Unit acreage is positively correlated with both growing stock stems/ac and percent of points stocked, which indicates that small units more often have inadequate sprouting (table 3).

The effects of heavy browsing or grazing on aspen sprouts are made more severe by units that are small. Small units are much more likely to be objects of concentrated use, especially by cattle, but by elk and deer as well. If the units are surrounded by closed-canopy forest, cattle use may be facilitated by a path through the forest in the form of an old haul road or skid trail. If there are many small units in a local area, the effects of heavy grazing or browsing are lessened, apparently because more forage and browse is available.

Small units are also more likely to have inadequate sprouting, because necessary logging facilities such as roads and landings take up a larger proportion of those units.

Soils

In units with adequate sprouting, average Mollic thickness was 32.3 cm (12.7 in); but in units with inadequate sprouting, average Mollic thickness was only 17.8 cm (7.0 in) (table 2). Mollic thickness is positively correlated with height growth of sprouts and number of points stocked (table 3, figure 5), which indicates that average Mollic thickness is an important predictor of adequacy of aspen sprouting. Average Mollic thickness is also positively correlated with aspect x-coordinate ("easterly-ness"), meaning that soils with a thicker Mollic layer are more often east-facing; this is expected, since winds are predominantly from the west, depositing deeper soil on easterly aspects. The positive correlation between average Mollic thickness and sprout age is probably due to more recent timber sales being located on soils expected to have better aspen sprouting, by conscious design of the timber managers.

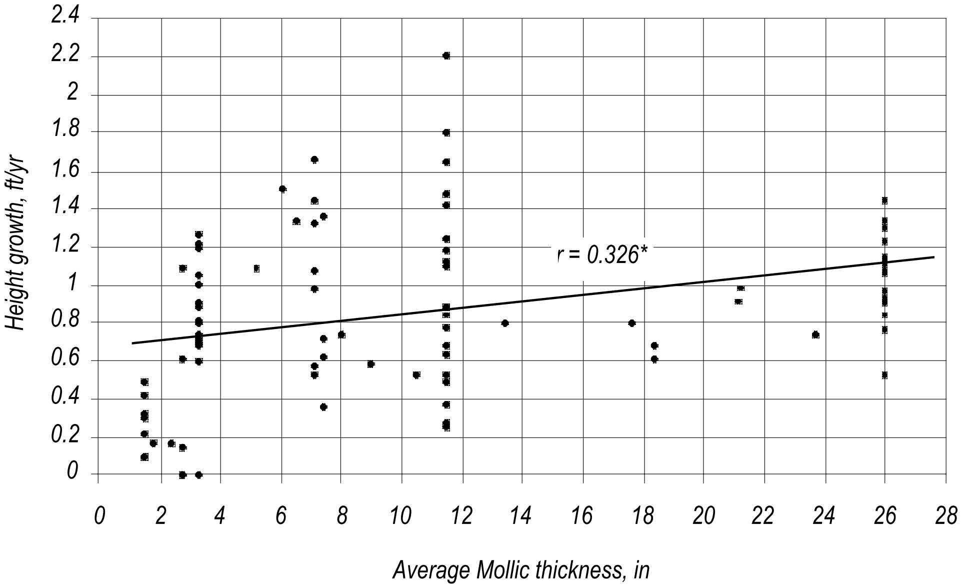

Figure 5—Height growth per year in aspen sprouts as a function of the thickness of the Mollic layer. *Significant correlation, *a* <1%.

Since soils were only superficially sampled for this study, I used the recent soil survey to evaluate soil map units for expected aspen sprouting (table 8; Hughes and others 1995). I used Mollic thickness, soil depth, soil temperature, and soil moisture as reported by Hughes and others (1995) to determine expected aspen regeneration quality for each soil map component (table 9), as implied in Cryer and Murray (1992). Based on table 9, I assigned each soil map unit a rating of "good" or "poor."

In the units with inadequate sprouting, soils were rated as poor for aspen regeneration (table 5). Also, about half of the units that came close to having inadequate sprouting had poor soils for aspen regeneration (table 7). These results confirm that soil is an important factor in determining potential for aspen sprouting.

The results by soil map unit were not as sharp as for unit size, slope, and stem size (table 9). *All* soil map units had adequate sprouting. The only soil map units that have >75% points stocked are 21 (Hapgood-Lamphier) and 22 (Hoosan-Lamphier-Leaps), although soil map units 25 (Lamphier-Hapgood) and 29 (Supervisor-Cebone) come close. These results indicate that soil map unit alone is insufficient for determining sprouting potential, yet soil map unit is still a useful criterion in combination with others.

Inadequate sprouting seems to be most certain with some combination of *more than one* of these negative factors, listed in priority order:

1. Seasonally high water tables, indicated by ≤ 9% slope, wet-site plants, and/or great snow accumulation.
2. Moderately heavy to heavy browsing by cattle or elk, sometimes made worse by small units <4 ha (<10 acres).
3. Soils with Mollic surface layer(s) <18 cm (<7 in) thick.
4. Logging practices that compact larger than normal portions of the unit, such as a large number of lateral haul roads or large, concentrated slash piles or landings. This may be complicated by small units in some places.

That more than one of these negative factors is necessary for inadequate sprouting is consistent with the hypothesis of Jacobi and others (1998) that these factors combine with one another to increase the amount of stress put on the aspen individuals. That is, these negative factors are in fact *stressors* that act additively (figure 6).

The hypothesis that increased stress is put on aspen by more than one negative factor is supported by the data in this study. The units where sprouting is inadequate or nearly inadequate are those where more than one negative factor is stressing the aspen. For sprouting to be inadequate, there could be as few as two negative factors, if those factors are especially intense (figure 7). There needs to be more than two negative factors if they are only moderately intense.

Is the stress of multiple factors brought to bear principally on the individual aspen stem, on the clone, or on some other unit? These data seem to show that stresses act both on the individual stem and on the clone. For example, browsing by animals leads to stress on the individual stems clipped by the animals, which leads to stress on the clone. This is indicated by the finding that live stems are one-third as tall in inadequate units as compared with adequate units. The height difference is likely due to animals browsing, since lightly browsed units have about the same height growth in all soil map units.

Areas where elk or cattle grazing or browsing pressure can be predicted are also at risk, but browsing is not as certain to lead to inadequate sprouting as seasonally high water tables are. Grazing and browsing pressure can usually be

Figure 6—Inadequate sprouting because of high water tables some years after cutting, as one stress factor in combination with the aspen disease Shepherd's Crook. Shepherd's Crook was found in several stands, but rarely was it responsible for significant mortality. Harvested by clearcutting in 1987, 9 years before the photo was taken. There are 2,940 live stems/ac, but only 375 GS stems/ac—most stems are dead or mostly dead culls. Jacobi and others (1998) studied this unit. Unit is 22 acres, on a 7% slope at 9,510 ft elevation. Soil Map Unit 15, considered good for aspen regeneration. Picture looking 291° magnetic (WNW), August 5, 1996.

Figure 7—Inadequate aspen regeneration because of low slope angle, heavy elk browsing, small unit size, and poor soils. Harvested by partial cutting in 1985, 11 years before the photo. Natural openings close by these units had no tree reproduction; in one of these openings, someone had dug a pond for watering animals, which had water in it in late season. It is likely that after 1985, the water table rose during one or more years. 125 GS stems/ac, growing 0.09 ft/yr, 0% of points stocked. Unit is 6 acres, on a 2% slope at 9,160 ft elevation. Soil Map Unit 27, considered poor for aspen regeneration. Picture looking 311° magnetic (NW), July 18, 1996.

predicted by asking the questions: "If a set of aspen clearcuts of a certain size and configuration are placed in a certain place, can we expect heavy use by elk (or deer)? Can we expect heavy use by cattle? Is this combined with other stress factors in the units to be cut?"

Overuse by elk is notable in several of the units in this study. An old timber haul road to several units in this study is now closed to motor vehicles to protect habitat. The elk population in this area has increased dramatically in recent years, and the aspen sprouting is suffering as a result. It is possible that the elk increase is due in part to fewer cattle here because of progressive changes in the management of the grazing allotment. But, the result in this area is that elk are being given preference and allowed to increase in numbers at the expense of aspen sprouting. Some kind of middle ground is desirable, where balance is achieved between elk herds and aspen regeneration, including consideration for other resources.

Browsing by cattle is an important factor in several units as well. For example, consider a unit that is divided into four parts by the pasture fence and the soil line that cross the unit (figure 8, figure 9, table 10). Elk use in this area is apparently at most moderate, even in intensity across all four parts.

In another unit of this study, an animal-proof exclosure was constructed in recent years in about a third of the unit. The fence is intact, and is apparently successful in keeping all herbivores out. In spite of poor soils for aspen regeneration in this unit, the sprouting was abundantly adequate *inside* the exclosure—though the sprouts are distributed in patches (figure 10). Outside the exclosure is an apparent disaster, with very heavy cattle pressure in the past, tapering off in recent years with improved grazing management, to which has been added intense pressure by elk, on soils unlikely to produce sprouting.

Soils that result in successful aspen regeneration can be predicted. Users should begin with a recent soil survey—in this case, Hughes and others 1995—and supplement this with field data as needed. A soil that usually results in poor aspen regeneration is an important negative factor leading to inadequate sprouting, but there are plenty of examples of units in this study that succeeded in spite of unlikely soils. It seems that unlikely soils are most important in combination with one of the other negative factors in high intensity. If a manager wishes to regenerate aspen on an unlikely soil for sprouting, other negative factors should be kept to a minimum such as low slope angles and grazing and browsing pressure. I recommend close coordination of timber management with wildlife and livestock management. Some modification of the previously preferred design may be required, such as changes of location, size, timing, and methods.

Local forest managers have incorporated many of these results into the site location and design of aspen timber sales. It has now become common practice to incorporate detailed soil, watershed, wildlife, and range management information into the location of proposed timber sales, as well as location and design of individual units.

Management of aspen is a multi-dimensional task; success often requires cooperation among many scientific disciplines and groups of partners. There are no substitutes for broad partnerships with common goals, consultation with interdisciplinary teams of scientists, and careful planning.

Figure 8—Fenceline contrast showing adequate aspen regeneration on the right side and very little on the left side. Unit was clearcut in 1987, 9 years before the photo was taken. The fence is a pasture division fence, with heavy grazing pressure (by cattle) on the left and light grazing pressure on the right. Pressure by elk is moderate on both sides, since the fence is a poor deterrent to them. The light line shows the boundary between Soil Map Unit 20, considered poor for aspen sprouting (left) and Soil Map Unit 21, considered very good for aspen sprouting (right). Aspen sprouting is barely adequate in the area left of the fence and right of the line. Circled numbers as in figure 9. Yellow-headed flower in abundance on the left side is orange sneezeweed (*Dugaldia hoopesii*), a noted increaser with livestock use. Picture looking east, July 29, 1996.

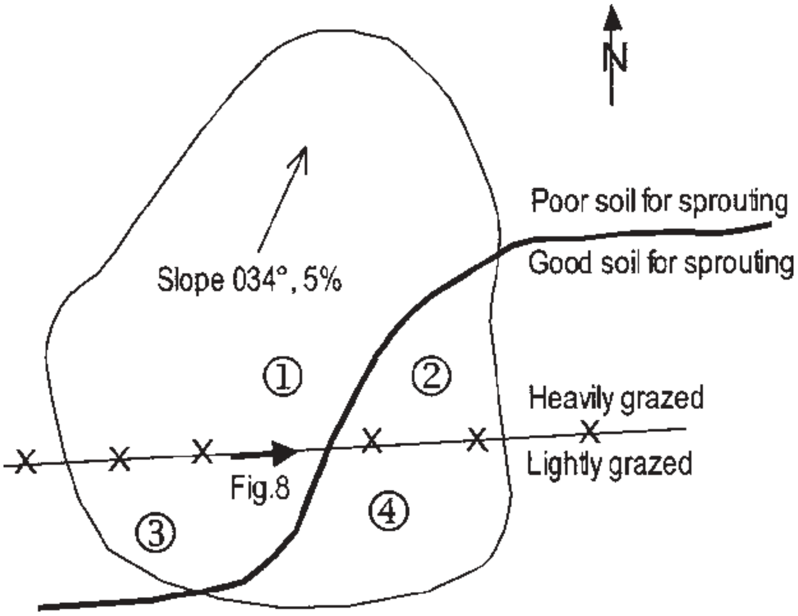

Figure 9—Diagram of Long Creek Sale, Unit No. 3. Photograph in figure 7, numbered zones in table 10.

Figure 10—Fenceline in a unit of poor soils, contrasting between heavily grazed and browsed by elk and cattle (right), and protected from grazing and browsing (left). The area to the left of the fence (the exclosure) has been protected from all animal use by this 9-foot fence for the past few years. This unit was clearcut in 1993, 3 years before photo was taken; methods of harvest were designed to meet research objectives, so those methods were not the same as usual. The fence was built as a research demonstration. On the left, protected side, the aspen regeneration is noticeably patchy, but still regenerating successfully, with 11,300 GS stems/ac. On the right, unprotected side, the aspen regeneration is clearly inadequate, with only 670 GS stems/ac. Overall, the unit (including both inside and outside the exclosure) has 4,220 GS stems/ac, but only 56% of the points are stocked. The unit was mapped in Soil Map Unit 29, but by the photo and my observation these soils are light-colored on the surface and probably have poor potential for aspen sprouting. Unit is 30 acres, on a 14% slope at 8,960 ft elevation. Picture looking south-southwest from the northwest corner of the exclosure, August 29, 1996.

Table 1—Summary of aspen regeneration in 113 timber sale units.

	Average age, yr	Percent of points stocked	Growing stock	Live stems
			stems/ac	*per acre*
Averages ± SE	5.82 ± 0.25	64.81 ± 3.10	3,963 ± 300	7,010 ± 418

Table 2—Factors influencing aspen regeneration. Numbers are shown as mean ± Standard Error (*N*), where *N* is number of units (GS = growing stock).

Factor	>1,200 GS/ac and >75% points stocked	>1,200 GS /ac	<1,200 GS /ac and <75% points stocked	All units
Unit size, ac	25.2 ± 1.9 (61)	24.3 ± 1.6 (84)	11.8 ± 1.3 (29)	21.1 ± 1.4 (113)
Slope, %	12.9 ± 0.6 (55)	12.5 ± 0.6 (70)	6.4 ± 0.7 (20)	11.1 ± 0.6 (90)
Mollic thickness, in	13.9 ± 1.4 (42)	12.7 ± 1.1 (64)	7.0 ± 1.3 (29)	10.9 ± 0.8 (93)
Aspect x-coordinate	60.7 ± 4.5 (55)	59.9 ± 4.1 (70)	50.5 ± 7.4 (20)	57.8 ± 3.6 (90)
Aspect y-coordinate	57.8 ± 4.7 (55)	59.5 ± 4.1 (70)	80.2 ± 5.3 (20)	64.1 ± 3.5 (90)
Age, yr	5.5 ± 0.3 (61)	5.6 ± 0.3 (84)	6.3 ± 1.3 (29)	5.8 ± 1.4 (113)
Height growth, ft/yr	1.20 ± 0.05 (61)	1.13 ± 0.04 (84)	0.42 ± 0.05 (28)	0.95 ± 0.05 (113)

Table 3—Selected correlation coefficients: units for which aspect, slope, and soil are known. *N* = 70.

	Age	Aspect x-coordinate	Aspect y-coordinate	Growing stock	Height growth	Total live	Mollic thickness	Number of points stocked
				stems/ac	*ft/yr*	*stems/ac*	*inch*	
Aspect x-coordinate	–0.006							
Aspect y-coordinate	**0.235**	–0.116						
Growing stock, stems/ac	–0.054	0.089	0.008					
Height growth, ft/yr	–0.223	–0.018	–0.179	**0.516***				
Total live stems/ac	**–0.315***	–0.007	0.012	**0.670***	**0.412***			
Thickness Mollic layer, in	**0.374***	**0.284**	–0.200	0.159	**0.326***	0.020		
Number of points stocked	–0.070	0.024	–0.104	**0.806***	**0.630***	**0.703***	**0.279**	
Slope, %	0.020	–0.052	**–0.321***	**0.340***	**0.464***	**0.341***	**0.374***	**0.435***

Bold–Significant at 5%. **Bold***–Significant at 1%.

Table 4—Selected correlation coefficients: units surveyed in 1996. *N* = 90.

	Growing stock	Age	Percent of points stocked	Unit	Acres with inadequate sprouting
	stems/ac	*yr*		*acres*	
Age, yr	–0.290				
Percent of points stocked	**0.783***	**–0.236**			
Unit acres	**0.298***	0.025	**0.362***		
Acres with inadequate sprouting	**–0.515***	0.172	**–0.695***	–0.180	
Acres with adequate sprouting	**0.443***	–0.039	**0.562***	**0.938***	**–0.511***

Bold–Significant at 5%. **Bold***–Significant at 1%.

Table 5—Factors in units that had <1,200 growing stock stems/ac and <75% points stocked.

Unit	Slope angle(s)	Unit acres	Plant species from table 6 conspicuous	Cattle grazing/ browsing	Elk or deer grazing/ browsing	Soils for aspen regen.[a]	Comments
1, 2, 3	2%, 2%, 5%	6, 8, 5	PEFL15, ABBI2–dead saplings	Moderate	Very heavy (elk)	Poor	Natural openings with ponds in area; major elk range; poor soils
4, 5	3%, 8%	6, 9	BRAR	Heavy	Light	Poor	Much human activity, open road through units; poor soils
6, 7, 8, 9, 10	7%, 5%, 8%, 9%, 7%	8, 10, 16, 8, 12	ABBI2-dead saplings, AGROS2	Moderately heavy	Moderately heavy (elk)	Poor	Elk activity heavy in some units; poor soils
11	4%	21	LIPU6, HESP6, SESE2	Light	Heavy (elk)	Poor	Poor soils
12	3%	10	LIPU6, HESP6, SESE2	Heavy	Moderately heavy (elk)	Poor	See comments for Unit 15; poor soils
13	12%	13	HESP6	Light	Moderate (elk)?	Good	The only mystery yet remaining
14	7%	22	VETE4	Light	Moderate (elk)?	Good	Documented site: death of sprout crop from combined high water and shepherd's crook (Jacobi and others 1998)
15	7%	32	None from table 6	Heavy	Moderately heavy (elk)	Poor	This and unit 12 are the only openings in heavily grazed cattle range; poor soils
16	14%	7	VETE4, SESE2, CAUT, SALU2	Moderately heavy	Heavy (elk)	Good	Slump blocks, scarps, ponds common in and around unit; snow depths considerable, snow damage common
17	7%	4	None from table 6	Moderate	Heavy (elk)	Good	Much mortality and cull damage from shepherd's crook
18	6%	27	None from table 6	Moderate	Very Heavy (elk)	Good	Major elk range
19	4%	10	None from table 6	Light	Heavy (elk)	Poor	Major elk range; poor soils
20	6%	10	None from table 6	Moderate	Heavy (elk)	Mostly poor	Major elk range; heavy, mostly (2/3) poor soils

[a] Rating according to the criteria in table 9.

Table 6—Plant species indicating seasonally high water tables.

Code[a]	Growth form	Species name[b]	Common name
ABBI2	Sapling	*Abies bifolia* (*A. lasiocarpa*)	Subalpine fir, saplings dead from high water (poor form, twisted, many lower branches)
AGROS2	Grass	*Agrostis* species	Bentgrasses
CACA4	Grass	*Calamagrosis canadensis*	Bluejoint reedgrass
CAUT	Grasslike	*Carex utriculata*	Beaked sedge
BRAR	Forb	*Breea arvense*	Canada thistle
DECE	Grass	*Deschampsia cespitosa*	Tufted hairgrass
HESP6	Forb	*Heracleum sphondylium*	Cow-parsnip
LIPU6	Forb	*Ligularia pudica*	Groundsel
PEFL15	Shrub	*Pentaphylloides floribunda*	Shrubby cinquefoil (called potentilla in trade)
SALU2	Shrub	*Salix lutea*	Yellow willow (and other shrub willows)
SESE2	Forb	*Senecio serra*	Butterweed groundsel
VETE4	Forb	*Veratrum tenuipetalum*	False-hellebore, cornhusk lily (sometimes called skunk cabbage in error)

[a] After USDA Natural Resources Conservation Service (1997).
[b] After Weber and Wittmann (1996).

Table 7—Factors in units that had >1,200 growing stock stems/ac but were <9% slope angle.

Unit	Slope angle(s)	Unit acres	Plant species from table 6 conspicuous	Cattle grazing/ browsing	Elk or deer grazing/ browsing	Soils for aspen regen.[a]	Comments
A, B	7%, 5%	18, 12	BRAR, DECE, CACA4	Moderately heavy	Light	Poor	Poor soils mostly; both units close to inadequate
C	4%	11	None from table 6	Moderate	Moderate (elk)	Good	Some conifers left; compaction by timber haul roads—no aspen sprouting there
D	5%	7	POTR5—this year's sprouts	Moderately heavy	Moderately heavy (elk)	Poor	Poor soils; unit close to inadequate
E	5%	10	None from table 6	Very heavy (2/3 of unit)	Moderate (elk)	Good	Pasture division fence separates heavily grazed cattle pasture (lower 2/3 of unit) from lighter-grazed pasture; line between good/poor soils also divides unit; most of unit (lower 2/3) inadequate, especially number of points stocked
F, G	8%, 7%	90, 45	VETE4, BRAR, ABBI2—dead saplings	Heavy only around edges, light in middle	Light	Good	Large units; compaction from timber haul roads and slash piles, especially in unit G; unit F is great success, unit G obviously success outside roads and slash piles
H, I	7%, 6%	60, 60	None from table 6	Moderately heavy	Heavy (elk)	Good	Logging design included too many lateral haul roads, increasing area compacted and reducing aspen sprouts; both units close to inadequate on number of points stocked
J	7%	33	None from table 6	Light	Heavy (elk)	Poor	Elk use is on tops of tall sprouts; elk were standing on snow; Poor soils
K, L	6%, 6%	16, 9	None from table 6	Heavy	Heavy (deer and elk)	Good	Low-elevation sites, near deer-elk winter range; unit L inadequate in number of points stocked
M	8%	36	None from table 6	Heavy only at edges	Heavy (deer and elk)	Good	Low-elevation sites, near deer-elk winter range
N	6%	5	None from table 6	Light	Heavy (elk)	Poor	Small unit, 5 ac; many conifers left; shepherd's crook in sprouts; poor soils
O, P	5%, 3%	8, 12	PEFL15, DECE, VETE4	Light	Light	Poor	Small units, 8-12 ac; shepherd's crook conspicuous in sprouts; poor soils
Q	8%	32	None from table 6	Moderate to heavy	Moderately heavy (elk)	Both	East ½ is nearly flat, with heavy cattle pressure and poor soils, poor sprouting; west ½ is 16% slope, light cattle pressure, moderately heavy elk pressure, good sprouting
R	3%	38	ABBI2—dead saplings	Light	Heavy (elk)	Poor	Many sprouts bent with snow damage; poor soils

[a] Rating according to the criteria in table 9.

Table 8—Summary by Soil Map Unit.

SMU[a]	No. units	Acres	Points stocked	Growing stock	Total live	Average height	Height growth	Slope
				stems/ac	*stems/ac*	*ft*	*ft/yr*	*%*
13 & 15	3.0	44.0	52.5%	1,938	3,944	5.9	0.7	10.8
20	11.3	214.9	52.1%	2,875	5,247	4.2	0.7	8.6
21 & 22	8.6	206.8	83.5%	4,971	7,923	6.5	0.9	11.0
25	11.2	354.5	72.5%	3,475	5,006	12.6	1.1	12.0
27	8.5	104.3	47.6%	1,816	9,278	2.0	0.4	5.7
29	30.1	684.5	71.2%	4,391	8,583	5.1	1.0	9.2
31	20.4	245.0	58.3%	3,183	6,651	3.8	0.9	3.1

[a] See table 4 for explanation of the Soil Map Unit codes, from Hughes and others 1995.

Table 9—Assignment of Soil Map Units to aspen regeneration classes.

SMU	Soil component	Taxonomic class	Mollic thickness	Aspen regeneration	Comments
			inch		
	Chilson	Lithic Argiboroll, Clayey, Mixed	5	Poor	Very clayey, shallow
13	Delson	Typic Argiboroll, Fine, Montmorillonitic[a]	11	Moderate	Very clayey, warm
	Beenom	Lithic Argiboroll, Loamy, Mixed	8	Poor	Clayey, shallow
	Delson	Typic Argiboroll, Fine, Montmorillonitic[a]	11	Good	Very clayey, warm
15	Kubler	Pachic Argiboroll, Fine, Montmorillonitic[a]	33	Very good	Very clayey, warm
	Showalter	Aridic Argiboroll, Clayey-Skeletal, Montmorillonitic[a]	11	Good	Very clayey, warm, dry
20	Gralic	Typic Cryorthent, Loamy-Skeletal, Mixed, Nonacid	<2	Poor	Shallow
	Grenadier	Dystric Cryochrept, Loamy-Skeletal, Mixed	4	Mostly poor	Shallow and cold
21	Hapgood	Pachic Cryoboroll, Loamy-Skeletal, Mixed	17	Very good	
	Lamphier	Pachic Cryoboroll, Fine-Loamy, Mixed	35	Very good	
	Hoosan	Pachic Cryoboroll, Fine, Mixed	22	Very good	
22	Lamphier	Pachic Cryoboroll, Fine-Loamy, Mixed	35	Very good	
	Leaps	Typic Cryoboroll, Fine, Montmorillonitic[a]	14	Good	
25	Lamphier	Pachic Cryoboroll, Fine-Loamy, Mixed	35	Very good	
	Hapgood	Pachic Cryoboroll, Loamy-Skeletal, Mixed	17	Very good	
27	Overgaard	Typic Cryoboralf, Fine, Mixed	<2	Poor	Clayey, shallow
	Olathe	Lithic Cryochrept, Loamy, Mixed	<2	Poor	Shallow
29	Supervisor	Typic Cryoboroll, Loamy-Skeletal, Mixed	11	Good	
	Cebone	Boralfic Cryoboroll, Fine, Montmorillonitic[a]	12	Moderately good	Very clayey
	Ula	Mollic Cryoboralf, Fine-Loamy, Mixed	7	Moderate	Clayey at depth
31	Agneston	Typic Cryoboralf, Loamy-Skeletal, Mixed	<2	Poor	Clayey, Shallow
	Pendergrass	Lithic Cryorthent, Loamy-Skeletal, Mixed, Nonacid	<2	Poor	Shallow

[a] Now called “Smectitic.”

Table 10—Zones in Long Creek Sale, Unit 3 (see figure 9).

Zone no.	Cattle grazing intensity	Soil	Aspen sprouting
1	Heavy	Poor	Very few, all culls, heavily browsed
2	Heavy	Good	Large number, mostly culls, heavily browsed
3	Light	Poor	Moderate sprouting, barely successful
4	Light	Good	Vigorous sprouting, very successful

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Nitrogen Mineralization in Aspen/Conifer Soils After a Natural Fire

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Abstract—*We measured the effects of the 1996 Pole Creek fire, Fishlake National Forest, Utah, on available soil N and net N mineralization for three summers after the fire using an ion exchange membrane (IEM) soil core incubation method. Fire in mixed aspen/conifer increased the amount of available* NH_4*, and a subsequent net increase in soil nitrification was observed. Release of* NH_4 *from the ash and a net increase in soil nitrification were still observed 3 years after the fire. The fire-caused increase in available soil N provides a source of N for aspen regrowth.*

Introduction

Aspen (*Populus tremuloides*) provide many ecological benefits to resource users, including protection of watersheds from erosion, some protection against rapid wildfire advance, increased biological diversity in the species-rich grass-forb understory, wood fiber, wildlife habitat, forage for domestic livestock and native ungulates, recreational sites, aesthetic considerations (e.g., fall leaf colors), and more water yield than conifers (Bartos and Campbell 1998a). Some authors have suggested that aspen are in decline throughout the Interior Western United States (Bartos and Campbell 1998a), although the extent of decline has been the subject of much debate. National Forest inventory and analysis data indicate that about 60% of aspen stands have disappeared since the mid-19th century (Bartos and Campbell 1998b). Decline of aspen stands is attributed to natural succession (e.g., invasion of conifers) (Harniss 1981), fire suppression (Jones and Debyle 1985), and overbrowsing by domestic livestock and native ungulates (Kay 1990).

Western aspen, which reproduce primarily by suckering from lateral roots, often need disturbances to stimulate the suckering response (Schier 1981). In the past, these disturbances included lightning-caused fires that killed mature aspen, and insects and diseases that weakened old decadent stands before toppling by wind. Suppression of human-caused and lightning-caused fires throughout the twentieth century has greatly reduced one of the main forces of aspen regeneration from the landscape. Even when a disturbance such as fire or wind does stimulate aspen regeneration, overbrowsing of new aspen suckers by domestic livestock and native ungulates quickly suppresses regeneration. Evidence indicates that overbrowsing and conifer invasion of declining aspen stands have led to the precarious state of aspen in the Interior Western United States, although this assessment is not universally accepted.

In addition to stimulating aspen suckering, fire can also exert a large influence on soil properties in burned stands, depending on the intensity of the burn. Increases in plant available nutrients usually occur following fire because of the transfer of nutrients from the ash to the soil (Schlesinger 1997). These

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increases are usually considered to be short lived because of nutrient uptake by new vegetative growth and losses from leaching (primarily NO_3) and erosion.

During June and July of 1996, an 8,000-acre natural fire (the Pole Creek fire) occurred in the area of Betenson and Grindstone Flats on the Beaver Ranger District of the Fishlake National Forest, Utah. This moderate-intensity fire burned in mixed stands of older aspen and invading conifers, primarily subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). After the fire, some cutting of fire-killed aspen and conifers was done to thin the stands, and four exclosures were constructed by Utah Division of Wildlife Resources and Fishlake National Forest personnel to protect aspen suckers from browsing by domestic livestock and native ungulates. Two exclosures were built in the Grindstone Flat area and two in the nearby Betenson Flat area.

We present results of the effects of a natural fire on available soil N and net soil N mineralization during the first, second, and third summers after the fire year. In particular, we studied the effects of fire on the amounts of extractable soil NH_4 and NO_3, amounts and rates of leaching of NH_4 and NO_3 from plant litter or ash layers, and net changes in some reactions of the internal soil N cycle (e.g., nitrification, mineralization).

Methods

We measured net soil N mineralization/immobilization during the summer months in 1997, 1998, and 1999, following the 1996 Pole Creek fire using an ion exchange membrane (IEM) soil core incubation technique. The method was similar to that developed by DiStefano and Gholz (1986) except that we used ion exchange membranes (Ionics Inc., Watertown, MA) in place of ion exchange resin bags. The IEMs have identical ion exchange properties to the more familiar resin beads and have shown considerable promise for assessing soil nutrient availability (Cooperband and Logan 1994).

Ion Exchange Membrane Soil Core Method

The assembly of the soil cores with IEMs is shown in figure 1. The soil core is enclosed in a 2-inch diameter x 4-inch long plastic liner (Forestry Suppliers, Jackson, MS). End caps were used to hold the IEMs against each end of the soil core. Circular holes (1.5-inch diameter) were cut in the center of the 2-inch diameter end caps. Cation (CEM) and anion (AEM) exchange membranes were prepared by cutting 2-inch diameter circles from the original membrane sheets and drilling nine evenly spaced ⅛-inch holes in each circle to allow movement of air and slow percolation of water through the soil cores. The CEMs and AEMs were soaked five times in 1 M HCl and 1 M $NaHCO_3$, respectively, rinsed with deionized water, and sealed in zip-lock plastic bags for transport to the field. To protect the IEMs from abrasion and excessive desiccation and to direct infiltrating water to flow across the surfaces of the IEMs to increase the efficiency of ion exchange, porous screens were prepared by cutting 2-inch diameter circles from 114-um Spectra/Mesh polyethylene filter screens.

We installed the IEM soil cores in the following manner. Leaf litter (unburned areas) or ash layer (burned areas) was first removed from the soil surface and set aside. The soil coring head with a plastic liner was driven into the soil using a slide hammer attachment (Forestry Suppliers, Jackson, MS) until flush with the top of the soil. The intact soil core was removed from the coring

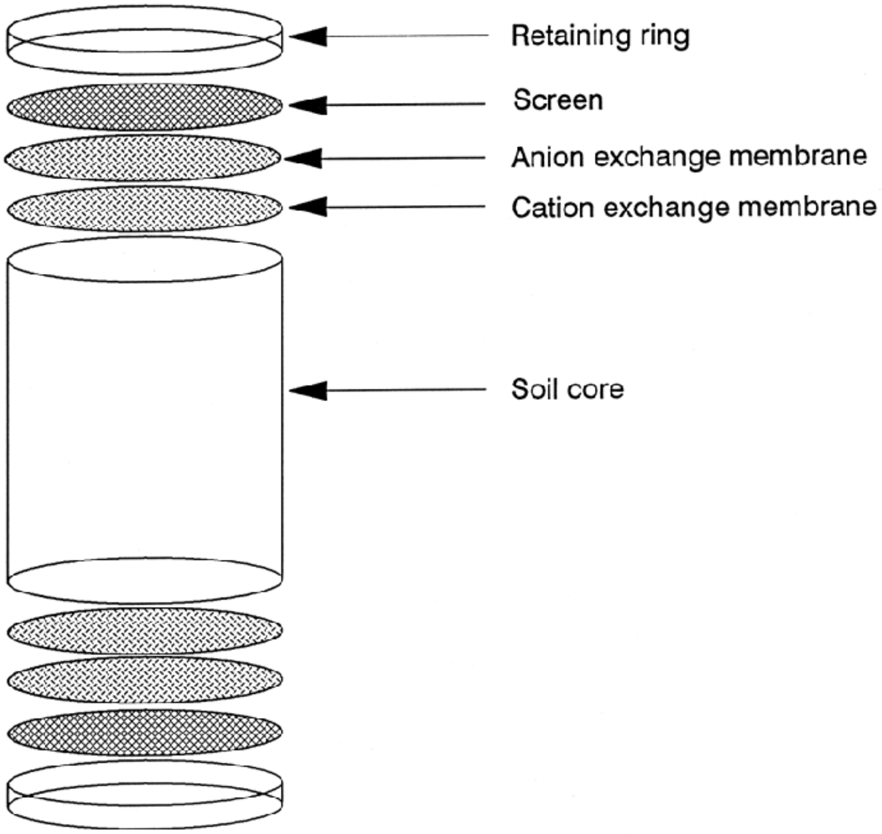

Figure 1–Ion exchange membrane soil core assembly.

head, the ends of the core were trimmed, and the excess soil was returned to the soil hole. The end caps, plastic screens, and IEMs were assembled as shown in figure 1, the IEM soil core was placed in the hole with the top end up, and the core was covered with leaf litter or ash. Core locations were marked with flagged rebar stakes. An additional soil core was taken adjacent to the installed IEM soil core to determine initial soil exchangeable NH_4 and NO_3 levels. The initial cores were removed from the coring tool and placed in labeled zip-lock plastic bags. The cores were transported to the laboratory in a cooler and stored at <4 °C until extraction (usually within 2 weeks of sampling).

The IEM soil cores were installed in burned and unburned areas on Grindstone and Betenson Flats: four cores were installed in each of the four exclosures in burned aspen/conifer stands, four cores were installed in each of three unburned aspen/conifer stands near the burned areas, and four cores were installed in each of two unburned aspen stands that regenerated as a result of a fire in 1958. Soil temperature in each area was monitored at a 4-inch depth using Optic StowAway temperature loggers (Onset Computer Corp., Bourne, MA).

Two incubation periods were used each summer: 6/25 to 7/22/97 (27 d), 7/22 to 9/23/97 (63 d), 6/23–24 to 7/21–22/98 (27–28 d), 7/21–22 to 9/19/98 (59–60 d), 7/1 to 7/29/99 (28 d), and 7/29 to 9/19/99 (52 d). At the end of each incubation period, the leaf litter or ash layer was removed from the tops of the cores and the cores were removed from the ground and placed in labeled zip-lock plastic bags. The cores were transported to the laboratory in a cooler and stored at <4 °C until extraction. New initial cores for the second incubation period were collected when the IEM soil cores from the first period were removed and the new IEM soil cores were installed.

The IEM soil cores were disassembled, and top and bottom CEM-AEM pairs were rinsed with deionized water to remove soil particles and placed in separate labeled petri dishes. The soil cores were removed from the plastic liners, returned to the zip-lock bags, and mixed by kneading the bags. Each CEM-AEM pair was extracted with 100 mL of 2 M KCl in 250-mL wide-mouth plastic jars by shaking for 1 h on an orbital shaker at 150 rpm. The extracts were frozen until analysis.

Water content of a representative subsample of each soil core was determined gravimetrically at 105 °C. A representative field-moist subsample of each soil core equivalent to 10 g of oven-dry soil was extracted with 100 mL of 2 M KCl in a 250-mL wide-mouth plastic jar by shaking for 1 h on an orbital shaker at 150 rpm. The extracts were filtered through Whatman 40 filter paper and frozen until analysis. The 2 M KCl extracts of IEMs and soil cores were analyzed for NH_4–N and NO_3–N by the automated phenate and Cd reduction methods, respectively, using a LACHAT flow injection analysis system (Zellweger Analytics, Milwaukee, WI).

The remaining soil from each soil core was air dried at room temperature and weighed. The total weight of each soil core was calculated by summing the oven-dry weight of the subsample used for determining water content, the oven-dry weight of the subsample used for determining extractable NH_4 and NO_3, and the air-dry weight of the remaining soil in each core.

Amounts of NH_4–N and NO_3–N accumulated by the IEMs (ug/cm^2) were calculated by multiplying the NH_4 and NO_3 concentrations in the KCl extracts by the extract volume and dividing by the surface area of the IEM (20.27 cm^2). Rates of NH_4 or NO_3 accumulation by the cores (ug/cm^2/mo) were calculated by dividing the accumulated amounts by the incubation time in days and multiplying by 30 days per month. The IEMs at the top of the soil core remove NH_4 and NO_3 in precipitation or leachate passing through the leaf litter or ash layers. The IEMs at the bottom of the soil core remove NH_4 and NO_3 leached from the soil core. Concentrations of NH_4 and NO_3 in the top and bottom IEMs on a soil weight basis for the entire soil core (mg/kg) were calculated by multiplying the amounts on the IEMs by the IEM surface area and dividing by the dry weight of the soil core.

Total NH_4 and NO_3 concentrations in the IEM soil cores were obtained by summing the concentrations of NH_4 or NO_3 in the soil core plus the amounts extracted from the bottom IEMs. Following terminology and definitions given by Stevenson (1986) and DiStefano and Gholz (1986), net ammonification is equal to total NH_4 in the IEM soil core minus NH_4 in the initial soil core. Net nitrification is equal to total NO_3 in the IEM soil core minus NO_3 in the initial soil core. Net mineralization (or immobilization) is equal to net ammonification plus net nitrification. Net ammonification, nitrification, and mineralization rates were calculated by dividing the net amounts by the incubation time. An example of these calculations for one of the soil cores from the burn area is shown in table 1.

Data Analysis

Because the data were nonnormally distributed, a Kruskal-Wallis (K-W) analysis of variance on ranks was run on each measured or derived N variable for each incubation period in each year with stand type as the factor and unburned aspen, unburned mixed aspen/conifer, and burned mixed aspen/conifer as levels within stand type (SigmaStat, ver. 2.0, SPSS Science, Chicago, IL). If a statistically significant difference among stand types was found ($p < 0.05$), a pairwise multiple comparisons test was conducted using Dunn's method to isolate which stand type was different from the others ($p < 0.05$). Also,

Table 1—Net ammonification, nitrification, and mineralization/immobilization for an IEM soil core from the Betenson 1 exclosure (7/22–9/23/97).

Initial soil core NH_4–N, mg/kg	39.0
Final IEM soil core NH_4–N, mg/kg	107.7
Bottom CEM NH_4–N, mg/kg	0.3
Final total (bottom CEM + IEM soil core) NH_4–N, mg/kg	108.0
Net (final total – initial) NH_4–N, mg/kg	69.1
Net ammonification rate (net NH_4–N / incubation time), mg/kg/mo	32.9
Initial soil core NO_3–N, mg/kg	11.6
Final IEM soil core NO_3–N, mg/kg	2.0
Bottom AEM NO_3–N, mg/kg	10.0
Final total (bottom AEM + IEM soil core) NO_3–N, mg/kg	12.0
Net (final total – initial) NO_3–N, mg/kg	0.4
Net nitrification rate (net NO_3–N / incubation time), mg/kg/mo	0.2
Net mineralization/immobilization rate (net ammonification + net nitrification), mg/kg/mo	33.1

Kolmogorod-Smirnov (K-S) tests were run to determine if the distribution of each variable for each incubation in each year differed by stand type (SYSTAT ver. 8.0, SPSS Science, Chicago, IL).

Results

The Pole Creek fire affected the post-fire rates of accumulation of NH_4 and NO_3 by the top and bottom IEMs in the incubated soil cores (table 2, figures 2 and 3). Rates of NH_4 accumulation by top and bottom CEMs in burned area soil cores were significantly greater than those in unburned areas during the first 1997 incubation, but were not significantly different during the second.

Higher rates of NH_4 accumulation by the top CEMs in unburned areas were observed in 1998 than in 1997. This resulted in no significant differences

Table 2—Median rates of NH_4 and NO_3 accumulation by IEMs at the top and bottom of IEM soil cores for two incubations in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. Different letters indicate that the median values for each stand type are significantly different within each incubation and year.

	Incubation number and year					
	1997		1998		1999	
Stand	1	2	1	2	1	2
	- $ug/cm^2/mo$ -					
Top CEM NH_4–N						
Unburned aspen	1.5 a	3.2 a	4.5 a	3.6 ab	1.0 a	1.2 a
Unburned aspen/conifer	1.6 a	3.1 a	7.6 a	5.6 a	3.0 ab	1.7 a
Burned aspen/conifer	10.3 b	1.0 a	6.4 a	0.2 b	9.8 b	1.6 a
Bottom CEM NH_4–N						
Unburned aspen	1.5 a	0.8 a	1.3 a	0.8 a	0.6 a	0.5 ab
Unburned aspen/conifer	1.7 a	0.4 a	1.3 ab	1.1 a	1.2 a	0.2 a
Burned aspen/conifer	4.5 b	0.8 a	2.6 b	1.0 a	1.2 a	0.8 b
Top AEM NO_3–N						
Unburned aspen	0.8 a	0.2 a	0.9 a	0.4 a	1.0 a	0.4 a
Unburned aspen/conifer	0.6 a	0.4 a	0.8 a	1.0 a	1.4 a	0.2 a
Burned aspen/conifer	0.6 a	44.4 b	78.6 b	91.0 b	29.1 b	26.6 b
Bottom AEM NO_3–N						
Unburned aspen	0.5 a	0.2 a	0.8 a	0.5 a	0.8 a	0.0 a
Unburned aspen/conifer	0.6 a	0.3 a	0.9 a	0.3 a	0.8 a	0.1 a
Burned aspen/conifer	4.8 b	94.6 b	26.6 b	85.6 b	4.6 b	7.2 b

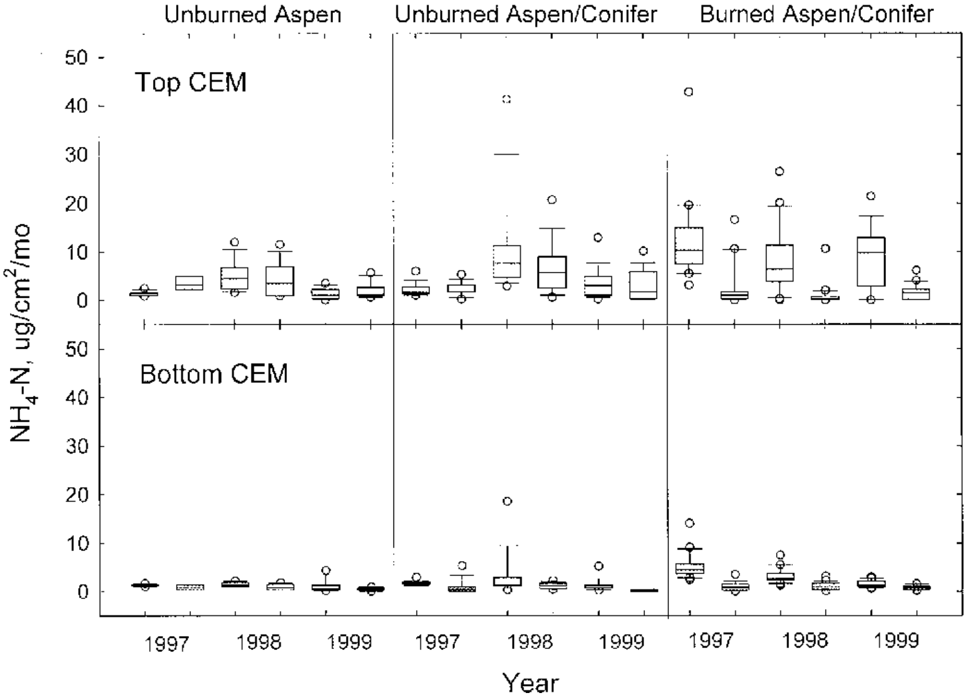

Figure 2—Box plots of rates of NH_4 accumulation by cation exchange membranes (CEM) at the top and bottom of IEM soil cores for two incubation periods in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points.

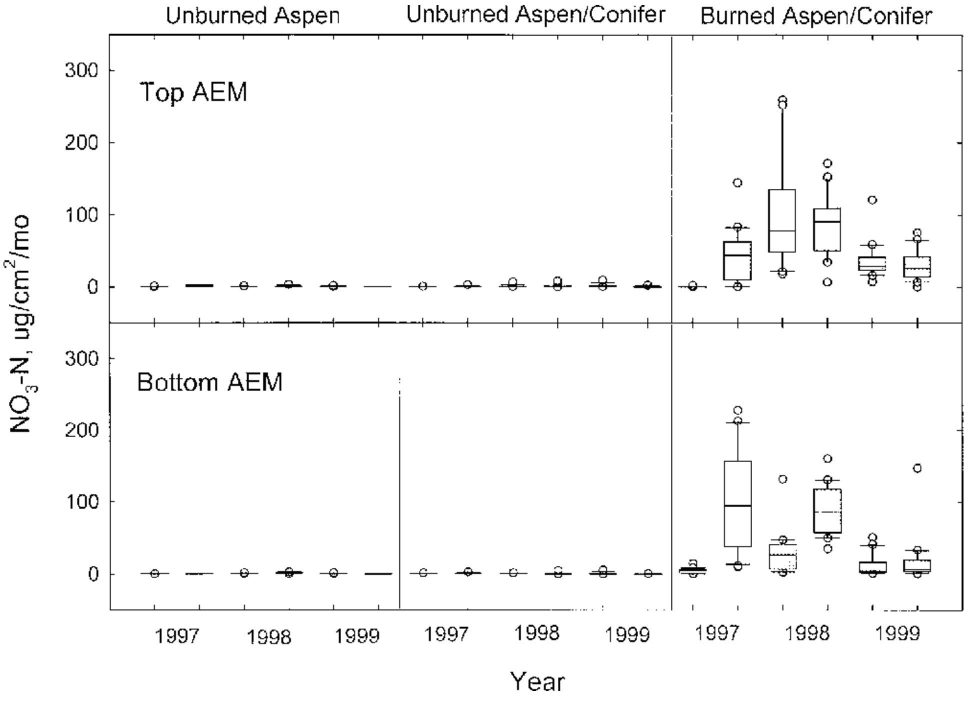

Figure 3—Box plots of rates of NO_3 accumulation by anion exchange membranes (AEM) at the top and bottom of IEM soil cores for two incubation periods in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points.

between burned and unburned areas for rates of NH_4 accumulation by the top CEMs during the first 1998 incubation. During the second 1998 incubation, higher rates of NH_4 accumulation by the top CEMs were found in unburned than burned areas. In contrast, higher rates of NH_4 accumulation by the bottom CEMs were found in burned areas than unburned areas during the first 1998 incubation. No significant differences between burned and unburned areas were found in NH_4 accumulation rates by the bottom CEMs during the second 1998 incubation.

Higher rates of NH_4 accumulation were again found in the top CEMs in burned areas compared to unburned areas during the first 1999 incubation, but not during the second. Stand type had no effect on NH_4 accumulation rates by the bottom CEMs during the first incubation in 1999, and although significant differences due to stand type were observed during the second 1999 incubation, these differences were minor because accumulation rates were low during this period.

During the first 1997 incubation, NO_3 accumulation rates by the top AEMs in burned areas were not significantly different from those in unburned areas. However, NO_3 accumulation rates by bottom AEMs were significantly greater in burned areas than unburned areas during the first 1997 incubation. During the second 1997 incubation, NO_3 accumulation rates by both top and bottom AEMs were significantly greater in burned areas than in unburned areas. The higher rates of NO_3 accumulation by top and bottom AEMs in burned areas compared to unburned areas continued in 1998 and 1999.

Higher rates of NH_4 accumulation by the CEMs were found during the first incubation than during the second, whereas higher rates of NO_3 accumulation by the AEMs were found during the second incubation than during the first. The longer second incubation allowed more time for greater quantities of NH_4 and NO_3 to accumulate on the IEMs, but the quantities accumulated on the IEMs are divided by incubation time to obtain rates of accumulation to adjust for the time difference between the first and second incubation. This shift in the rates of accumulation by the IEMs and relative distribution of inorganic N species from the first to the second incubation period indicates an increase in net soil nitrification rates in burned areas as summer progressed. This pattern continued for NH_4 in top and bottom CEMs and NO_3 in bottom AEMs in 1998 and 1999, but not for NO_3 in top AEMs. Rates of NO_3 accumulation by top AEMs during the first incubation were similar to those during the second incubation in 1998 and 1999.

The distribution of NH_4 and NO_3 among the top and bottom IEMs tended to follow the relative mobility of the ions. Nitrate is more mobile than NH_4, so similar rates of NO_3 accumulation were found in top and bottom AEMs in burned areas. In contrast, higher rates of NH_4 accumulation were found in top than bottom CEMs.

During the first 1997 incubation, significantly more NH_4 and NO_3 were extracted from IEM soil cores (including bottom IEMs) in burned areas than from those in unburned areas (table 3, figure 4). Extractable NH_4 in IEM soil

Table 3—Median soil + bottom CEM NH_4 and soil + bottom AEM NO_3 in IEM soil cores for two incubation periods in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. Different letters indicate that the median values for each stand type are significantly different within each incubation and year.

	Incubation number and year					
	1997		1998		1999	
Stand	1	2	1	2	1	2
	mg/kg					
Soil + CEM NH_4–N						
Unburned aspen	3.8 a	2.0 a	2.2 a	3.2 a	1.8 ab	1.4 ab
Unburned aspen/conifer	5.1 a	5.2 a	10.8 a	13.0 a	3.5 a	4.0 a
Burned aspen/conifer	22.3 b	7.2 a	1.0 b	1.0 b	1.0 b	0.6 b
Soil + AEM NO_3–N						
Unburned aspen	0.6 a	0.6 a	1.5 a	4.6 a	0.1 a	2.1 a
Unburned aspen/conifer	0.5 a	0.8 a	1.4 a	1.7 a	0.2 a	2.0 a
Burned aspen/conifer	10.2 b	35.4 b	13.9 b	32.7 b	3.8 b	8.8 b

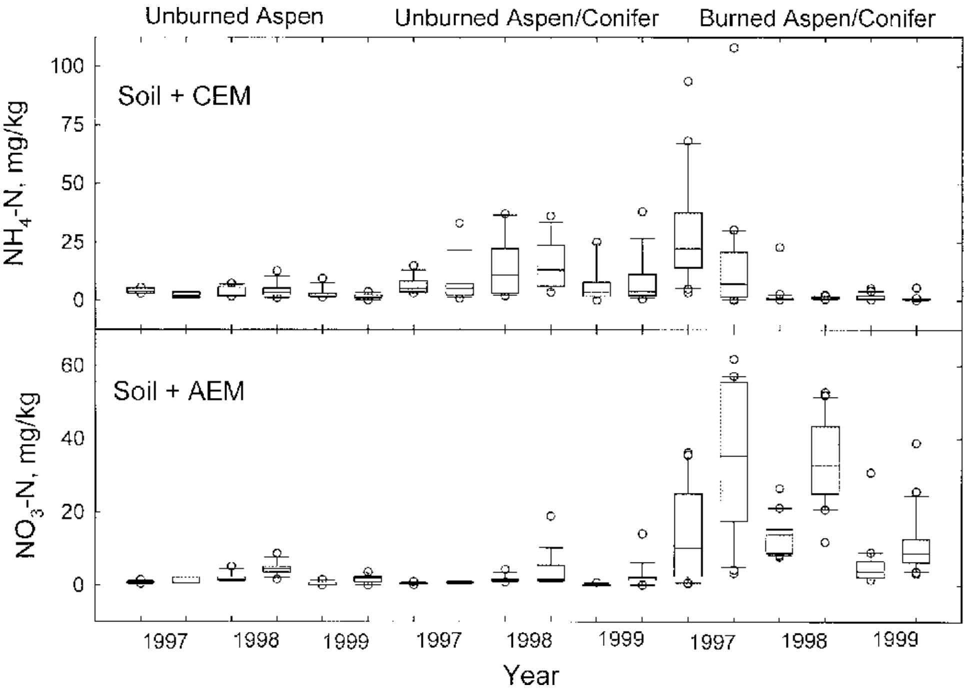

Figure 4—Box plots of soil + CEM NH_4 and soil + AEM NO_3 in IEM soil cores for two incubation periods in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points.

cores was not significantly different between burned and unburned areas during the second 1997 incubation. Significantly more NO_3 was extracted from IEM soil cores in burned areas than those from unburned areas during both 1997 incubations (table 3, figure 4). No significant differences were found between unburned aspen and unburned aspen/conifer for IEM soil core NH_4 or NO_3 during the first or second 1997 incubations.

In contrast with the 1997 results, more NH_4 tended to be extracted from IEM soil cores in unburned areas than in burned areas in 1998. Soil core NO_3 levels in burned areas in 1998 were similar to those observed in the same areas in 1997. Soil core NO_3 levels in unburned areas in 1998 tended to be higher than those observed in 1997, but were still significantly less than those in burned areas. The pattern of higher soil core NH_4 levels in unburned areas than burned areas and higher soil core NO_3 levels in burned than unburned areas continued in 1999.

To obtain an estimate of the total supply of inorganic N available for plant uptake or microbial activity during the summer months, the total amounts of NH_4 and NO_3 accumulated by the top and bottom IEMs from the first and second incubations were added to the total amounts of these ions remaining in the soil cores at the end of the second incubation period (table 4, figure 5).

Table 4–Median total IEM (top and bottom CEMs and AEMs from first and second incubations) + soil (IEM soil core from second incubation) NH_4 + NO_3–N in unburned aspen, unburned aspen/conifer, and burned aspen/conifer in 1997, 1998, and 1999. Different letters indicate that the median values for each stand type are significantly different within each year.

	Year		
Stand	**1997**	**1998**	**1999**
	- - - - - - - - - - - - - *mg/kg* - - - - - - - - - - - - -		
Unburned aspen	4.6 a	10.1 a	4.4 a
Unburned aspen/conifer	9.0 a	21.1 a	8.2 ab
Burned aspen/conifer	69.4 b	67.8 b	20.2 b

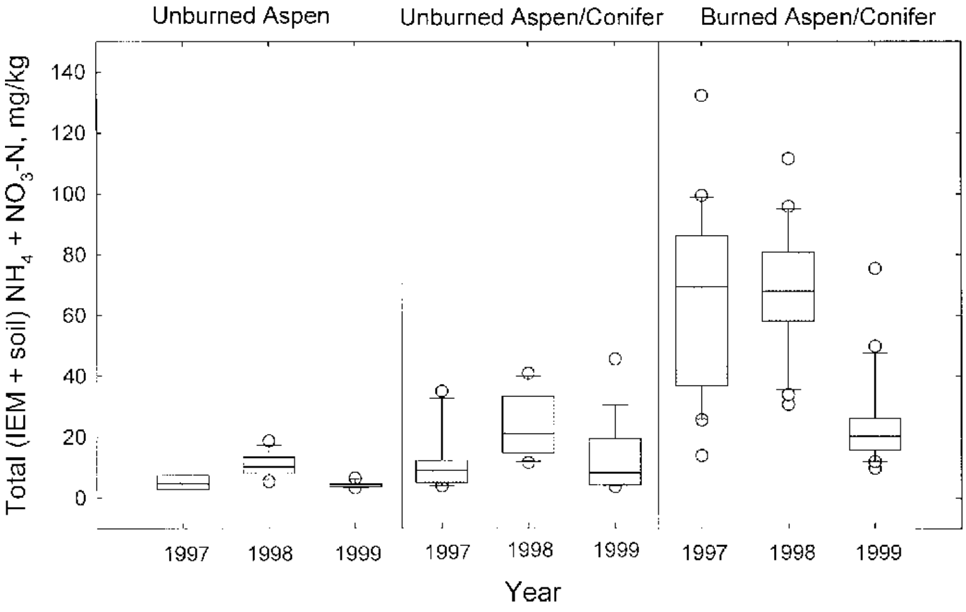

Figure 5–Box plots of total IEM (top and bottom CEMs and AEMs from first and second incubations) + soil (IEM soil core from second incubation) $NH_4 + NO_3$–N in unburned aspen, unburned aspen/conifer, and burned aspen/conifer in 1997, 1998, and 1999. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points.

Similar levels of $NH_4 + NO_3$–N were available for plant uptake or microbial activity in burned areas in 1997 and 1998, and these levels were significantly greater than those in unburned areas. In unburned areas, more $NH_4 + NO_3$–N was observed in 1998 than in 1997. In 1999, $NH_4 + NO_3$–N in unburned areas had declined to levels observed in 1997. Amounts of $NH_4 + NO_3$–N in burned areas also decreased in 1999, but were still significantly higher than those in unburned aspen but not in unburned aspen/conifer.

In 1997, net ammonification, nitrification, and mineralization/immobilization rates were not significantly different between burned and unburned areas or between unburned aspen and unburned aspen/conifer stands (table 5, figure 6). Even though median rates were not significantly different, there tended to be a greater net loss of NH_4 in burned areas during the early part of summer (first incubation) than later in the summer (second incubation). Net gains in soil NO_3 in burned areas tended to be greater during the latter part

Table 5—Median net ammonification, nitrification, and mineralization/immobilization rates in IEM soil cores for two incubation periods in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. Different letters indicate that the median values for each stand type are significantly different within each incubation and year.

	Incubation number and year					
	1997		1998		1999	
Stand	1	2	1	2	1	2
	mg/kg					
Net ammonification rate						
Unburned aspen	0.7 a	–0.2 a	0.9 ab	1.2 ab	1.5 a	0.6 ab
Unburned aspen/conifer	1.8 a	1.4 a	4.2 a	5.4 a	0.8 a	1.6 a
Burned aspen/conifer	–6.3 a	–7.3 a	–0.2 b	0.1 b	–0.5 a	–0.1 b
Net nitrification rate						
Unburned aspen	–0.2 a	0.2 a	0.5 a	1.8 ab	–0.3 a	0.5 a
Unburned aspen/conifer	–0.3 a	0.2 a	0.2 a	0.2 a	–0.9 a	0.8 a
Burned aspen/conifer	4.2 a	12.2 a	2.6 a	7.5 b	–0.6 a	2.7 b
Net N mineralization rate						
Unburned aspen	0.5 a	0.5 a	1.8 a	3.0 a	1.6 a	1.4 a
Unburned aspen/conifer	1.6 a	1.8 a	4.2 a	6.9 a	0.2 a	3.4 a
Burned aspen/conifer	8.4 a	3.9 a	2.4 a	7.4 a	–0.5 a	2.5 a

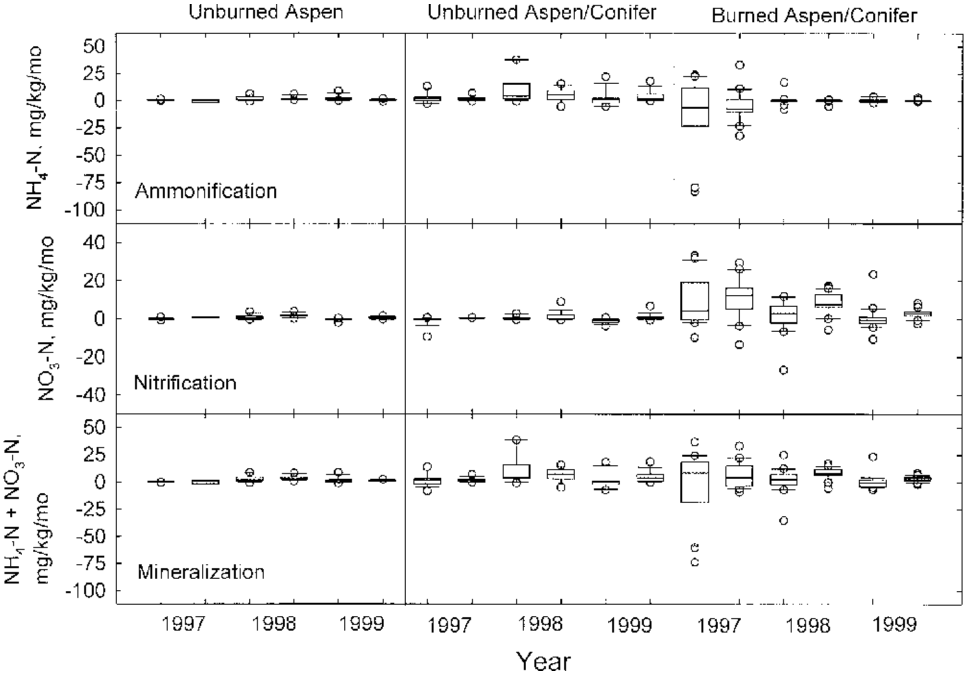

Figure 6—Box plots of net ammonification, nitrification, and mineralization/immobilization rates in IEM soil cores for two incubation periods in each of 3 years in unburned aspen, unburned aspen/conifer, and burned aspen/conifer. The 25th and 75th percentiles are shown as a box centered about the median (50th percentile), the 10th and 90th percentiles are shown as error bars, and the 5th and 95th percentiles and outliers are shown as points.

of summer than in the early part. The loss in NH_4 was largely balanced by the gain in NO_3 (nitrification), although some loss of NH_4 may have been from direct microbial utilization of this form of N. In 1998 and 1999, net ammonification rates tended to be higher in unburned areas than burned areas, whereas, the opposite was observed for net nitrification rates. Because of the relative balance of net ammonification and net nitrification rates, net mineralization/immobilization rates in burned and unburned areas tended to be similar in 1998 and 1999.

For cases where the K-W tests revealed that median values of the various N variables for the different stand types differed significantly, K-S tests showed that the data distributions also differed as the Box plots indicate (figures 2, 3, 4, 5, and 6). The range of values tended to be much greater in burned than in unburned areas.

Discussion

In undisturbed (unburned) aspen and mixed aspen/conifer soils, the various microbial mineralization and immobilization reactions of the internal soil N cycle tend to be balanced. There is usually little free NH_4 and NO_3 in the mineral soil (bottom of figures 2 and 3, figures 4 and 5) because it is quickly utilized by microorganisms or taken up by plant roots. Thus, net mineralization/immobilization rates tend to be low (figure 6). Low or unchanged levels of NH_4 and NO_3 and low or unchanged rates of net mineralization do not mean that active mineralization is not taking place or that the internal soil N cycle is not operating (Stevenson 1986). Gross rates of the microbially mediated reactions may be high, but since the reactions tend to be balanced, net rates are low (Stevenson 1986).

Depending on its intensity, fire alters many soil properties including exerting a strong influence on soil microbial mineralization/immobilization processes (Schlesinger 1997). Losses of gaseous and particulate N occur during combustion of leaf litter and soil organic matter. Microbial populations and enzyme activity may decrease, but available nutrients are also returned to the soil by the residual ash (Schlesinger 1997). Even though total soil N may be lower because of combustion, residual N in the ash is subjected to rapid mineralization and nitrification provided the fire is not too intense and microbial and enzyme populations can recover (Schlesinger 1997).

The source of the high amounts of NH_4 accumulated by the CEMs and in the soil cores in the burn area the first summer after the fire may include NH_4 as a combustion product in the ash layer, release from mineral sources of NH_4, and rapid mineralization of combustion products. Much of this available NH_4 was probably carried over in the soil from the summer in which the fire occurred (6 to 7/96). Nitrification (microbial oxidation of NH_4 to NO_3) occurred mostly during the first summer after the fire (6 to 9/97) because of the observed decrease in NH_4 and increase in NO_3 accumulated by the IEMs and soil cores from the first to the second incubation period. The IEM soil core incubation method provides a snapshot of soil N mineralization/immobilization for the incubation periods studied, but since we did not have soil cores in place immediately after the fire, we could not quantify soil N transformations in late summer and fall of the fire year (7 to 9/96).

Nitrification is influenced by many factors, including temperature, moisture, and the substrates NH_4, O_2, and CO_2 (Stevenson 1986). The high amounts of available NH_4 found in burn area soils provide a ready substrate for surviving or post-fire invading populations of nitrifying microorganisms. Summertime soil temperature ranges and means in the burn area were higher than in unburned areas because the relatively open canopy and dark colored ash served to trap heat (data not shown), thus helping to accelerate nitrification. Adequate soil moisture was available in burned areas (mean soil core water content of 24.1% in 1997) for nitrification to occur throughout the summer.

Although denitrification and leaching can potentially remove much of the NO_3 produced by post-fire nitrification, the large amounts of available soil NH_4 and NO_3 present during the growing season provide a ready source of mineral N for uptake by aspen suckers. A strong aspen suckering response was observed on Betenson and Grindstone Flats and in other burned areas on the Fishlake National Forest during the first summer after the fires (Amacher and Bartos 1998). Leaching of NH_4 from the ash layer and subsequent nitrification of the leached NH_4 continued through the second and third summers after the fire. A longer residence time of post-fire soil NO_3 provides more opportunity for regenerating aspen clones to exploit this source of N. Thus, available N from ash may be an important source of N to young aspen until N mineralization in leaf litter and soil organic matter can resupply the nutritional needs of aspen.

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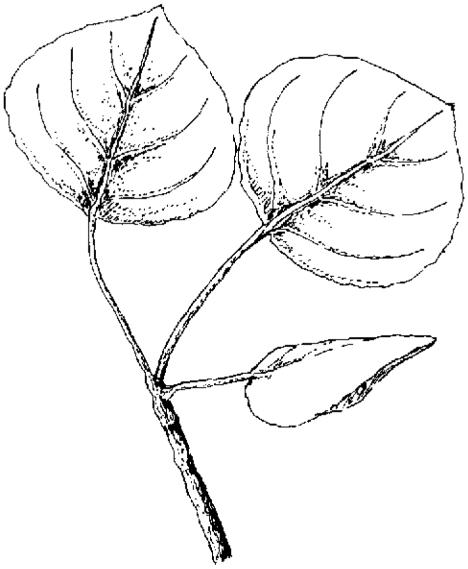

Aspen Forest Products

The Effect of Aspen Wood Characteristics and Properties on Utilization

Kurt H. Mackes[1] **and Dennis L. Lynch**[2]

Abstract*—This paper reviews characteristics and properties of aspen wood, including anatomical structure and characteristics, moisture and shrinkage properties, weight and specific gravity, mechanical properties, and processing characteristics. Uses of aspen are evaluated: sawn and veneer products, composite panels, pulp, excelsior, post and poles, animal bedding, animal food supplements, fuel applications, and novelties. Aspen is a preferred species for paneling, veneer products including matchsticks and chopsticks, waferboard and oriented strandboard (OSB), fiberboard, pulp, excelsior, research animal bedding, animal food supplements, and tourist or gift items.*

Introduction

Quaking aspen (*Populus tremuloides*) is widely distributed and commonly found in Colorado and throughout the Rocky Mountain Region. Although aspen up to 120 feet tall and 4 feet in diameter have been reported (Perala and Carpenter 1985), mature trees are typically smaller, averaging in the range of 60 to 80 feet tall with a diameter of 11 inches diameter at breast height (d.b.h.) or larger (Baker 1925). Although aspen trees are fairly straight, have little taper, and are relatively free of limbs, limb scars persist and trees in some stands can be very contorted (Perala and Carpenter 1985). Aspen continues to be an underutilized species for wood products in the Rocky Mountain West.

The purpose of this paper is to review characteristics and properties of aspen wood, including anatomical structure and characteristics, moisture and shrinkage properties, weight and specific gravity, mechanical properties, and processing characteristics. Then, based on these characteristics and properties, traditional and potential uses for aspen are evaluated. Assessments are presented for a wide range of uses, including sawn and veneer products, composite panels, pulp, excelsior, post and poles, animal bedding, animal food supplements, fuel applications, and tourist or gift items.

Characteristics and Properties

Anatomical

Aspen is a diffuse-porous hardwood. The pores are small and evenly distributed throughout annual growth increments. The heartwood is white to light brown or creamy. The sapwood is typically whiter and blends into the heartwood with no clear lines of demarcation. Annual growth increments are delineated by slight color differences between earlywood and latewood. The density gradient between earlywood and latewood is small, giving uniform texture. Rays are extremely fine and hardly visible even with a hand lens. Aspen wood is straight grained, light, and soft. Dry aspen has no characteristic taste or

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odor. However, green aspen can have both, which is most likely due to the presence of wetwood.

Both tension wood and wetwood are commonly found in aspen. Tension wood is a type of reaction wood. Wetwood is a water-soaked condition commonly found in both the sapwood and heartwood of aspen (Knutson 1973). However, in the Rocky Mountains, wetwood seems to occur primarily in heartwood (Ward 1976). Wetwood is usually discolored from normal wood and dark-colored heartwood that are usually associated with wetwood (Boone 1989). Although wetwood typically harbors high populations of bacteria and yeast, their role in wetwood formation is not clear.

Moisture Content

Water in freshly harvested green wood is located within the cell lumen and the cell wall. The point where all the water in the lumen has been removed but the cell wall is still saturated is termed the fiber saturation point (FSP). As wood is dried, water leaves the lumen although some water vapor still remains, and water begins to leave the cell walls.

The amount of water in wood is usually expressed as the moisture content. Typically, moisture content is determined by weighing the green sample, drying it to oven-dry status, and then weighing the oven-dry sample. The oven-dry weight is subtracted from the green weight and divided by the oven-dry weight to calculate moisture content. Thus, moisture content can often exceed 100%.

The average green moisture content for aspen given in the *Wood Handbook* (USDA 1999) is 95% for heartwood and 113% for sapwood. The moisture content of aspen wood in standing trees varies considerably, depending on the season and the amount of wetwood present in the wood. Wengert (1976) reported that the moisture content of aspen sapwood can range from 65% in the summer to 110% in the winter. Wengert et al. (1985) reported an average summer heartwood moisture content of 71% and sapwood moisture content of 91% for aspen logs from southwestern Colorado. The moisture content of wetwood is considerably higher than that of normal wood and can be as high as 160% (Bois 1974).

Shrinkage

Aspen has relatively low shrinkage from the FSP to OD condition. From the FSP to OD conditions, quaking aspen shrinks on average 3.5% in the radial direction and 6.7% in the tangential direction. The volumetric shrinkage is 11.5% (USDA 1999). The ratio of radial-tangential shrinkage is relatively high, which can cause drying defects. Because tension wood is commonly found in aspen, longitudinal shrinkage can be significant. The longitudinal shrinkage of tension wood is up to five times that of normal wood (USDA 1999). This can also cause a variety of drying defects. From the FSP to OD condition, longitudinal shrinkage can range from 0.16 to 0.72% (Kennedy 1968).

Specific Gravity

For a given wood sample, specific gravity is defined as the ratio of oven-dry sample weight to the weight of a volume of water equal to the sample volume at a specified moisture content (USDA 1999). Since specific gravity is a relationship or index, it has no units. Specific gravity is typically based on green volume or volume at 12% moisture content. The *Wood Handbook* (USDA 1999) reports an average specific gravity for quaking aspen of 0.35 based on green volume and 0.38 based on volume at 12% moisture content. This compares to an average specific gravity value of 0.38, with a variation from 0.30 to 0.46, reported for quaking aspen in the West by Wengert et al. (1985). An average value of 0.45, varying from 0.38 to 0.57, was reported green for aspen bark. The specific gravity of wetwood is 0.03 to 0.04 less than normal wood (Haygreen and Wong 1966).

Weight

Green aspen wood typically weighs 40 to 45 pounds per cubic foot, although the presence of wetwood can increase weight to 50 pounds per cubic foot or more. Wengert et al. (1985) reported average summer values for aspen of 41 pounds per cubic foot sapwood and 44 pounds per cubic foot for heartwood. Green aspen bark is heavier, averaging about 55 pounds per cubic foot. An average cord of green aspen will weigh between 4,000 and 4,500 pounds. Approximately 15% of this weight is bark.

Lynch and Jones (1998) found that green aspen logs hauled from the forest weighed approximately 82 pounds per merchantable cubic foot based on scaled sample loads. This means that if a merchantable cubic foot of wood actually weighs 40 to 45 pounds, up to 50% or more of the aspen being transported is bark or wood considered unmerchantable in the scale. Thus, hauling weights per merchantable cubic foot may be considerably higher than weights of green wood cited in tables. See the *Foresters Field Handbook* (Larrabee et. al. 1994) for information on scaling and log rules.

Wengert (1985) reported an average oven-dry weight of 24 pounds per cubic foot for aspen wood and 27 pounds per cubic foot for oven-dry bark. The weight of aspen wood at 12% moisture content averages 27 pounds per cubic foot. This equates to roughly 1,800 pounds per thousand board feet of lumber at 12% moisture content.

Mechanical Properties

Although mechanical properties specifically determined for quaking aspen from the Rocky Mountain West are not available, table 1 summarizes values given for quaking aspen in the *Wood Handbook* (USDA 1999). Aspen has a relatively low specific gravity, which tends to correlate with strength and stiffness properties. Therefore, aspen mechanical properties are low relative to most North American hardwoods.

Table 1—Mechanical properties of quaking aspen (source: Wood Handbook [USDA 1999]).

	Moisture content	
Property	**Green**	**12%**
Specific gravity	0.35	0.38
Static bending properties		
Modulus of rupture (psi)	5,100	8,400
Modulus of elasticity (psi)	860,000	1,180,000
Work to maximum load (inch lb/cubic inch)	6.4	7.6
Compression parallel to grain		
Maximum crushing stress (psi)	2,140	4,250
Compression perpendicular to grain		
Stress at proportional limit (psi)	180	370
Shear parallel to grain		
Maximum stress (psi)	660	850
Tension perpendicular to grain		
Maximum stress (psi)	230	260
Hardness		
Side (lbs)	300	350

Nailing Characteristics

Aspen accepts nails well and does not have a tendency to split. However, because nail joint strength is correlated to wood density, low-density wood species such as aspen do not tend to perform as well as higher density species. This is especially true regarding the resistance of wood to the withdrawal of nails. In addition, the withdrawal resistance of nails driven into green wood decreases as the wood seasons. The nail withdrawal resistance of aspen can decrease up to 90% during the seasoning process (Johnson 1947).

Processing Characteristics

Drying

Normal sapwood of aspen is easily dried. Aspen sapwood is typically dried rapidly. One-inch aspen lumber has been successfully dried in 36 hours using kiln temperatures up to 240 °F (Wengert et al. 1985). Aspen heartwood and wetwood are considerably more difficult to dry. Normal heartwood dries slower than sapwood because of tyloses present in the vessels. Using conventional kiln-drying schedules to dry 1¾-inch aspen lumber, Ward (1976) found that it took 90 hours to dry sapwood, 115 hours to dry heartwood, and 179 hours to dry wetwood.

Aspen wood is usually conditioned at the end of drying to reduce the effects of tension wood and case hardening. To accomplish this, a dry-bulb temperature of 180 °F is typically used. The wet-bulb temperature used varies based on the desired final moisture content (Wengert et. al 1985). Although the conditioning time required to relieve stresses in 1-inch boards varies, 6 to 12 hours is usually adequate.

Aspen wetwood is difficult to dry, requiring more time. Ward (1976) attributed this to higher moisture content and bacteria slime occluding the vessels of the wood. Numerous defects, including collapse, honeycomb, and ring failure, can occur as aspen wetwood is dried. Collapse is commonly associated with aspen wetwood. Collapse can occur during both air drying (Clausen et al. 1949) and kiln drying (Ward 1976).

Warp is a common defect associated with drying normal aspen wood. Warp occurs because aspen has a high tangential-to-radial shrinkage ratio and the presence of tension wood, which can be abundant in aspen. Rasmussen (1961) reported that the amount of warp experienced during drying can be minimized by using proper stacking practices.

The saw-dry-rip (SDR) curing process has been used to dry aspen studs (Maeglin 1979). In this process, logs are initially sawed into 1¾-inch flitches. The flitches are kiln-dried to the desired moisture content and then sawn into studs. This method eliminates most of the warp that usually occurs when drying aspen. However, when using the SDR method to process aspen, sorting is necessary to select optimum log diameter and to remove logs with wetwood (Boone 1990).

Machining

Machining includes sawing, planing, shaping, boring, turning, and sanding. Generally, aspen machines easily. The power consumption required to machine aspen is relatively low and tools dull slowly. Under appropriate conditions, good quality turnings, borings, and planed and sanded surfaces can be produced with aspen wood (Wengert 1976; Wengert et. al. 1985).

Numerous factors are known to affect the quality of machined surfaces (Davis 1962). Moisture content of wood can dramatically affect the quality of planed and sanded surfaces. Aspen wood should be machined at a moisture content of less than 12% and preferably less than 6%. Specific gravity can also be a factor. Wood species such as aspen with low specific gravity tend to yield poorer turning quality. Machine settings and processing conditions affect quality. The quality of planed surfaces are affected by knife angle, feed rate versus cutter head speed, and cutting depth. Based on data presented by Davis (1962), knife angles should be maintained at 25 to 30 degrees when machining aspen. A slow feed rate and a high cutter head speed (peripheral speed above 5,000 feet per minute) that maintains at least 22 cuts per inch should be used. Final cutting depth should be shallow, approximately 1⁄32-inch. When boring, a slow axial feed should be used.

One common defect that commonly occurs when planing or sanding aspen is “fuzzy” or “whiskered” grain. This occurs because aspen fibers often do not sever cleanly. This is partly due to the presence of tension wood. Wengert (1976) also concluded, based on limited personal observation, that wetwood machines poorly in comparison to normal wood. Sanding aspen with fine grit sand paper increases the severity of the fuzziness. Wengert (1976) suggested using special abrasives, anti-fuzz sealer, or a wash coat of sizing prior to final sanding.

Gluability

Aspen is one of the easiest types of wood species to glue. It bonds well with a variety of wood adhesives under a wide range of bonding conditions (USDA 1999). Because aspen wood has good absorptive properties, rapid assembly is usually required to avoid glue-starved joints (Wengert et. al. 1985). Additional water is also needed with some water-based adhesives to prevent premature drying.

Preservative Treatment

Both the heartwood and sapwood of aspen have little natural decay resistance. Because of this, aspen wood must be treated prior to use in applications where conditions are favorable for decay. Generally, only the sapwood is readily treatable, and small diameter aspen logs comprised almost entirely of sapwood usually treat best (Wengert et. al. 1985). Aspen is generally considered a relatively refractory species because heartwood has low permeability. Wetwood also has low permeability. Because of this, Cooper (1976) found that it was difficult to get uniform preservative penetration using a pressure treatment. However, double diffusion treatments have proven to treat aspen to satisfactory levels. Puetmann and Schmidt (1997) were able to adequately treat aspen boards with water-soluble borate preservatives that were applied using traditional dip-diffusion methods.

Finishing

Aspen holds paint well and is one of the best hardwoods to paint. Fiest (1994) reported that aspen accepts finishing, including stains and paint, similar to softwoods such as fir, pine, hemlock, and spruce. Aspen also absorbs stains readily, although absorption can occur unevenly causing a “blotchy” appearance. Wengert et al. (1985) suggested using a sealer or wash coat before staining to alleviate this problem. Aspen accepts ink well and can be printed using the direct application of ink on the wood.

Weathering

Aspen is moderately resistant to weathering (USDA 1999). Aspen weathers to a light gray color. The weathered wood tends to have moderate sheen. Weathering checks are usually small and inconspicuous. Testing conducted by Fiest (1994) revealed that aspen weathering characteristics are comparable to those of softwoods such as ponderosa pine, fir, hemlock, and spruce. Generally, finished rough-sawn surfaces weathered better than finished smooth surfaces and two coats performed better than one. Acrylic latex paint gave the best protection after 10 years of service. Semitransparent oil-based stains and solid-color stains also performed well. Transparent stains provided the least protection against weathering. Long-term weathering tests conducted on finished aspen waferboard by Carll and Fiest (1989) showed that finished panels generally had good weathering resistance, although evidence of decay was present in over 20% of vertically exposed painted panels tested in Mississippi and Wisconsin after 7 years.

Wood Products

Sawn Products

Quaking aspen logs have been processed into boards, dimension lumber, and timbers at sawmills in Colorado and the Rocky Mountain Region. Although some aspen is manufactured into studs, most aspen lumber is used to produce secondary products. End uses include construction framing (studs), pallets, boxes and crates, paneling, mine timbers, furniture, toys, and lumber core. Significant amounts of aspen have been used to produce studs, pallets, paneling, and mine timbers in Colorado.

Because aspen has a low specific gravity and correspondingly low strength and stiffness, aspen studs are not suitable for many structural applications and are used primarily for light frame construction (Thompson 1972). In addition, aspen studs are difficult to dry defect free. This is because of the high ratio of radial to tangential shrinkage and the abundance of tension wood and wetwood found in aspen. As a result, aspen is not a preferred species for stud manufacturing.

Virtually all Colorado pallet manufacturers consider aspen to be a suitable raw material for building pallets (Mackes and Lynch 1997). Aspen can be used to manufacture both permanent reusable pallets and expendable one-trip pallets. No special nailing is required if aspen is used only for deckboards. However, even though the majority of Colorado manufacturers said they would use aspen to build pallets if available at competitive prices, aspen currently constitutes less than 1% of the 50 million board feet used to build pallets annually in Colorado (Mackes and Lynch 1997).

Aspen is utilized to produce paneling. Aspen paneling is typically ½-inch thick, 4 to 6 inches wide, and cut to random length. Green aspen boards of various grades are normally used. No wane or rot is allowed. The boards are dried, usually in a kiln. After drying, the wood must be resawn, planed, shaped, cut to length, and in some instances stained. Paneling is marketed nationally either stained or natural.

Another use for aspen paneling is in saunas (Koepke 1976). Aspen is used as a substitute for redwood. Aspen is desirable because it does not readily splinter, stain in the presence of sweat, or undergo significant dimensional change with variations in environment. It is also more economical than redwood.

Products used in mines, including cribbing, caps, and wedges, can be made from aspen lumber. These tend to be applications where bending and resiliency is desirable. Mines prefer dry wood, but may accept green low-grade material (Koepke 1976). This material can have discoloration, some rot, and large knots.

Veneer and Plywood

Two principal types of plywood are manufactured: hardwood and decorative plywood, and construction and industrial plywood (USDA 1999). Aspen can be used to make both types. Hardwood and decorative plywood must conform to American National Standard ANSI/HPVA-1-1994 (HPVA 1994). Construction and industrial plywood is covered in Product Standard PS-1-95 (NIST 1995). Under this standard, aspen is classified as a Group 4 species based on strength and stiffness. Although quaking aspen from the Rocky Mountain West is considered suitable for making plywood, no aspen from Colorado forests is currently used for this purpose.

In addition to plywood, other products can be produced from aspen veneer. These include containers, matchsticks, and chopsticks. Material for chopsticks, for example, must be completely free of defect and very white in color to be offered for sale in the Japanese market. In our research (unpublished) of aspen product potential, we found that this rigid demand for quality and the tremendous quantity of wood required to service this market made Colorado aspen an unlikely supply source. Nearly all chopsticks are made from Canadian aspen. Aspen veneer is also used to manufacture stamped veneer products, including tongue depressors, spoons, and ice cream sticks.

Troxell (1976) summarized characteristics that make aspen desirable for veneer products. Aspen wood has relatively low density, soft texture, good machining properties, and dimensional stability. It is easily glued, has a lack of characteristic odor, and has good appearance. Important factors limiting aspen use were also given. These included small average log size, relatively low veneer yield, relatively high harvesting and processing costs, and low strength properties compared to most other veneer species.

Particleboard

Numerous types of particleboard, having a wide range of properties, are produced for a variety of end uses identified in the *Wood Handbook* (USDA 1999). Particleboard can be used for furniture cores. It can also be used in flooring systems, manufactured housing, stair trends, and underlayment. Thin panels of particleboard can be used as a paneling substrate.

Aspen wood is an excellent raw material for manufacturing particleboard. Aspen can be mixed with softwoods and other hardwoods to make particleboard (Gertjejansen et al. 1973; Stayton et al. 1971). Because aspen particles are low in density and bond well at relatively low pressure, aspen is particularly well suited for making low density boards that are strong and durable. Aspen particleboard is also produced with sufficient density and working properties, including adequate smoothness, dimension stability, machinability, and screw-holding capacity, for use in furniture and cabinet manufacture. Another desirable characteristic of aspen is its light color that is aesthetically appealing for particleboard.

Oriented Strandboard

Oriented strandboard (OSB) is a structural composite board (flakeboard). OSB has gained acceptance as a substitute for plywood in sheathing, decking, and decorative applications. Flakes or strands forming the panel are bonded together parallel to the plane of the panel. The strands forming OSB are longer than they are wide and are oriented in alternate layers that are perpendicular to each other. Typical strand size is 4.5 to 6 inches long, 0.5 inches wide, and 0.023 to 0.027 inches thick (USDA 1999). This differs from waferboard where flakes are approximately as long as they are wide and have random orientation in the panel.

Aspen is a preferred species for producing OSB in the United States. Because of its relatively low density, waferboard and OSB produced from aspen wood has a high compression ratio (Geimer 1976). This results in high bending strength and low porosity. Other wood properties that make aspen desirable include absence of resinous extractives and straight grain (Wengert et. al. 1985).

Pulp Products

Aspen wood is easily pulped by all commercial processes (Perala and Carpenter 1985). With regards to fiber morphology, aspen has an excellent length-to-diameter ratio, and fiber wall thickness is characterized as thin to medium. Aspen pulp is used to produce book, newsprint, and fine printing papers. The highest quality groundwood pulps are produced from aspen. Aspen pulp is also well suited for enhancing the structure of fine papers produced from kraft and sulfite pulps. Chemimechanical pulps produced from aspen are used primarily for hardboards and fiberboards. Because aspen has a relatively low density, it is desirable for producing low- to medium-density fiberboards.

Although used extensively for pulp in the Lake States and Canada, practically no aspen from Colorado forests is pulped. Wengert (1976) concluded that aspen pulping technology used in the Lake States and Canada is generally applicable to aspen from the Rocky Mountain Region; therefore, the lack of technology and basic research should not be a barrier to pulping aspen from Colorado forests. Barriers are more likely the result of marketing, economic, and/or environmental factors.

Excelsior

Excelsior is composed of long curly strands of wood that have been mechanically shaved from dry blocks of aspen. Aspen is the preferred species used to manufacture excelsior products. Excelsior is used primarily in evaporative cooler pads, packaging, erosion control mats for reseeding along highways, archery targets, and decorative material. Aspen wood is desirable for excelsior because it is lightweight and easily processed. Good absorbency properties, lack of characteristic odor, and neutral color are also beneficial.

Posts and Poles

Aspen is not a preferred species for posts and poles. However, some aspen is utilized for these types of products, including corral poles. As noted previously, aspen has little natural decay resistance and must be treated for most exterior applications. Because the heartwood is difficult to treat, small-diameter logs comprised primarily of sapwood are most commonly treated.

Animal Bedding

Aspen is an excellent choice for animal bedding and litter for many household pets, with the exception of ferrets, and is considered superior to both pine and cedar products. Curiously, aspen bedding is not available in retail pet stores. Pine and cedar products have gained acceptance in these markets and currently dominate. Both pine and cedar emit aromatic hydrocarbons that tend to mask animal odors. Pine currently dominates the horse and turkey bedding markets as well, although some aspen and cottonwood is used to bed horses.

Aspen is the preferred wood for use as bedding and litter for small laboratory mammals. Aspen is preferred to cedar and pine bedding products commonly found in retail pet stores because of health considerations and the potential impact of these considerations on test results. The wood of cedar contains plicatic acid and pine contains abietic acid. Prolonged exposure to these aromatic hydrocarbons can contribute to respiratory diseases such as asthma and liver or kidney disease.

Once dried, aspen has no characteristic taste or odor even after subsequent exposure to moisture. In addition, the wood is relatively neutral in color. It is low in specific gravity (light) with good absorbency. Toxicology studies conducted on aspen products reveal that the wood is typically low in biological toxins (fungi, aerobic plate counts, and coliform). The wood is also normally absent of pesticides and low in heavy metals such as arsenic, lead, mercury, and cadmium.

Animal Food Supplements

Wood and bark from species of the genus Populus have been used as an animal feed. Baker (1976) estimated the digestibility of aspen wood by ruminants at 35%. If properly supplemented, aspen can effectively be the equivalent of medium-quality hay. As part of ongoing research being conducted at Colorado State University, the use of aspen bark as a food supplement for captive wild and domestic animals is being investigated (Irlbeck et al. 2000).

Fuel

Although aspen is used extensively for fuel in the Lake States, fuel use in the Rocky Mountain Region is relatively low due to the lack of industrial users. Fuel use in this region is limited primarily to a few wood processors and home fireplaces.

Aspen has a heating value of approximately 8,000 BTUs per bone-dry pound (Lowry 1976). Harder and Einspahr (1976) reported a heating value of 8,897 BTUs per pound for quaking aspen bark. Because aspen has a relatively low specific gravity (0.37) compared to denser eastern hardwoods, a greater volume of aspen is required to yield the same amount of heat. Because of its low natural decay resistance, storing large amounts of aspen in piles for extended periods of time can cause problems, including a reduction in the heating value of the wood.

Moisture content has a significant impact on recoverable heat from combustion (Ince 1979). Moisture in the wood evaporates and absorbs heat of combustion. As a result, green aspen wood does not burn well. Panshin et al. (1950) reported that 3,440 pounds of green aspen wood yielded 10.3 million BTUs compared to 2,160 pounds of air-dried wood that yielded 12.5 million BTUs. This emphasizes the benefits of properly seasoning aspen wood prior to combustion.

Tourist and Gift Items

At least three firms are manufacturing and marketing tourist and gift products made from Colorado aspen (Lynch and Mackes 2000). These products are usually handcrafted from the wood of standing dead aspen. They are typically turned, sawed, or left in the round. Products such as candleholders, artwork, boxes, turned vases or bowls, and jewelry are common items. Although aspen has good working properties, the main reason that aspen is the preferred wood for novelties is because it sells, and primarily for emotional reasons (Koepke 1976). People (primarily tourists) relate these products to the positive experience of visiting the Rocky Mountains.

Summary and Conclusion

Although widely distributed, quaking aspen continues to be an underutilized species in Colorado and the Rocky Mountain West. Aspen has relatively low density and correspondingly low strength and stiffness. As a result, aspen is not well suited for many structural applications. However, because aspen is lightweight and has adequate strength it is desirable for many applications. Combined with other characteristics such as straight grain, resistance to splintering, neutral color, lack of characteristic odor (nonresinous), and good processing characteristics, aspen is a preferred wood species for many products. These include paneling, veneer products, including matchsticks and chopsticks, waferboard and OSB, fiberboard, pulp, excelsior, pallets, research animal bedding, animal food supplements, and tourist or gift items.

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Summary: Aspen Decline in the West?

Dennis H. Knight[1]

No other tree in the Rocky Mountain region is more highly valued for its amenities than aspen (*Populus tremuloides*). In Colorado, New Mexico, Arizona, and southern Utah, aspen covers entire mountain slopes and plateaus, sometimes forming the landscape matrix in which other cover types occur as patches. Northward aspen occurs in patches (figure 1), forming small groves that can be thought of as a *keystone cover type*—one that has more significant effects on species diversity and ecological processes than would be expected considering the comparatively small amount of land area that it occupies.

Much appreciated by many for the color and habitat diversity that it provides, aspen also has a remarkable suite of adaptations. It is a deciduous tree that survives where evergreen conifers are far more common. Notably, aspen bark has chlorophyll that is capable of photosynthesis in the late fall and early spring, making it a rather novel *deciduous evergreen* tree. Another adaptation is its longevity. The literature commonly refers to aspen's short-lived shoots (the ramets), but the plant itself (the genet) could be thousands of years old because of root sprouting. Indeed, aspen may live longer than any other tree. Seedlings are rarely encountered over much of aspen's range, but only a few successful seedlings are necessary to maintain the populations of such long-lived plants. The rate of genet mortality seems very low.

The ecological characteristics of aspen and aspen forests have been the topic of numerous workshops and conferences. Norbert DeByle and Robert Winokur edited the most notable review. In this fine book, published in 1985 (*Aspen: Ecology and Management in the Western United States*; USFS General Technical Report RM-119), we have access to information on the paleobotany, genetics, physiology, and reproductive biology of aspen; the effects of climate, fire, insects, diseases, and herbivores on aspen forests; the various resources for which aspen is valued; and traditional management strategies.

But much has been learned in the interim. Scientists and managers now have new tools for their work, such as geographic information systems, and they have made better use of repeat photography, remote sensing, and dendrochronology. There also has been an influx of new ideas generated by landscape ecologists and conservation biologists. Moreover, global climate change is now thought by most of the scientific community to be inevitable if not already occurring; and some managers are worried about the decline of aspen, whether due to climate change, fire suppression, or too many elk. At our conference in Grand Junction, managers were urged to "take action now" and "take action often" to counteract the loss of aspen in some areas (Bartos, this proceedings; Campbell and Bartos, this proceedings; Bartos and Campbell 1998).

Threats to existing aspen forests, whether from timber harvesting, disease, heavy browsing, or natural succession, are viewed with alarm. However, it is important to take a long-term perspective on the kind of changes that have been observed. Aspen is a species that responds quickly to disturbances. Widespread disturbances caused by timber harvesting and fires in the late 1800s and early 1900s may have enabled aspen to become unusually abundant in the Rocky

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Figure 1—Two photos illustrating the patchy growth of aspen in some parts of the Rocky Mountains. (a) The Black Hills of South Dakota, where browsing by deer can be heavy. (b) The foothills of the Wind River Mountains near Pinedale, Wyoming; there are no fences protecting the aspen groves in this area.

Mountains during the last century. If aspen is now declining, the explanation may lie in natural processes that have caused similar declines in the past—one phase in a series of natural fluctuations. There is no basis to suggest that aspen is threatened globally, nor are most aspen groves likely to be lost in the near future.

Change in Rocky Mountain ecosystems certainly will occur because of human activity as well as other phenomena. To illustrate, recent research suggests that Utah juniper and ponderosa pine have occurred on the land area known as Wyoming for less than 2,000 years (Stephen T. Jackson, personal communication). Both are expanding their distribution, probably due to the kinds of climatic changes that have characterized the Earth for millennia. Considering their probable longevity, individual aspen clones surely have survived many episodes of climate change.

The effect of climate change on aspen can be manifested in various ways. For example, the populations of large herbivores such as elk may have increased due to less winter mortality during periods of mild climate. Browsing on aspen twigs and bark would undoubtedly increase during such times, and the number of aspen saplings might have declined. Alternatively, if longer dry periods accompany such episodes, then fires could have been more common. More frequent fires would enable the aspen to become more abundant, at least in areas that are some distance from winter ranges where browsing would be intensive. Papers presented at the Grand Junction conference suggested that distance from high concentrations of elk is correlated with the growth of aspen saplings into trees (for example, Barnett et al.; Kaye et al., this proceedings).

A second example that illustrates the effects of climate pertains to seedling establishment. In Arizona, successful aspen establishment is more likely to occur following fire if the annual postfire precipitation is above average for several years (Moore, this proceedings; Romme, this proceedings). Drought, in contrast, could prevent seedling establishment. As important, drought could diminish the abundance of root sprouts after a disturbance, possibly because of a higher susceptibility to insects and pathogens during droughts (Jacobi, this proceedings).

In contrast to climate, the succession of aspen forests to coniferous forests can be altered through management. Aspen groves have been invigorated using prescribed burning, clearcutting, and the selective cutting of invading conifers, largely because of root sprouting. Some managers would pursue such options more widely for sustaining aspen forests and providing a source of wood (Bartos and Campbell 1998; Mackes and Lynch, this proceedings). This kind of active management is opposed by those who feel the rate of harvesting has been excessive on some national forests, that no additional roads should be constructed, and that the invasion of aspen by conifers is a natural process that very likely will be reversed by fires and other disturbances in the future.

In resolving this debate, it is important to recognize that aspen is a widespread species and that a decline in the cover of aspen forests has been documented only in a few areas, such as in parts of Utah and adjacent to some national parks (Kay, this proceedings; Smith, this proceedings; Weisberg and Coughenour, this proceedings). Also, while some aspen forests are seral to conifers (figure 2), others are self-perpetuating stands. The abundance of aspen forests in a landscape should be considered as well. In some areas, aspen is so rare that it might be classified as a sensitive species. Maintaining the species and its associates through active management could be the logical alternative, especially if the stands are seral in nature. Elsewhere, aspen may be so common that having

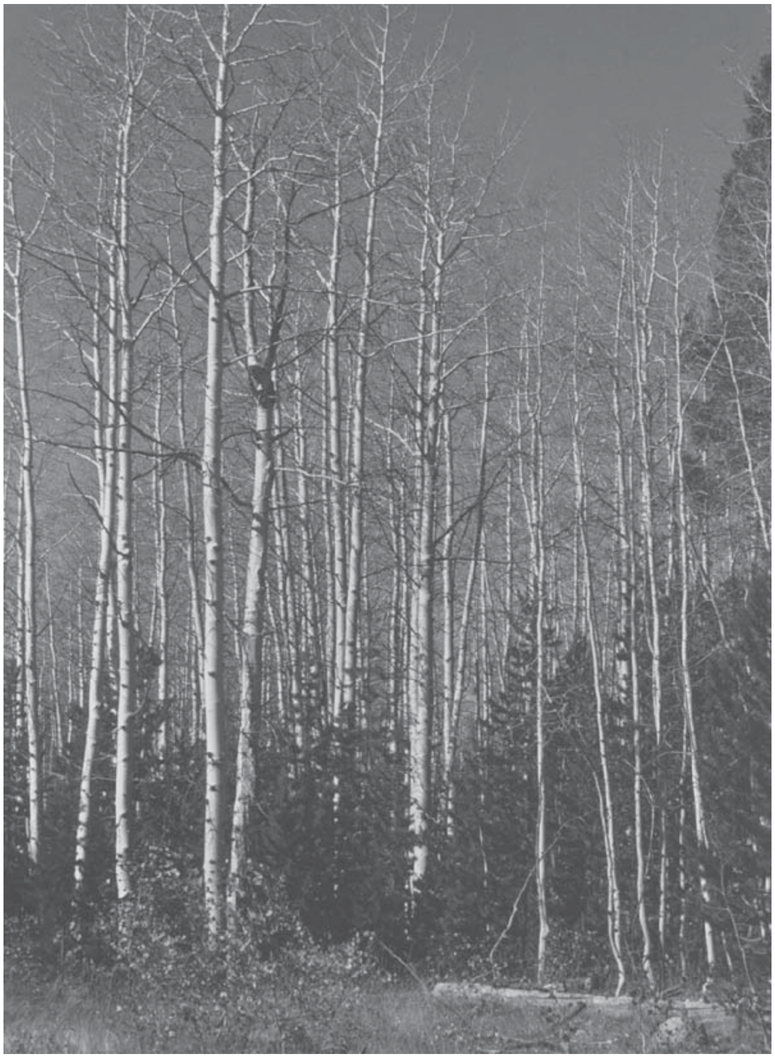

Figure 2—An aspen grove in the Sierra Madre, Wyoming, with an understory of lodgepole pine (*Pinus contorta*). Aspen may be seral to other conifers as well, but aspen forests in some areas are self-perpetuating and have no conifers (Mueggler 1985).

a portion of the forests change to conifers would not have significant effects for most people—ecologically or aesthetically.

As important, managers should consider the prevailing sentiment with regard to the interested public's desire for the future condition of the landscapes in which aspen occurs. The building of additional roads is now a big issue. Will new roads be required to sustain aspen in specific areas through the harvesting of conifers, or to better control prescribed fires? Similarly, will the shooting of elk in national parks be required to reduce browsing pressure? Will the number of domestic livestock have to be reduced in the vicinity of aspen groves? If the answers to such questions are affirmative, then the arguments for active management in each case must be convincing and site specific. Extrapolations from other areas will not be adequate.

Therein lies the controversy. Some groups simply want aspen forests that are green in the summer and yellow in the fall, preferably with a minimum of "wasted wood" in the form of dead trees and coarse woody debris. For them, fires should be suppressed, partly to protect the second homes that are located adjacent to federal lands (the presence of such structures greatly complicates forest management activities). Others place high value on roadless areas,

Figure 3—Aspen grove affected severely by elk browsing near Yellowstone National Park. Small root sprouts can be found among the dying ramets, indicating that the genet is not dead. However, the habitat provided by a stand of mature ramets (aspen trees) is no longer available. Placing a fence around this clone probably would allow the restoration of this stand.

dispersed recreation, rare species, and the biodiversity that can be sustained in wildlands. Such amenities have become so uncommon during the last 50 years that they are now considered scarce resources.

Notably, roadless areas already have been influenced by management activities such as fire suppression and changes in the natural fluctuations of large herbivore populations. This is just another expression of what Garrett Hardin has termed the first law of ecology—we can never do merely one thing. Actions taken on a specific area will affect adjacent areas. Similarly, if fires are suppressed, conifers will continue to overtop the aspen in some areas. And, with more evergreen conifers growing where the deciduous aspen once occurred, there will almost certainly be less streamflow because transpiration from the conifers occurs for a longer period each year. Fewer fires may not be simply the result of extinguishing lightning- or human-cause ignitions, when we are able, but also the result of fuel load reductions, such as through livestock grazing.

And if the abundance of carnivores such as wolves and cougars are reduced, then elk populations could increase, or move less frequently from one place to another, with the effect that there is more browsing on aspen. This in turn could cause more disease because of wounds to the bark. Supporting this hypothesis, Larsen and Ripple (this proceedings) concluded that aspen seedling establishment became less frequent at about the time when wolves were removed from Yellowstone National Park. The interactions are further complicated with timber harvesting. When wood is removed, there surely will be fewer downed trees, thereby providing less-dense patches of tangled timber where aspen are protected from browsing long enough to enable growth into new trees. As in other kinds of forest, the removal of timber creates an ecosystem that is different from one that burns (where most of the large wood remains after the disturbance event).

Natural fluctuations in ecosystem variables such as downed wood and aspen abundance are natural and important, yet it is human nature to look for consistency from one year to the next. A striking example is the desire to have a consistently high number of elk hunting permits year after year. This is accomplished in some areas by feeding elk in the winter, routinely or only during harsh winters, and making determinations on the number of elk that can be harvested each fall. The result can be unusually long periods of continuously high levels of browsing that prevent the growth of aspen saplings into trees (DeByle 1979; figure 3).

Fortunately, aspen continues to persist in the western states. It may be declining in some areas, possibly for reasons related to human activity. Alternatively, climatic changes beyond human control may be the cause. Aspen is still very abundant over much of its range and it could rebound in the future where it is now becoming less common. The interactions affecting the dynamics of aspen are worthy of continued investigation. Much has been learned since the 1985 review edited by DeByle and Winokur, but additional, spatially explicit information is required on the history and causes of episodes of recruitment and mortality for both aspen genets and ramets in specific areas. Many will be interested in the results.

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Poster Abstracts

100 Years of Landscape Change in the North Fork of the Gunnison River Valley, Colorado

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Vegetative changes on western landscapes continue to be questioned, discussed, and debated. The author researched historic writings describing presettlement explorations, surveys, and studies to determine vegetative conditions at the time of American settlement. Research included rephotographing 46 landscape photographs taken from 1887 to 1916. Results indicated (1) most vegetative changes have occurred in and around the towns and settlements; (2) sagebrush grasslands have been extensively modified by intensive agriculture; and (3) widespread increases in woody vegetation. These include increases in pinyon/juniper woodlands; increases in the mountain shrub communities; and three distinct trends in the aspen forests: (a) most aspen are older, mature, and becoming decadent, (b) some aspen have increased into meadows and parks, (c) conifers have invaded some aspen stands that existed 100 years ago, and (d) subalpine conifer forests are bigger, older, and healthier.

Aspen Regeneration in the Book Cliffs

Sarah Benanti, Helga Van Miegroet, and Fred Baker, Forest Resources Department, Utah State University, Logan, UT

In the Book Cliffs of eastern Utah, the Bureau of Land Management noticed that Douglas-fir appear to be increasing in abundance at the expense of quaking aspen in the Douglas-fir/aspen ecosystem. The purpose of this study is to assess the vigor of the aspen stands. In order to do this, the Douglas-fir/aspen ecosystem, a 30 mile x 2 mile (46 km x 3 km) study area, was divided into three sections. Eighty-six stands larger than 0.1 ha were delineated on topographic maps. For each stand selected, a transect was established that bisects its long axis. Sample points, representing plot centers, were then placed at 40 m intervals along the transect and GPS referenced, allowing for a 20 m buffer from the edge of the stand. Twenty-six stands were sampled with a grand total of 157 plots. Each sample stand was rated for vigor as follows: (1) vigorous, pure aspen; (2) declining, pure aspen; (3) declining aspen with Douglas-fir in the understory; (4) declining aspen with Douglas-fir in the overstory; and (5) predominantly Douglas-fir with declining aspen. No stands were found in the first category, 73 stands were found in the second category, 55 were found in the third category, 14 stands were found in the fourth category, and 15 stands were found in the fifth category. Most of the aspen stands need to be rejuvenated, but the animal pressure needs to be considered before anything is done—otherwise all of the aspen suckers will be eaten.

Genetic Variation Among Isolated Populations of Quaking Aspen: Implications for Species Conservation and Management

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In the Blue Mountains of eastern Oregon, aspen stands representing the western fringe of the species range are in rapid decline and at risk of extirpation. We investigated the genetic structure of these stands to develop recommendations for the management and conservation of aspen genetic resources. We also were interested in using genetic information to make inferences about the historical distribution of aspen in this area. Forty-five stands were analyzed for isozyme variation at 18 loci. Overall, we found relatively high levels of allozyme variation, with 72% of the loci polymorphic and an average of 2.4 alleles per locus. Individual stands were much less variable, with 24% of the loci polymorphic, and an average of 1.3 alleles per locus. About half (47%) of the stands appeared to be single clones, while only a few contained more than 10 clones, indicating that sexual reproduction has played a minor role in aspen regeneration. We also found genetic evidence that one or more geographically disjunct clones may well have been part of a large contiguous stand in historical times. The level of genetic differentiation among stands was very high, which has several implications for conservation and ecological restoration efforts. Most importantly, we have allocated our limited resources to locate and protect as many relict stands as possible, rather than trying to conserve all the clones within the larger stands. We discussed additional applications of these results to the conservation and management of aspen in the Blue Mountains, including the development of plant materials for artificial regeneration, and silvicultural methods to enhance stand regeneration.

Restoring Fire Process and Function at the Site and Landscape Scale

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The Powell Ranger District, Dixie National Forest (R4), completed a landscape scale vegetation analysis for the Sevier Plateau. The focus of this 310,000 acre assessment, including multiple land ownership, was to determine vegetation changes that had occurred over the past 100–150 years as a result of management practices and the exclusion of fire. The assessment looked at ecosystem processes of disturbance pattern, structure, and composition to determine if this landscape is functioning and that vegetation patterns are sustainable. The findings of the interdisciplinary team assessment showed that many vegetation types on the Sevier Plateau were being impacted by successional change, which was placing many of these types at risk due to insect, disease, and wildfire potential. It was noted that the aspen ecosystem had been modified to the point that as much as 60% of the landscape had changed from aspen dominance to late seral conifer dominance. The outcome of this assessment was a proposal to reintroduce disturbance patterns into the landscape through the use of prescribed fire and wildfire for resource benefit (PNF). The plan was intended to treat many of the vegetation types to create change over the entire landscape rather than just focusing on a small portion of the Plateau. The first project to be implemented was the Jones Corral Vegetation Project encompassing 26,000 acres of the assessment area. Approximately 6,000 acres were targeted for burning. In June 1997, approximately 1,000 acres of aspen-conifer, in patch sizes from ¼ acre to 150 acres in size, were prescribe burned in a stand replacement treatment to initiate new aspen regeneration. During a 1998 monitoring visit to the treatment area, it was determined that as many as 150,000 aspen suckers per acre had regenerated with growth of the dominant suckers reaching 3 feet in height. During a 1999 visit, growth of the dominant suckers was approaching 6 feet. Additional burning was completed in 1999 (currently totaling 15,000 acres across the Plateau). Additional planning efforts are ongoing to implement additional treatments over the next decade.

Production and Total Root Carbon Allocation for Single-Storied and Multi-Storied Aspen Stands in Southern Wyoming

Paula J. Fornwalt, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO; and Skip Smith, Department of Forest Sciences, Colorado State University, Fort Collins, CO

We compared aboveground net primary production (ANPP) and total root carbon allocation (TRCA) of vigorous, single-storied aspen stands to that of mature, multi-storied stands to address the issue of long-term aspen stand stability in the central Rocky Mountains. We also examined differences in leaf area efficiency (LAI) and growth efficiency (E_{ANPP}) between the two stand structures.

The single-storied sites were young and even-aged, with a mean age of 19 years. Tree heights, diameters, and ages were normally distributed. The multi-storied sites were uneven-aged, with tree ages ranging from 23–146 years; the stands exhibited negative exponential, or "inverse-j" shaped age, diameter, and height distributions. Total ANPP at the single-storied sites was approximately half of the total ANPP at the multi-storied sites (112 g C m^{-2} y^{-1} and 240 g C m^{-2} y^{-1}, respectively). Stemwood and foliage production at the single-storied sites were also only half of that at the multi-storied sites. The single-storied sites produced 44 g C m^{-2} y^{-1} of stemwood and 59 g C m^{-2} y^{-1} of foliage, while the multi-storied sites produced 113 g C m^{-2} y^{-1} of stemwood and 117 g C m^{-2} y^{-1} of foliage. LAI was 1.0 at the single-storied sites and 2.0 at the multi-storied sites. E_{ANPP} for the two stand structures did not differ ($p = 0.47$); E_{ANPP} was 111 g C per m^2 of leaf area (LA) at the single-storied aspen sites, and 120 g C per m^2 LA at the multi-storied sites. Soil respiration was significantly higher at the multi-storied sites than at the single-storied sites for all months that it was measured. Growing-season soil respiration was 400 g C m^{-2} at the single-storied sites and 561 g C m^{-2} at the multi-storied sites ($p = 0.03$). When the estimated below-snow values were added, annual soil respiration was 502 g C m^{-2} at the single-storied sites and 664 g C m^{-2} at the multi-storied sites ($p = 0.03$). TRCA was also higher at the multi-storied sites, although the difference was not significant. The single-storied sites allocated 394 g C m^{-2} to the roots, while multi-storied sites allocated 500 g C m^{-2} ($p = 0.14$).

Results from this study do not provide any evidence of lowered productivity at the older, multi-storied sites. These findings shed a positive light on the possibility of long-term persistence of Rocky Mountain aspen stands growing in a multi-storied stand structure.

Environmental Influences on Aspen Regeneration Failure

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Seven study sites were established on the San Juan, Grand Mesa, Uncompahgre, and Gunnison National Forests and State lands near the Routt National Forest to determine what environmental conditions predisposed aspen sprouts to infection by two canker-causing fungi (*Cytospora chrysosperma* and *Dothiora polyspora*). Each site was located where >95% aspen sprout mortality occurred in 1983, 1987, or 1990 and consisted of whole stands or portions of stands that ranged from two to 10 acres. At each site, a plot with >95% sprout mortality was paired with a plot within the stand or within 2 miles where at least 50% of the sprouts survived. Measurements of past meteorological conditions, current soil conditions, soil hydrologic factors, and current and previous stand conditions were taken during the summers of 1990 to 1993. Two scenarios explain the aspen regeneration failure at the seven study sites: (1) On "wet" sites, excess soil moisture (resulting from deep and late spring snowpacks on poorly drained soils) predisposed aspen trees to infection by canker pathogens. Root mortality from soil flooding and drought in mid summer may have caused drought stress. (2) On dry sites, drought conditions from low spring snowpacks and reduced summer precipitation on soils with poor water-holding capacity predisposed aspen trees to infection by canker pathogens. In addition, shallow rooting induced by a high water table appears to be related to potential drought on dry sites.

Predicting where mortality will occur is difficult because previous stand characteristics were not different between areas with or without sprout mortality. Soil differences were specific to a site and thus the soil conditions were not similar on all sites. Predicting when mortality will occur may be feasible with additional research that relates sprout health to the amount of water in spring snowpacks, summer precipitation, and Palmer Drought Index data. Failure of aspen regeneration will probably continue to occur. Based on 8 to 60 years of meteorological data, deep May snowpacks occur about 26% of the years at the study sites and shallow snowpacks occur 8% of the years.

Influences on Regional Timing of Aspen Regeneration in the Colorado Front Range

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Regional patterns in quaking aspen establishment can be influenced by a variety of factors, including climate, human land-use, and forest dynamics. We looked at the timing and frequency of aspen regeneration between 1860 and 1990 in Rocky Mountain National Park and the Roosevelt National Forest in the Front Range of Colorado. We related spatial and temporal patterns of aspen regeneration with regional climate and grazing history. A drought severity index was used to represent regional climate. Historical elk populations for the National Park and cattle populations for the National Forest were used to reconstruct grazing intensity. We found that climate explained approximately 30% of the variance ($p < 0.05$) of aspen establishment at high elevations in the elk summer range and in Rocky Mountain National Park. We found that aspen regeneration was consistently higher in the elk summer range than in the winter range and that regeneration was more frequent in Rocky Mountain National Park between 1900 and 1970 than in the Roosevelt National Forest. In the 1970s and 1980s aspen regeneration was more frequent in the National Forest. We conclude that in the absence of grazing pressure, climate has an influence on aspen regeneration. However, when grazing is present, it plays a dominant role in influencing aspen regeneration.

Effects of Prescribed Fire on Aspen Within a Mixed Ponderosa Pine/White Fir Forest at Grand Canyon National Park

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Grand Canyon National Park's fire effects monitoring program collects data throughout the Park before and after prescribed fire. As part of this program, the Park's forests have been divided into several types, each of which has relatively homogeneous vegetation and can be burned similarly throughout. One of the types found on the north rim of the canyon is composed of ponderosa pine mixed with white fir and, often, with aspen. The primary objectives of prescribed fire in this type are to reduce fuel loads, to reduce white fir pole density, and to maintain large ponderosa pine. We are interested in determining whether the fire prescription currently used to meet these objectives will also maintain aspen as a component within these stands. From 1993 to 1998, we collected data on overstory, pole, and seedling/sucker density for all species in 0.1 hectare rectangular plots. Because not all plots contained aspen, data are somewhat limited, but currently, we have data from 5 years postburn on two plots, 2 years postburn on four plots and 1 year postburn on six plots. These earliest results suggest that competition from white fir seedlings may limit aspen regeneration.

Aspen Regeneration Following Two Episodes of Wildland Fire on Shadow Mountain, Wyoming

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The regenerative response of aspen was monitored following two spatially overlapping wildland fire events on Shadow Mountain, Wyoming. The two fires occurred 6 years apart. The fires left a landscape mosaic of unburned, once-burned, and twice-burned aspen stands ranging in size from approximately 1.0 to 12.0 hectares. Aspen suckering in burned areas was significantly greater than that observed in unburned areas. Less regeneration occurred on plots that burned for a second time than on those which burned only once; however, by the second year postfire, sucker numbers on the reburned plots were not significantly lower than on the plots that burned only once. Self-thinning of suckers observed on the plots that burned only in the first fire suggests that sucker numbers on once-burned and twice-burned plots will converge over a 6- to 10-year period. Sucker numbers on burned plots appear sufficient for stand replacement, while those on unburned plots are very low, consistent with seral aspen stands that, in the absence of disturbance, may be subject to significant conifer encroachment or replacement.

Old Aspen Trees in Colorado

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In 1999, seven mixed-species stands composed of aspen, Engelmann spruce, and subalpine fir were sampled to determine establishment patterns, height growth rates, and shifts in dominance. Five out of the seven stands sampled contained aspen trees at least 220 years of age, including five trees over 250 years old and one tree that was at least 276 years old. The site of this oldest known aspen tree occurs on a northern aspect at 2,830 meters elevation on the Paonia Ranger District, Gunnison National Forest. Before this study, the oldest aspen tree recorded was 249 years of age (Abolt, R.A.P. 1997. Fire histories of upper elevation forests in the Gila Wilderness, New Mexico via fire scar and stand age structure analyses. M.S. thesis, The University of Arizona, Tucson. 120pp.).

Classification of Vegetation and Fuels in Aspen Communities in the Area of Los Alamos, New Mexico

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As part of an ongoing vegetative community classification/fuel hazard estimation project in and around Los Alamos National Laboratory, several aspen communities were sampled. Some differences in understory community structure were found, and the various communities did not always fit into current classification systems. Evaluation of fuel loads within these communities were lower than adjacent spruce/fir communities. The lower canopy density, with the resultant increase in understory vegetation, along with a reduction in ladder fuels when compared to spruce/fir forests, confirm that these communities could act as firebreaks if wildfires were to ignite in this area.

Modeling Understory Light in Young Trembling Aspen Stands

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The purpose of this study was to calibrate and validate the MIXLIGHT forest light model for use in immature aspen stands in boreal mixed wood forest of Alberta. This will allow the prediction of understory light regimes for stands of a range of height and density. Individual aspen tree characteristics needed to calibrate the light model include: leaf area, crown radius, crown length, height, diameter, and crown class. These were measured along with stand level attributes such as basal area, leaf area index, and stem density in 96 plots within relatively pure aspen stands ranging in age from 2 to 30 years old. Actual understory light as a percentage of above canopy light was also measured instantaneously in 17 separate plots during either overcast or clear sky conditions in order to validate the light model. Individual tree crown characteristics, such as leaf area, leaf area density, crown radius, and crown length, were best predicted by exponential functions of diameter at 30 cm; R^2 ranging from 0.59–0.69 for intermediate trees and from 0.78–0.87 for canopy trees. Including a measure of intraspecific competition, such as density or basal area, or using crown characteristics as a proportion of total tree height did not improve the prediction. Horizontal crown overlap was estimated for stands of various heights and was found to decline with increasing height. The validation of MIXLIGHT and subsequent prediction of light in young aspen stands of differing height and density is ongoing.

Status of Aspen and Manipulation of Stands in the Sierra Nevada of California

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Few studies have been conducted on the status of aspen in the Sierra Nevada in contrast to the Rocky Mountains and Intermountain West. There is a paucity of landscape-scale condition information and accurate vegetation classification of the aspen community type in the Sierra bioregion. We conducted aspen stand condition inventories on three National Forests across the Sierra Nevada to get an indication of the status of aspen. Our results indicate that the majority of aspen stands in the three forests are subject to the same factors implicated in the decline of aspen in the Rocky Mountains and Intermountain West. We also examined pretreatment and posttreatment conditions in stands manipulated for aspen restoration. Stands manipulated with conifer removal or prescribed fire treatments appeared to largely achieve restoration objectives with some exceptions. We speculate that moisture regime and uncontrolled livestock browsing were the factors that most influenced the failure to meet regeneration objectives. We recommend a Sierran-wide aspen condition inventory, development of an accurate vegetation classification map, and controlled research studies on treatment options in the Sierra if the ecological restoration of this community type in the Sierra Nevada is to be successful.

Population Biology of Aspen (*Populus tremula*)

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Approximately 30,000 mature aspens (d.b.h. >15 cm) as well as dead standing trunks and logs have been spatially mapped in an area of over 100 km^2, including both virgin areas with large amounts of aspen and ordinary managed forests, in east-central Finland (northern Europe). Trees with d.b.h. <15 cm, as well as small saplings, will be mapped on sample plots within the area in 2000–2001. Experiments will also be set up to study the establishment of root suckers in canopy gaps, browsing by moose, and minimum gap size for successful vegetative recruitment. The temporal and spatial dynamics of dead aspen in different decay classes will also be included in the analysis.

I will work at two hierarchical levels. At the individual tree and stand levels, key questions are reproductive biology and seed dispersal and regeneration in old-growth forests without large-scale disturbances. At the landscape level, the focus is on the clonal structure, dynamics, and spatial aggregation of mature aspen populations in managed and virgin forests.

A Remotely Sensed Aspen Deterioration Classification for the Study and Management of Quaking Aspen in the Intermountain West

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It has been shown that quaking aspen is quickly disappearing in the Intermountain West, thus altering the structure, function, and composition of the landscape into the foreseeable future. Before management action can be taken to restore the presence of this keystone species, cross-scale knowledge of the distribution and health of aspen clones must be obtained. Drawing upon a recently developed, field-tested aspen stand deterioration classification, a remotely sensed aspen deterioration classification is proposed. Five deterioration classes have been defined in a Douglas-fir/aspen ecosystem in the Book Cliffs of eastern Utah, and these will be correlated to LANDSAT-TM imagery to generate a supervised classification. This remotely sensed classification will be tested using other vegetation patches in the study area and may with equal ease be applied and tested in similar landscapes across the Intermountain West. After integration into a GIS, the classification will provide valuable information on the spatial distribution and health of aspen stands, environmental variables regulating aspen presence, and other information for the development of future silvicultural prescriptions.

Landscape Scale Restoration of Aspen and Mountain Brush Communities in Northern Utah

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Historically, periodic disturbances such as wildfire and windthrow played an important role in the vigor of aspen and mountain brush communities, contributing to a diversity of stand ages and structure. Cultural land management practices such as fire suppression and domestic livestock grazing introduced by Europeans since the late 1800s have translated into increasingly homogeneous landscapes, reduced biodiversity, and landscapes dominated by catastrophic disturbance. The change in forest structure and composition has caused a decline in ecological health in aspen and mountain brush communities. A long-term, landscape-scale aspen and mountain brush treatment project initiated on the Wasatch-Cache National Forest in northern Utah serves to target those aspen and mountain brush communities across a two district area that are approaching late successional stages due to a lack of natural disturbances. Disturbance was reintroduced in the form of prescribed fire to encourage the restoration of composition, structure, and function by allowing for periodic disturbance. Additional objectives of the treatment applications were to reduce hazardous natural fuels, increase biodiversity, increase the number of wildlife species (specifically big game, nongame, and upland game), maintain the long-term habitat stability at the landscape level, and increase the resistance of the landscape to insects and disease. Permanent monitoring plots were installed in all three areas. Monitoring will allow for adaptive management by reviewing effectiveness and applying appropriate variations to future applications. Monitoring variables include target species' regeneration success measured by species and number of stems, increase in species diversity, change in stand structure and composition, and change in fuel loading. Data collected will also provide for the development of custom fuel models for aspen-dominated stands. Future analysis will seek to validate these models.

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RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

Research Locations

Flagstaff, Arizona
Fort Collins, Colorado*
Boise, Idaho
Moscow, Idaho
Bozeman, Montana
Missoula, Montana
Lincoln, Nebraska
Reno, Nevada
Albuquerque, New Mexico
Rapid City, South Dakota
Logan, Utah
Ogden, Utah
Provo, Utah
Laramie, Wyoming

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