

VEGETATION ASSOCIATIONS

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Aspen trees grow along moist stream bottoms as well as on dry ridges and southerly exposures, on talus slopes, and on shallow to deep soils of varied origins. Quaking aspen is one of the few plant species that can grow in all mountain vegetational zones from the alpine to the basal plain (Daubenmire 1943). As a consequence, aspen dominated communities are found intermixed with such divergent vegetation as semiarid shrublands and wet spruce-fir forests.

The broad latitudinal and environmental range of aspen (discussed in the DISTRIBUTION chapter) brings it into association with a diversity of other plant species. Consequently, understory composition varies from place to place and reflects both regional floristics and adjacent vegetation types.

A characteristic element among aspen communities in the West is the luxuriant undergrowth that it supports compared to that in adjacent coniferous forests. This undergrowth frequently consists of three layers: tall shrubs, medium shrubs/tall herbs, and low herbs. Forbs generally dominate the herb component; but occasionally, grasses and sedges are equally abundant.

The complexity and diversity of aspen-dominated communities are compounded by the occurrence of aspen as a dominant seral as well as climax tree. The proportion and even presence of many understory species changes drastically as the climax trees (usually conifers in the West) regain dominance and alter the microenvironment and competitive relationships.

There have been only a few, geographically narrow attempts to classify aspen communities into recognizable associations based upon floristics and/or environment. Although interest in classifying aspen communities is increasing (Hoffman and Alexander 1980,

Mueggler and Campbell 1982, Severson and Thilenius 1976, Youngblood and Mueggler 1981), descriptions of community composition are too incomplete to permit reliable categorization of aspen associations throughout the West or even on a regional basis.

Seral Versus Stable Aspen Communities

Aspen generally has been regarded as a fire-induced successional species able to dominate a site until it is replaced by less fire-enduring but more shade tolerant and environmentally adapted conifers. (The role of fire in aspen succession is discussed in the FIRE chapter.)

The successional status of much western aspen land is evidenced by aspen's relatively rapid replacement by conifers within a single aspen generation (fig. 1). This is a major concern to many resource managers who anticipate the loss of multiple resource values (grazing, wildlife habitat, water production) accompanying such type conversion. In many areas, however, conifer invasion can be so slow that more than 1,000 years without fire may be required for aspen stands to progress to a conifer climax.

Recent studies suggest that although the majority of aspen forests may be seral to other types of vegetation, climax aspen communities occur throughout the West. Lynch (1955) described stable aspen groves in northern Montana; aspen appears to be a climax dominant in parts of western Wyoming (Beetle 1974, Reed 1971, Youngblood and Mueggler 1981), southern Wyoming (Wirsing and Alexander, 1975), eastern Idaho (Mueggler and Campbell 1982), and in parts of northern Utah (Henderson et al. 1977); both Hoffman and Alexander (1980) and Langenheim (1962) concluded that many of the aspen forests in central and northern Colorado are stable; and Severson and Thilenius (1976) found stable aspen communities in the Black Hills of North Dakota.

The uneven age distribution of aspen trees in some stands (fig. 2) indicates that aspen can be self-perpetuating without necessarily requiring a major rejuvenating disturbance such as fire. Whether such stands qualify as "climax" is unclear. An uneven-aged structure of the aspen overstory, lack of evidence of successional change in the understory, and absence of invasion by trees more shade tolerant than aspen are indicators of community stability. Such relatively stable stands that are able to persist for several centuries without appreciable change should be considered at least *de facto* climax, and should be managed as stable vegetation types.



Figure 1.—A seral aspen community in northern Utah rapidly being replaced by Engelmann spruce and subalpine fir climax forest.

The environmental conditions which differentiate stable and seral aspen communities have not been determined. Harper¹ found that seral aspen stands were not consistently associated with soil parent material. Instead, they appeared to be associated with sandstone soils on the Wasatch Plateau of central Utah, with basaltic soils on the Aquarius Plateau, and with granitic soils in the LaSal Mountains of south-central and southeastern Utah. Aspen tends to form relatively stable communities at mid-elevations and on southerly exposures; at high elevations and on northerly exposures, it usually is seral to conifers. However, these relationships have not been verified.

The most valid indicator of a seral aspen situation appears to be incipient or actual prominence of conifers, which suggests active replacement of the aspen overstory by more shade tolerant trees. Conifers, however, must be prominent, not merely present. Occasional conifers can be found in a basically stable aspen community because of highly unusual and temporary conditions which favored their establishment. In such cases, a stable aspen community might contain a few scattered conifers but lack subsequent conifer reproduction, even though a seed source is present. An uneven-aged conifer understory generally is reliable evidence of a seral aspen site.

Seral aspen communities in the West usually change eventually to forests dominated by coniferous trees if plant succession is permitted to progress without disturbance. Conifers such as *Picea engelmannii*, *P. pungens*, *Abies lasiocarpa*, *A. concolor*, *Pinus contorta*, *P. ponderosa*, and *Pseudotsuga menziesii* form an increasing part of the tree canopy as succession progresses.

Sometimes, however, aspen communities are replaced by grasslands and shrublands (fig. 3). This usually occurs where aspen fails to regenerate on sites not suited for the establishment and growth of conifers. Regeneration can fail when apical dominance prevents suckering

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Figure 2.—A stable, uneven-aged aspen community in northern Utah.



Figure 3.—A degenerating aspen community in southern Montana being replaced by mountain grassland vegetation.

during gradual deterioration of the clones (Schier 1975a) (see the VEGETATIVE REGENERATION chapter). Regeneration also can fail because of animal use. Where suckering does occur in a decadent clone, continued heavy browsing by wildlife or livestock can prevent suckers from developing into trees and cause a gradual conversion to grasslands or shrublands. (See the ANIMAL IMPACTS chapter.)

Community Structure

All aspen communities are multilayered. Sufficient light is able to penetrate the canopy to support abundant undergrowth, in contrast to the general paucity of herbs and shrubs in adjacent coniferous forests.

Most aspen stands are even-aged because of the rapid reproduction by suckering after major disturbance. Uneven-aged stands are likely to form under stable aspen conditions where the overstory gradually disintegrates with disease or age and is replaced by suckers. Uneven-aged stands also occur where individual clones gradually expand into adjacent grasslands or shrublands. At maturity (80 to 100 years) tree heights range from roughly 30 to 100 feet (10 m to 30 m), depending upon site and clonal genotype. A tall shrub stratum sometimes grows beneath this tree canopy layer. Where present, tall shrubs form a very open and intermittent layer from 6 to 12 feet (2 m to 4 m) in height. Medium height shrubs and tall herbs frequently form a rather continuous layer at about 3 feet (1 m). An even lower layer of herbs is always part of the understory. Although scattered mosses and lichens may be on the forest floor, they seldom form a conspicuous layer. Some aspen communities in the West consist of only a tree layer and a low herbaceous layer of forbs and/or graminoids; more commonly, however, a medium shrub and/or tall herb layer also is present.

In seral aspen stands, the tree canopy usually consists almost exclusively of aspen for 50 to 150 years, un-

til the slower growing conifers are able to penetrate the aspen canopy. As the conifer layer thickens, less light penetrates to lower levels of vegetation, competitive relationships are altered, and the understory shrubs and herbs progressively decrease in abundance until few remain.

A tall shrub undergrowth component can be found associated with aspen along the Rocky Mountains and high plateaus from Canada to Mexico. Species of *Prunus* and *Amelanchier* frequently are major constituents of this layer throughout the range of aspen in the West. Other genera, such as *Acer*, *Quercus*, and *Corylus*, however, are more restricted geographically. Usually the shrubs are scattered and do not form a well-defined layer. Occasionally, however, these tall shrubs are so abundant that they impede movement of livestock and humans through the stands. The environmental controls on the tall shrub component are uncertain; but, for whatever reasons, this layer appears to frequent aspen communities more on southerly than on northerly exposures, and more at lower than at upper elevations.

Most aspen stands contain an undergrowth layer consisting of a mixture of medium-high shrubs and tall herbs. A variety of shrub genera may be found in this layer (e.g. *Pachistima*, *Ribes*, *Shepherdia*, *Juniperus*, *Ceanothus*, and *Spiraea*). Various species of *Symphoricarpos* and *Rosa*, however, usually are most frequent and abundant. These latter two genera appear to typify the shrub component of aspen communities throughout the West. The tall herb component in this layer consists of a wide variety of genera. Those most common are: *Agastache*, *Aster*, *Delphinium*, *Senecio*, *Ligusticum*, *Hackelia*, *Heracleum*, and *Rudbeckia*. Species composition of the medium shrub/tall herb layer varies greatly between locations. In some stands, it may be composed almost exclusively of *Symphoricarpos oreophilus*. In others, shrubs may be lacking, and the layer will be composed of tall forbs, such as *Senecio serra*, *Rudbeckia occidentalis*, *Agastache urticifolia*, and *Delphinium occidentale*.

The low herb layer, always present in aspen communities, varies in composition. It generally is composed of an abundance of forbs and lesser amounts of graminoids. Occasionally, low-growing shrubs, such as *Berberis* and *Arctostaphylos*, also are present. The graminoids associated throughout the geographical distribution of aspen consist of members of the genera *Agropyron*, *Bromus*, *Poa*, *Elymus*, and *Carex*. The most generally encountered forb genera in this layer are *Thalictrum*, *Achillea*, *Aster*, *Fragaria*, *Osmorhiza*, *Lupinus*, *Galium*, and *Valeriana*; however, the diversity of forbs is great. *Thalictrum* is the only low forb that really typifies aspen communities throughout the West. Annual forbs, such as *Nemophila breviflora* and *Galium bifolium*, are rather common in this layer. In some locations, species of *Lathyrus* and *Vicia* form a rather unique, sprawling net of lush growth partly elevated by their tendency to cling to and climb over low shrubs and upright forbs.

Aspen Associations

An understanding of the similarities and differences in aspen communities throughout the West can be facilitated by a regional summarization of available information. The regional breakdown used here (fig. 4) is based primarily on broad physiographic provinces (Fenneman 1931). The amount of information available on aspen communities for any one region differs considerably and tends to reflect the prevalence of aspen in the region.

The undergrowth of aspen communities is highly diverse even within subregional areas. Extensive surveys of aspen communities indicate that only about 10% of the species encountered are found in more than 50% of the stands (table 1). For example, of 114 important shrubs and herbs found in eastern Idaho aspen communities, only 11 were present in more than one-half of the 319 stands sampled (Mueggler and Campbell 1982). Frequently, species that dominate the undergrowth of some stands are absent in others. This reflects the ability of aspen to serve as an overstory dominant under a broad range of environmental conditions.

Despite the highly varied composition of undergrowth in aspen communities throughout the West, certain genera appear repeatedly regardless of geographical location. Shrub genera typically growing in aspen communities are *Symphoricarpos*, *Rosa*, *Amelanchier*, *Prunus*, and *Berberis*. Forbs that repeatedly are found in aspen communities regardless of region are *Thalictrum*, *Osmorhiza*, *Geranium*, *Aster*, *Lathyrus*, *Achillea*, *Ligusticum*, *Galium*, and *Senecio*. The few graminoids commonly found in aspen understory are members of the genera *Bromus*, *Elymus*, *Poa*, and *Carex*.

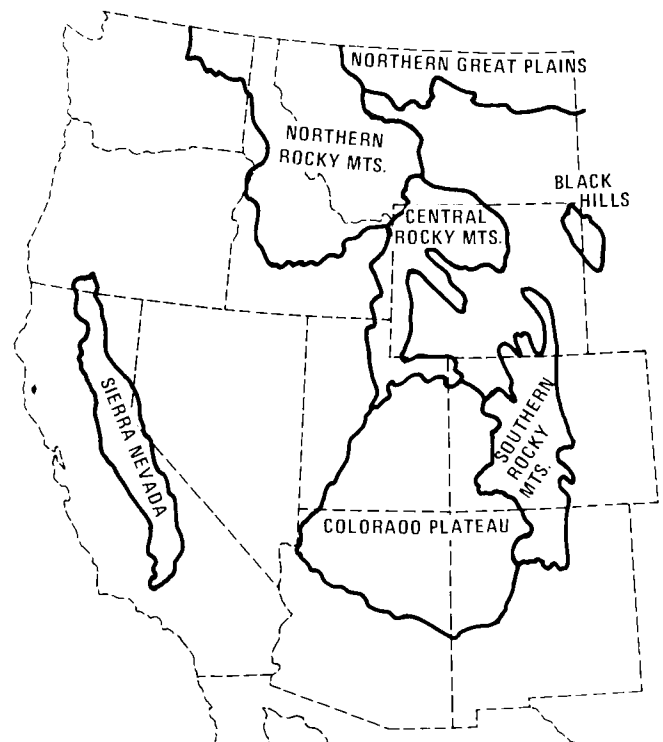


Figure 4.—Regions of western United States in which aspen exists in unique, described vegetation associations (Fenneman 1931).

Table 1.—Percentage cover¹ by undergrowth species growing in 50% or more of the aspen stands sampled in separate studies in the central Rocky Mountains (southeastern Idaho and western Wyoming) and southern Rocky Mountains (northern Colorado).

Species	Central Rocky Mountains		Southern Rocky Mountains
	(E. Idaho) ²	(W. Wyoming) ³	(N. Colorado) ⁴
<i>Achillea millefolium</i>	1	1	4
<i>Amelanchier alnifolia</i>	12		
<i>Aster engelmannii</i>			4
<i>Bromus ciliatus</i>			8
<i>Carex geyeri</i>			15
<i>Calamagrostis rubescens</i>	33		
<i>Elymus glaucus</i>	9	5	13
<i>Fragaria</i> spp.		4	3
<i>Galium boreale</i>			2
<i>Geranium richardsonii</i>			9
<i>G. viscosissimum</i>	12	8	
<i>Lathyrus leucanthus</i>			6
<i>Ligusticum porteri</i>			16
<i>Lupinus argenteus</i>	7	5	
<i>Osmorhiza</i> spp.	6		6
<i>Rosa woodsii</i>	4	7	
<i>Symphoricarpos oreophilus</i>	14	9	
<i>Taraxacum</i> spp.	2		7
<i>Thalictrum fendleri</i>	10	13	20
<i>Vicia americana</i>			6
Total stands sampled	319	177	47
Total species reported	114	99	103

¹Average canopy cover of the species in those stands where present.

²Data compiled from Mueggler and Campbell (1982).

³Data compiled from Youngblood and Mueggler (1981).

⁴Data compiled from Hoffman and Alexander (1980).

Northern Great Plains

The aspen parklands that sweep across Canada as a broad ecotone between the northern boreal forests and the prairies of the Northern Great Plains penetrate southward into northern Montana. Aspen groves on the eastern edge of Glacier National Park, where the east slope of the Northern Rocky Mountains meet the plains, are a southwesterly extension of these parklands (Lynch 1955).

Aspen in the northern parklands is considered a climax species that was held in check naturally by repeated wildfires (Moss 1932). It now appears to be aggressively expanding into adjacent prairies. Between 1907 and 1966, aspen groves in the parkland regions of south-central Alberta expanded 60% (Bailey and Wroe 1974). This invasion by aspen appears partly related to periods of higher than normal growing season temperatures. Expansion of the aspen groves is a major concern of livestock producers in Canada, because only 10% to 25% as much forage is produced in the aspen understory as was produced in the prior grasslands (Bailey and Wroe 1974).

The dynamics of these northern parkland aspen communities contrasts with those for the aspen forests in the Rocky Mountains and Colorado Plateau regions. Fire apparently suppressed expansion of aspen in the northern parklands; but fire perpetuated the seral aspen forests

farther south. The herbaceous understory in mature aspen parkland communities is characteristically meager; but it is usually lush in the aspen forests farther south.

Moss (1932) described what he termed an aspen consociation in the parklands of Alberta. This consociation contained a mixed understory of shrubs, forbs, and grasses (table 2). Such a simplistic categorization inevitably has substantial within-category differences in composition.

Table 2.—Common plants occurring in the undergrowth of aspen communities in the parklands of Alberta (Moss 1932).

SHRUBS	FORBS
<i>Symphoricarpos pauciflorus</i>	<i>Aralia nudicaulis</i>
<i>Amelanchier alnifolia</i>	<i>Aster lindleyanus</i>
<i>Prunus</i> sp.	<i>Cornus canadensis</i>
<i>Rosa</i> sp.	<i>Epilobium angustifolium</i>
<i>Corylus rostrata</i>	<i>Fragaria americana</i>
<i>Viburnum pauciflorum</i>	<i>Galium triflorum</i>
	<i>Lathyrus ochroleucus</i>
	<i>Vicia americana</i>
	<i>Mertensia pilosa</i>
	<i>Rubus triflorus</i>
	<i>Thalictrum venulosum</i>
GRASSES	
<i>Agropyron richardsonii</i>	
<i>A. tenerum</i>	
<i>Bromus ciliatus</i>	
<i>Calamagrostis canadensis</i>	

The southerly extension of parklands into Montana consists of a rather narrow mosaic of aspen groves and grasslands where the mountains meet the plains. Lynch (1955) recognized three stable aspen associations in this area (table 3). His *Populetum Symphoricarpetosum* association occupies sloping lands and has a pronounced shrub stratum. His *Populetum Asteretosum* association occurs in intermorainal troughs and depressions and has an understory consisting principally of forbs; shrubs are of minor importance. Lynch's *Populetum Osmorhizetosum* association is restricted to moist slopes and narrow valley bottoms; it is conspicuous, because the tree layer consists of a mixture of *Populus tremuloides* and *P. trichocarpa*.

Northern Rocky Mountains

Aspen communities in the Northern Rocky Mountains and adjacent Columbia Plateau are relatively infrequent and small. Generally, they are small clones along mountain streams and meadow fringes, or are a very patchy transitional type between coniferous forest and grasslands on mountain slopes. The size of individual stands seldom exceeds 5 acres (2 ha). Habeck (1967) considered much of the aspen in the mountains of northwestern Montana to be seral to *Pseudotsuga menziesii* and *Picea*

engelmannii, but acknowledged the existence of stable groves. Pfister et al. (1977) indicated that small patches of climax aspen probably occur farther south in Montana near the Continental Divide. Permanent or climax aspen communities also have been identified in central Idaho (Schlatterer 1972) and in the Blue Mountains of eastern Oregon (Hall 1973).

Descriptions of aspen communities of the Northern Rocky Mountains and Columbia Plateau are sketchy. Those in Montana mentioned by Habeck (1967) contain a distinct shrub layer consisting of such species as *Symphoricarpos occidentalis*, *Amelanchier alnifolia*, *Rosa woodsii*, *Prunus virginiana*, *Shepherdia argentea*, and *Ribes setosum*; the herb layer consists of an unspecified mixture of grasses and forbs. Peek (1963) indicated that dominant understory species in some southwestern Montana aspen stands were *Thalictrum occidentale*, *Geranium viscosissimum*, *Heracleum lanatum*, *Bromus marginatus*, and *Calamagrostis rubescens*.

Schlatterer (1972) described a single *Populus tremuloides*/*Symphoricarpos oreophilus*-*Carex geyeri* habitat type for central Idaho. This habitat type represents the climax aspen communities (table 4), in contrast to those in central Idaho which are seral to *Pseudotsuga menziesii* and *Abies lasiocarpa*. Occurrence of climax aspen in this area appears to be strong-

Table 3.—Prominent undergrowth species in three aspen associations east of Glacier National Park, Montana (Lynch 1955).

	Associations		
	<i>Populetum Symphoricarpetosum</i>	<i>Populetum Asteretosum</i>	<i>Populetum Osmorhizetosum</i>
SHRUBS			
<i>Amelanchier alnifolia</i>	X*	X	
<i>Berberis repens</i>	X		X
<i>Prunus virginiana</i>	X		
<i>Rosa acicularis</i>	X*	X	
<i>Symphoricarpos albus</i>	X*	X	
<i>S. occidentalis</i>		X	X
GRAMINOIDS			
<i>Agropyron subsecundum</i>			X
<i>Bromus carinatus</i>			X
<i>Calamagrostis rubescens</i>	X*		
<i>Carex</i> spp.	X		X
<i>Elymus glaucus</i>		X*	X
FORBS			
<i>Achillea millefolium</i>	X	X	
<i>Aster foliaceus</i>	X	X*	X
<i>A. conspicuus</i>	X	X	X
<i>Fragaria virginiana</i>	X	X*	X
<i>Galium boreale</i>	X	X	X
<i>Geranium richardsonii</i>		X*	X
<i>G. viscosissimum</i>	X		
<i>Heracleum lanatum</i>		X	X*
<i>Lathyrus ochroleucus</i>	X*	X	X
<i>Osmorhiza occidentalis</i>			X
<i>Smilacina stellata</i>	X	X	X*
<i>Thalictrum occidentale</i>		X*	X
<i>Vicia americana</i>	X	X	X
<i>Viola canadensis</i>		X	X*

*An asterisk denotes where the species is most abundant.

Table 4.—Undergrowth plants common in the *Populus tremuloides*/*Symphoricarpos oreophilus*-*Carex geyeri* habitat type in central Idaho (Schlatterer 1972).

SHRUBS	FORBS
<i>Symphoricarpos oreophilus</i>	<i>Achillea millefolium</i>
<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	<i>Fragaria virginiana</i>
	<i>Geranium viscosissimum</i>
	<i>Hydrophyllum capitatum</i>
	<i>Lupinus</i> spp.
	<i>Osmorhiza occidentalis</i>
	<i>Potentilla glandulosa</i>
	<i>Senecio serra</i>
	<i>Smilacina stellata</i>
	<i>Thalictrum occidentale</i>
	<i>Valeriana sitchensis</i>

ly governed by temperature and the amount of available soil moisture. Schlatterer (1972) noted that species composition of the habitat type varied greatly, depending upon amount of disturbance by livestock grazing.

Hall (1973) described a *Populus tremuloides*-meadow community type in northeastern Oregon that occurs most often as groves on moist meadow sites. The understory of these meadow groves consists primarily of the following graminoids: *Deschampsia caespitosa*, *Carex festivella*, *Danthonia californica*, *Poa pratensis*, and *Agrostis* spp. Forbs such as *Veratrum californicum* become abundant with overgrazing.

Central Rocky Mountains

Aspen communities of western Wyoming and adjacent portions of Idaho and northern Utah can be either small patches or large stands. This central Rocky Mountain region appears to be a zone of transition from the sporadic, small groves in the northern Rocky Mountains to the extensive aspen forest of the Colorado Plateau and southern Rocky Mountains. The typical small, scattered aspen stands of southern Montana and northwestern Wyoming are replaced by larger and more frequent stands farther south. Extensive aspen forests are frequently found in southeastern Idaho, southern Wyoming, and northern Utah.

Most descriptions of aspen communities in this region are generalizations from community composition in local areas. Reported composition of understory vegetation differs greatly. For example, only *Symphoricarpos oreophilus*, *Senecio serra*, and *Thalictrum fendleri* are common to at least half of the descriptions from 18 different sources. Although species composition is highly varied, the communities can be categorized according to structure. Some contain a tall shrub layer, others are without tall shrubs but possess a conspicuous layer of medium to low shrubs, and others have a predominantly herbaceous understory.

The most prevalent species in the tall shrub layer in this region are *Prunus virginiana* and *Amelanchier alnifolia*. Aspen communities containing a dispersed stratum of these tall shrubs were observed by Beetle

(1974), Gruell and Loope,² and Youngblood and Muegler (1981) in the Jackson Hole area, and by Reed (1971) in the Wind River Mountains of western Wyoming. Mueggler and Campbell (1982) found tall-shrub undergrowth in eastern Idaho, as did Crowther and Harper (1965) and Henderson et al. (1976) in northern Utah. A community with tall shrubs almost always has a medium to low shrub layer as well. The herb layer in the tall shrub aspen communities (table 5) is composed of a mixture of forbs and grasses that generally decrease in productivity as the density of the shrub layer increases.

Communities that lack a tall shrub stratum but have a distinct medium to low shrub stratum have been noted in the Bighorn Mountains of northern Wyoming (Hoffman and Alexander 1976), throughout western Wyoming (Youngblood and Mueggler 1981), eastern Idaho (Mueggler and Campbell 1982), in the Uinta Mountains of Northern Utah (Hayward 1945, Henderson et al. 1977, Winn 1976), and generally throughout the central Rocky Mountains (Houston 1954). Such communities contain most of the species listed in table 5, except the tall shrubs. In addition, *Juniperus communis*, *Poa nervosa*, *Galium boreale*, and *Geranium viscosissimum* frequently grow in these communities. The medium and low shrubs, particularly species of *Symphoricarpos*, may form a rather dense cover. Productivity of the herb stratum usually varies inversely with the density of shrubs.

Aspen communities lacking a well-defined shrub layer, although infrequent, are found in the central Rocky Mountains. Both Reed (1952) and Youngblood and Mueggler (1981) found such communities on moist sites in western Wyoming, as did Mueggler and Campbell (1982) in eastern Idaho. Beetle (1974) mentioned "aspen savannah" communities in Teton County, Wyoming, with an understory dominated by the grass *Calamagrostis rubescens* and the forb *Lupinus argenteus*.

²Gruell, G. E., and L. L. Loope. 1974. *Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming*. USDA Forest Service, Intermountain Region, and U.S. Department of the Interior, National Park Service, Rocky Mountain Region. 33 p.

Table 5.—Typical undergrowth species present in tall shrub aspen communities in the central Rocky Mountains.

SHRUBS	FORBS
<i>Amelanchier alnifolia</i>	<i>Achillea millefolium</i>
<i>Berberis repens</i>	<i>Agastache urticifolia</i>
<i>Pachistima myrsinites</i>	<i>Aquilegia coerulea</i>
<i>Prunus virginiana</i>	<i>Aster engelmannii</i>
<i>Rosa nutkana</i>	<i>Geranium</i> spp.
<i>Rosa woodsii</i>	<i>Lathyrus</i> spp.
<i>Shepherdia canadensis</i>	<i>Lupinus</i> spp.
<i>Symphoricarpos albus</i>	<i>Osmorhiza</i> spp.
<i>S. oreophilus</i>	<i>Rudbeckia occidentalis</i>
<i>S. vaccinioides</i>	<i>Senecio serra</i>
	<i>Thalictrum fendleri</i>
	<i>Valeriana occidentalis</i>
GRASSES	
<i>Agropyron subsecundum</i>	
<i>A. trachycaulum</i>	
<i>Bromus anomalus</i>	
<i>B. marginatus</i>	
<i>Calamagrostis rubescens</i>	
<i>Elymus glaucus</i>	

Table 6.—Aspen community types according to seral status on the Caribou and Targhee National Forests in eastern Idaho (Mueggler and Campbell 1982).

STABLE

Populus tremuloides/*Amelanchier alnifolia*-*Pachistima myrsinites*
Populus tremuloides/*Amelanchier alnifolia*-*Spiraea betulifolia*
Populus tremuloides/*Amelanchier alnifolia*-*Symphoricarpos oreophilus*
Populus tremuloides/*Amelanchier alnifolia*-*Calamagrostis rubescens*
Populus tremuloides/*Pachistima myrsinites*-*Calamagrostis rubescens*
Populus tremuloides/*Pachistima myrsinites*-*Geranium viscosissimum*
Populus tremuloides/*Spiraea betulifolia*-*Calamagrostis rubescens*
Populus tremuloides/*Symphoricarpos oreophilus*-*Calamagrostis rubescens*
Populus tremuloides/*Artemisia tridentata*-*Festuca idahoensis*
Populus tremuloides/*Calamagrostis rubescens*
Populus tremuloides/*Geranium viscosissimum*
Populus tremuloides/*Wyethia amplexicaulis*

SERAL (to conifers)

Populus tremuloides-*Abies lasiocarpa*/*Symphoricarpos oreophilus*
Populus tremuloides-*Abies lasiocarpa*/*Thalictrum fendleri*
Populus tremuloides-*Pseudotsuga menziesii*/*Amelanchier alnifolia*
Populus tremuloides-*Pseudotsuga menziesii*/*Symphoricarpos oreophilus*
Populus tremuloides-*Pseudotsuga menziesii*/*Calamagrostis rubescens*
Populus tremuloides-*Pinus contorta*/*Calamagrostis rubescens*

SERAL (abusive grazing)

Populus tremuloides/*Symphoricarpos oreophilus*-*Poa pratensis*
Populus tremuloides/*Symphoricarpos oreophilus*-*Rudbeckia occidentalis*
Populus tremuloides/*Calamagrostis rubescens*-*Poa pratensis*
Populus tremuloides/*Poa pratensis*
Populus tremuloides/*Rudbeckia occidentalis*

Although Beetle suggested that such stands represented a grazing disclimax situation, similar composition has been found where ungulate use has been minimal historically.³ In northern Utah, the understory may be dominated by a luxuriant mixture of such tall forbs as *Senecio serra*, *Agastache urticifolia*, *Hackelia floribunda*, and *Delphinium occidentale*. These aspen/tall forb communities frequently also possess an abundance of low forbs such as *Valeriana occidentalis*, *Thalictrum fendleri*, *Osmorhiza occidentalis*, *Osmorhiza depauperata*, *Osmorhiza chilensis*, *Nemophila breviflora*, *Galium triflorum*, and *Galium boreale*.

Several researchers have attempted to develop phytosociological classifications for stable aspen communities in various parts of the central Rocky Mountain region. Hoffman and Alexander (1976) named stable aspen communities in the Bighorn Mountains of Wyoming the *Populus tremuloides*/*Lupinus argenteus* habitat type. These communities contain a rich mixture of grasses and forbs with the shrubs *Juniperus communis*, *Ribes lacustre*, and *Potentilla fruticosa* conspicuous in some stands. Reed (1971) classified the aspen forest in the Wind River Mountains of Wyoming into a single *Populus tremuloides*/*Symphoricarpos oreophilus* habitat type. However, only 10 of the 19 stands so classified contained *S. oreophilus*; and shrubs as a class were prominent in only 13, suggesting considerable compositional variability within the habitat type. Henderson et al.

(1977) discerned two climax aspen habitat types in the Uinta Mountains of northern Utah: *Populus tremuloides*/*Carex geeyeri* h.t. and *Populus tremuloides*/*Juniperus communis* h.t. Both are found in the lower forest zone—the former on easterly and southerly exposures and the latter primarily on north slopes.

Comprehensive classifications of aspen communities have been developed for eastern Idaho (Mueggler and Campbell 1982) and western Wyoming (Youngblood and Mueggler 1981). The Idaho classification was based upon a detailed examination of 319 aspen stands on the Caribou and Targhee National Forests. Of 23 community types described, 11 were considered stable and 12 seral, either to coniferous forests or because of major alteration caused by abusive livestock grazing (table 6). The Wyoming classification, based on 177 aspen stands sampled on the Bridger-Teton National Forest, identifies 26 community types of which 9 were considered stable and 17 seral (table 7).

Colorado Plateau

Aspen forests in the Colorado Plateau region of central and southern Utah, western Colorado, northwestern New Mexico, and northern Arizona frequently cover broad areas. According to Cottam (1954), aspen dominates more mountainous terrain between 7,000 and 10,000 feet (2,100 m and 3,000 m) elevation in Utah than any other forest tree. Although the aspen in much of this area is gradually being replaced by conifers, many of the extensive aspen stands show little evidence of such

³Personal observation by Walter F. Mueggler, Principal Plant Ecologist, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Logan, Utah

Table 7.—Aspen community types according to seral status on the Bridger-Teton National Forest, Wyoming (Youngblood and Mueggler 1981).

STABLE

Populus tremuloides/Artemisia tridentata
Populus tremuloides/Symphoricarpos oreophilus
Populus tremuloides/Wyethia amplexicaulis
Populus tremuloides/Juniperus communis
Populus tremuloides/Thalictrum fendleri
Populus tremuloides/Astragalus miser
Populus tremuloides/Calamagrostis rubescens
Populus tremuloides/Heracleum lanatum
Populus tremuloides/Ranunculus alismaefolius

SERAL

Populus tremuloides/Spiraea betulifolia c.t.
Populus tremuloides-Pseudotsuga menziesii/Spiraea betulifolia c.t.
Populus tremuloides-Pseudotsuga menziesii/Calamagrostis rubescens c.t.
Populus tremuloides/Berberis repens c.t.
Populus tremuloides-Abies lasiocarpa/Berberis repens c.t.
Populus tremuloides/Shepherdia canadensis c.t.
Populus tremuloides-Abies lasiocarpa/Shepherdia canadensis c.t.
Populus tremuloides/Arnica cordifolia c.t.
Populus tremuloides-Abies lasiocarpa/Arnica cordifolia c.t.
Populus tremuloides/Rudbeckia occidentalis c.t.
Populus tremuloides-Abies lasiocarpa/Rudbeckia occidentalis c.t.
Populus tremuloides/Prunus virginiana c.t.
Populus tremuloides-Abies lasiocarpa/Prunus virginiana c.t.
Populus tremuloides/Ligusticum filicinum c.t.
Populus tremuloides-Abies lasiocarpa/Ligusticum filicinum c.t.
Populus tremuloides-Abies lasiocarpa/Pedicularis racemosa c.t.
Populus tremuloides/Equisetum arvense c.t.

a successional trend. Understory vegetation may provide clues to successional status of these stands. In central Utah, for example, the presence of *Bromus polyanthus*, *Collomia linearis*, *Galium bifolium*, *Stellaria jamesiana*, *Vicia americana*, and *Viola nuttallii*, suggests stable aspen communities, whereas *Berberis repens*, *Pachistima myrsinites*, and *Viola adunca* indicate seral communities.¹

Barnes (1975) found that aspen on the Colorado Plateau not only is more abundant but exhibits larger individual clones than it does farther north. Kemperman (1970) measured a single clone in southern Utah that occupied 107 acres (43 ha) and consisted of 47,000 stems. Stands composed of numerous contiguous clones are common in this region; whereas in the Northern Rocky Mountain region, the clones are relatively small and frequently isolated. Regional floristics contribute to the uniqueness of aspen communities in the Colorado Plateau region. Species such as *Quercus gambelii*, *Symphoricarpos palmeri*, *Festuca thurberi*, and *F. arizonica* may be present in the understory there, but not farther north.

Despite the prevalence of aspen forests in this region, few descriptions of community composition have been published. Mueggler and Bartos (1977) described an aspen community at 8,500 feet (2,600 m) and another at 10,500 feet (3,200 m), near its lower and upper elevational limits, in the Tushar mountains of southern Utah (table 8). The lower elevation community possessed a pronounced medium to low shrub stratum consisting of *Symphoricarpos vaccinioides*, *Rosa woodsii*, and *Berberis repens*. The upper elevation community lacked

a shrub stratum; the understory consisted of approximately 10% graminoids and 90% forbs.

Elevationally related differences in understory composition also are apparent on the Wasatch Plateau in central Utah. Data from 14 stands near 8,000 feet (2,450 m) elevation, near the lower limits of the aspen zone in this area, show a pronounced shrub stratum in contrast to data from 10 stands at about 10,000 feet (3,050 m) near the upper limits of the zone.⁴ Differences in composition of the herbaceous layer at the different elevations is equally pronounced (table 9).

Warner and Harper (1972) found understory composition differences between sites of high and low quality for aspen growth (table 10), as determined from Jones' (1967b) site index curves. Warner and Harper's determinations were based on 43 stands in northern and central Utah within both the Central Rocky Mountain and Colorado Plateau regions. They found that low quality sites were characteristically more shrubby than high quality sites; the understory of high quality sites was dominated by forbs.

Paulsen (1969) described an aspen community at 9,500 feet (2,900 m) on Black Mesa, in western Colorado that had an almost exclusive herbaceous understory. The primary component was the sedge *Carex geyeri*, which accounted for about 25% of the total herbage production. Prominent grasses were *Bromus carinatus*, *Bromus anomalus*, *Festuca thurberi*, and *Agropyron trachycaulum*. Forbs comprised about 60% of the her-

⁴Data furnished by K. T. Harper, Department of Botany and Range Science, Brigham Young University, Provo, Utah

Table 8.—Differences in prominent undergrowth species in aspen stands at two elevations in the Tushar mountains of southern Utah (Mueggler and Bartos 1977).

8,500 feet elevation	Common to both	10,500 feet elevation
<i>Agropyron caninum</i>	<i>Achillea millefolium</i>	<i>Carex</i> spp.
<i>Berberis repens</i>	<i>Astragalus bourgovii</i>	<i>Festuca idahoensis</i>
<i>Cirsium undulatum</i>	<i>Bromus anomalus</i>	<i>Helenium hoopesii</i>
<i>Erigeron speciosus</i>	<i>Castilleja linariaefolia</i>	<i>Potentilla pulcherrima</i>
<i>Helianthella uniflora</i>	<i>Fragaria americana</i>	<i>Solidago decumbens</i>
<i>Rosa woodsii</i>	<i>Fraseria speciosa</i>	
<i>Smilacina stellata</i>	<i>Lupinus leucophyllus</i>	
<i>Stipa lettermani</i>	<i>Poa fendleriana</i>	
<i>Symphoricarpos vaccinioides</i>		

Table 9.—Differences in undergrowth species' in aspen communities at two elevations on the Wasatch Plateau in central Utah.

8,000 feet elevation	Common to both	10,000 feet elevation
<i>Aster engelmannii</i>	<i>Achillea millefolium</i> *	<i>Androsace septentrionalis</i>
<i>Aster foliaceus</i>	<i>Agropyron riparium</i> (upper*)	<i>Artemisia ludoviciana</i>
<i>Berberis repens</i> *	<i>Bromus polyanthus</i> (upper*)	<i>Chenopodium fremontii</i>
<i>Bromus ciliatus</i>	<i>Lathyrus lanzwertii</i>	<i>Collomia linearis</i>
<i>Carex rossii</i>	<i>Osmorhiza obtusa</i> *	<i>Descurainia californica</i> *
<i>Cynoglossum officinale</i>	<i>Stellaria jamesiana</i> (upper*)	<i>Galium bifolium</i> *
<i>Dactylis glomerata</i>	<i>Taraxacum officinale</i> *	<i>Melica bulbosa</i>
<i>Elymus glaucus</i>	<i>Vicia americana</i> *	<i>Osmorhiza occidentalis</i>
<i>Fragaria bracteata</i>	<i>Viola nuttallii</i> (upper*)	<i>Poa reflexa</i>
<i>Galium boreale</i> *		<i>Polemonium foliosissimum</i>
<i>Gentiana heterosepala</i>		<i>Polygonum douglasii</i>
<i>Geranium fremontii</i> *		<i>Ribes montigenum</i>
<i>Lathyrus pauciflorus</i> *		<i>Stipa lettermani</i>
<i>Pachistima myrsinites</i> *		<i>Thalictrum fendleri</i>
<i>Poa pratensis</i> *		<i>Trisetum spicatum</i>
<i>Rosa</i> sp.		
<i>Rudbeckia occidentalis</i>		
<i>Stipa columbiana</i>		
<i>Swertia radiata</i>		
<i>Symphoricarpos oreophilus</i> *		
<i>Viola adunca</i> *		

*All listed species had at least 5% average frequencies; those with asterisks had frequencies of at least 20%.

Table 10.—Effect of site quality differences on prominent undergrowth species in Utah aspen communities (Warner and Harper 1972).

Low quality site	Common to both	High quality site
<i>Aster engelmannii</i>	<i>Achillea millefolium</i>	<i>Elymus glaucus</i>
<i>Gayophytum ramosissimum</i>	<i>Agropyron trachycaulum</i>	<i>Lathyrus lanzwertii</i>
<i>Pachistima myrsinites</i>	<i>Bromus polyanthus</i>	<i>Mertensia arizonica</i>
<i>Polygonum douglasii</i>	<i>Chenopodium fremontii</i>	<i>Osmorhiza chilensis</i>
<i>Symphoricarpos oreophilus</i>	<i>Collomia linearis</i>	<i>Thalictrum fendleri</i>
	<i>Collinsia parviflora</i>	<i>Viola nuttallii</i>
	<i>Descurainia californica</i>	
	<i>Galium bifolium</i>	
	<i>Nemophila breviflora</i>	
	<i>Stellaria jamesiana</i>	
	<i>Vicia americana</i>	

Table 11.—Major undergrowth components of two major types of aspen communities in the Jarbridge mountains of Nevada.

Populus/forb type	Common to both	Populus/Symphoricarpos type
<i>Agropyron trachycaulum</i>	<i>Agastache urticifolia</i>	<i>Amelanchier alnifolia</i>
<i>Osmorhiza occidentalis</i>	<i>Aster perelegans</i>	<i>Carex hoodii</i>
<i>Potentilla glandulosa</i>	<i>Bromus marginatus</i>	<i>Ceanothus velutinus</i>
<i>Senecio serra</i>	<i>Geranium viscosissimum</i>	<i>Erigeron speciosus</i>
<i>Thalictrum fendleri</i>	<i>Hackelia mierantha</i>	<i>Prunus virginiana</i>
	<i>Symphoricarpos oreophilus</i>	<i>Ribes cereum</i>
	<i>Valeriana occidentalis</i>	

bage; the most abundant were *Ligusticum porteri*, *Lathyrus leucanthus*, *Thalictrum dasycarpum*, *Fragaria glauca*, *Osmorhiza obtusa*, *Geranium fremontii*, and *Galium boreale*.

Northwest of the Colorado Plateau region, in the Jarbridge Mountains of Nevada, Lewis (1975) found two major types of aspen communities. He designated those with an understory dominated by tall forbs the *Populus tremuloides*/forb type. He called those dominated by shrubs the *Populus tremuloides*/*Symphoricarpos* type (table 11). Lewis (1971) indicated that stable aspen communities in the nearby Ruby and East Humboldt Ranges had the following species common in the understory: *Agastache urticifolia*, *Agropyron trachycaulum*, *Bromus polyanthus*, *Castilleja miniata*, *Lupinus argenteus*, *Symphoricarpos oreophilus*, and *Thalictrum fendleri*.

Southern Rocky Mountains

The southern Rocky Mountain region extends along the mountain chain from southwestern Wyoming, through Colorado, and into north-central New Mexico. The majority of aspen forests in this region are along the west slope of the Rocky Mountains. As in adjacent regions, both seral and stable communities exist in small groves and as extensive forests. Many of the aspen forests in the region are successional to *Picea engelmannii* and *Abies lasiocarpa*.

Severson (1963) concluded that the aspen stands on the Hayden Division of the Medicine Bow National Forest in southeastern Wyoming are successional to coniferous forests. The most prominent species in the understory of these seral aspen communities are *Vicia americana*, *Carex geyeri*, *Taraxacum officinale*, *Stipa lettermani*, and *Calamagrostis rubescens*. Severson (1963) observed that variation in understory composition is influenced more by biotic factors, such as grazing, than by climatic or edaphic factors, with the exception of elevational extremes. Although Wirsing and Alexander (1975) indicated that aspen on the Medicine Bow National Forest may be a seral species in the *Abies lasiocarpa*/*Vaccinium* and *Abies lasiocarpa*/*Carex geyeri* habitat types, it also is found in stable communities, which they classified as the *Populus tremuloides*/*Carex geyeri* habitat type. This stable type generally occurs in small patches at the lower fringe of the coniferous forest zone. The understory of the type consists of a mixture of shrubs and herbs. Prominent members of the shrub

layer are *Juniperus communis*, *Rosa woodsii*, *Amelanchier alnifolia*, and *Berberis repens*. In contrast to most aspen communities elsewhere, *Symphoricarpos* is conspicuously absent as an important member of the shrub layer. Herbs characterizing the understory of this habitat type are *Carex geyeri*, *Elymus glaucus*, *Osmorhiza depauperata*, *Galium boreale*, and *Achillea millefolium*.

A complete description of aspen communities occurring in any portion of the southern Rocky Mountains is given by Hoffman and Alexander (1980). They identified five aspen-dominated habitat types on the Routt National Forest, in northwestern Colorado: *Populus tremuloides*/*Symphoricarpos oreophilus* h.t., *P. tremuloides*/*Thalictrum fendleri* h.t., *P. tremuloides*/*Heracleum sphondylium* h.t., *P. tremuloides*/*Veratrum tenuipetalum* h.t., and *P. tremuloides*/*Pteridium aquilinum* h.t. The majority of the 47 stands used to develop this classification were in the *P. tremuloides*/*T. fendleri* type. Species prominent in the undergrowth of most stands were *Bromus ciliatus*, *Elymus glaucus*, *Carex geyeri*, *Geranium richardsonii*, *Osmorhiza* spp., *Thalictrum fendleri*, and *Vicia americana*.

Both Langenheim (1962) and Morgan (1969) described relatively stable aspen forests in the Gunnison area of central Colorado, that have predominantly herbaceous understories. Characteristic species in these mature aspen communities are: *Bromus ciliatus*, *Erigeron elatior*, *Geranium richardsonii*, *Lathyrus leucanthus*, *Ligusticum porteri*, *Senecio serra*, *Thalictrum fendleri*, and *Vicia americana*. Morgan (1969) recognized that some communities differed because of the abundance of *Symphoricarpos utahensis*, *Aster engelmannii*, and *Pteridium aquilinum*. Langenheim (1962), however, identified situations where aspen is a transitional type with adjacent communities dominated by *Festuca thurberi* and *Artemisia tridentata*, and situations where aspen dominates talus slopes. Understory in the ecotonal and talus slope types contains shrubs such as *Symphoricarpos* spp., *Artemisia tridentata*, *Pachistima myrsinites*, *Acer glabrum*, and *Rosa* spp.

Moir and Ludwig (1979) considered aspen to be a major seral tree in 6 of the 8 spruce-fir habitat types and in 7 of the 11 mixed conifer habitat types that they identified for New Mexico and Arizona. They did not recognize aspen as either a major or minor climax dominant. Laysen and Schubert (1979) also recognized the seral status of aspen in the *Picea pungens*, *Abies lasiocarpa*, *A. concolor*, *P. engelmannii*, *Pseudotsuga menziesii*, and

Pinus ponderosa climax forest series in New Mexico and Arizona. Although they did not identify situations where aspen achieves climax status, they suggested that a climax aspen series might exist in certain edaphic situations.

Black Hills

Aspen is a conspicuous element in the vegetation of the Black Hills of South Dakota. The relatively low elevation of this isolated mountain mass, less than 7,480 feet (2,280 m), confines aspen almost entirely to the northerly exposures (Severson and Thilenius 1976). Both Kranz and Linder (1973) and Thilenius (1972) recognized aspen as seral to *Pinus ponderosa* in this area; however relatively stable communities also exist.

Severson and Thilenius (1976) classified 28 aspen stands in the Black Hills and adjacent Bear Lodge Mountains of north-eastern Wyoming into the following nine "aspen groups":

1. *Populus tremuloides*/*Spiraea lucida*/*Lathyrus ochroleucus*
2. *Populus tremuloides*/*Symphoricarpos albus*/*Pteridium aquilinum*
3. *Populus tremuloides*/*Berberis repens*/*Oryzopsis asperifolia*/*Aster laevis*
4. *Populus tremuloides*/*Ribes missouriense*/*Oryzopsis asperifolia*/*Aster laevis*
5. *Populus tremuloides*/*Rosa woodsii*/*Poa pratensis*/*Trifolium repens*
6. *Populus tremuloides*/*Physocarpus monogynus*/*Poa pratensis*/*Smilacina stellata*
7. *Populus tremuloides*/*Rubus parviflorus*/*Agropyron subsecundum*/*Aralia nudicaulis*
8. *Populus tremuloides*/*Corylus cornuta*/*Aralia nudicaulis*
9. *Populus tremuloides*/*Ostrya virginiana*/*Oryzopsis asperifolia*/*Aralia nudicaulis*.

Groups 8 and 9 are considered relatively stable aspen types. Groups 3 and 4 are seral stages that will revert to *Pinus ponderosa* or *Picea glauca*. The successional status of stands in the remaining groups was not defined. The indicator species for each group are contained in the name. As suggested by names, shrubs are generally important in the understory of most groups. Plants most commonly occurring as understory to aspen communities in this isolated mountain mass are shown in table 12.

Sierra Nevada

Aspen is only a minor element in the vegetation of the Sierra Nevada Mountains of California and northward into the Cascades of Oregon and Washington (Barry 1971, Franklin and Dyrness 1973). Scattered groves grow along riparian zones and on transitional areas between coniferous forests and mountain meadows. Occasionally, aspen can be found intermixed as scattered individuals or small clones within the coniferous forest

Table 12.—Common undergrowth species found in aspen communities in the Black Hills of South Dakota (Severson and Thilenius 1976).

SHRUBS	FORBS
<i>Amelanchier alnifolia</i>	<i>Aster laevis</i>
<i>Berberis repens</i>	<i>Fragaria ovalis</i>
<i>Rosa woodsii</i>	<i>Galium boreale</i>
<i>Spiraea lucida</i>	<i>Lathyrus ochroleucus</i>
<i>Symphoricarpos albus</i>	<i>Monarda fistulosa</i>
	<i>Thalictrum venulosum</i>
GRASSES	<i>Smilacina stellata</i>
	<i>Vicia americana</i>
<i>Oryzopsis asperifolia</i>	
<i>Poa pratensis</i>	

types. Barry (1971) considered most such groves in the Sierra Nevada to be relatively stable communities particularly adapted to ecotonal areas between forest and meadows. He indicated that aspen is a truly seral species only in the *Abies magnifica* forests where it may gain temporary dominance after logging.

Barry (1971) found substantial understory differences in four aspen parkland stands, in the Lake Tahoe area, on the California-Nevada border. The understory varied from very sparse to very dense. Of the total 54 species encountered in these communities, only *Thalictrum fendleri* was in the understory in all four stands. Other plants reported in the understory in at least two of the four stands were *Achillea millefolium*, *Alnus tenuifolia*, *Bromus marginatus*, *Lupinus* spp., *Poa pratensis*, *Monardella odoratissima*, *Osmorhiza chilensis*, and *Osmorhiza occidentalis*.

Grazing Disclimax

Aspen communities have long been recognized for their value as livestock range. However, a long history of sometimes abusive grazing on some areas has led to certain changes in undergrowth composition that persists despite conservative grazing in recent years. These changes often resulted in a more simple flora of fewer plant species than originally present in the undergrowth (Beetle 1974, Costello 1944, Houston 1954). The plants that remained, usually low in palatability to livestock, increased in abundance as competition from the more palatable plants decreased (see the FORAGE chapter).

With extreme abuse, the undergrowth may consist primarily of perennials such as *Rudbeckia* spp., *Lathyrus* spp., *Wyethia* spp., *Poa pratensis*, and *Taraxacum officinale*, and annuals such as *Madia glomerata*, *Nemophila breviflora*, *Galium bifolium*, and *Polygonum douglasii* (Beetle 1974, Houston 1954). The particular combination of species will differ with the environment.

Some of the current combinations of species in aspen communities might be considered relatively stable grazing disclimaxes. Such communities apparently are no longer able to return to their original compositions in the foreseeable future, either because of environmental changes caused by abusive grazing, or because of the competitive dominance of the invader species.