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Biotic and Abiotic Processes of Eastside Ecosystems:

The Effects of Management on Plant and Community Ecology, and on Stand and Landscape Vegetation Dynamics

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ABSTRACT

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Paleo-vegetation studies have shown that vegetation has changed in composition and extent in the intermountain Pacific Northwest over the past 20,000 years. Today, both natural and human-induced disturbances have long-term influence on the structure and composition of eastside vegetation. Disturbance may enhance landscape diversity, therefore, the scale of modifying events and activities needs to shift from species and stand to the landscape level. Knowledge of plant succession is the foundation of a sound vegetation management program where the primary goal is to retard, arrest, or accelerate the natural forces of vegetation change.

Keywords: Pleistocene vegetation, pollen analysis, disturbance, stand development, succession, steepe ecosystem, forest ecosystem, shrublands, scablands, landscape.

Contents

INTRODUCTION

Changing climates affect the distribution and composition of plant species indigenous to eastside forest, shrubland, grassland, and woodland ecosystems. Analysis of paleobotanical data from pollen records and woodrat middens describe major changes in vegetation and vegetation patterns on the east side in the last 20,000 years.

The kinds of plant communities in eastside ecosystems today are summarized. The premanagement era is the basis for describing the vegetation structure, composition, and patterns. Primary disturbances (fire, grazing, insects, diseases) that modified the vegetation are related to successional processes and pathways induced by these natural disturbances. These disturbances are not considered destructive; they altered plant communities and affected ecosystem function.

With settlement and increased modification of the landscape by Euro-Americans, natural processes were altered as land management activities intensified and periodic burning by natural fire was curtailed. Major management practices that have interacted with successional processes, landscape patterns, structures, and patch sizes and shapes are addressed. Eastside landscape patterns of the present day are contrasted with those of the recent past (last 100 years) and the prehistoric past (last 20,000 years), to emphasize the changing nature of eastside ecosystems as a result of disturbances. Stand dynamics, complex plant interactions, and the effects of management practices on vegetation development are emphasized. Degraded sites need to be restored to compositions and structures that will enhance biological diversity and ecosystem function across eastside landscapes.

LATE QUATERNARY PRECURSORS: THE LAST 20,000 YEARS-AN OVERVIEW

Late Pleistocene Environments

The striking vegetational shifts described for the Pacific Northwest during the last 20,000, 10,000, or 1000 years are not unusual. In fact, no vegetation on earth has escaped the repeated stress of glacial climates and interglacial adjustments or the short, sharp climatic shifts during each period. With each episode, species displaced by climate, ice, water, and competition responded through growth form, migration, or selection-or faced local extinction. At various paces in different places, species repeatedly abandoned and then reclaimed the same terrain, but not always with the same associates.

The last glaciation brought Laurentide or Cordilleran Ice sheets to Washington, Idaho, and Montana, and ice caps grew in the larger ranges (Waitt and Thorson 1983). The largest area of ice south of the continental ice sheets covered the Yellowstone Plateau; other ice caps formed over the Bitterroot and Sawtooth ranges, and along the spine of the Cascade Range. Other ranges supported small ice caps or cirque and valley glaciers that receded to near present limits by 10,000 B.P. Re-advances of alpine glaciers and downslope retreat of the upper tree line mark cold, moist episodes of the Holocene (Davis 1988).

Pleistocene lakes drowned vast areas of the Northwest and Great Basin and, along with glaciers, acted as barriers to plant movements. The lakes may also have contributed to restriction or demise of populations by their growth and by catastrophic draining. With final desiccation, plants colonized fine-grained substrates that had accumulated over thousands of years. Some lake floors (such as Glacial. Lake Missoula) were probably stabilized rapidly by grasses and sagebrushes, whereas others (such as Pluvial Lake Bonneville) still return windborne sediment to surrounding ranges and adjacent valleys. The late histories of these two lakes illustrate the rapidity and intensity with which brief climatic variability altered the Pleistocene landscape on a grand scale.

Along the margin of continental glaciers in Washington, Idaho, and Montana, proglacial lakes grew in ice-dammed drainages. The largest of these, Glacial Lake Missoula, formed when ice extended southward in the Purcell Trench and blocked the Clark Fork Valley with a 600-meter-high ice dam at the Montana-Idaho border. Rivers and melting glaciers fed the resulting lake until it spread over 3000 km^2, with a volume near that of Lake Ontario. Faint wave-formed beaches still mark the hillsides to 290 m above Missoula, Montana. Although estimates of the number vary, periodic catastrophic outburst floods or jokulhaups, began with failure of the ice-dam. With each "Spokane Flood," as much as 2150 km^3 of water poured through the breach, Pend Oreille Lake, and the Spokane Valley. Icy torrents, hundreds of meters deep, and tens of kilometers wide, then raged across central Washington, violating drainage divides, stripping Palouse loess, and raising gigantic basalt blocks from their beds. Washington's distinctive scablands are the product of some of the greatest floods known from the geologic record; the last of these occurred about 13,000 B.P. (Waitt 1985).

Volcanic ash layers (tephra) that allow precise correlation of vegetational events within the northern Rocky Mountains (Carrara 1989) and far beyond will prove the greatest asset of this region in deciphering patterns of Quaternary vegetation history. Multiple eruptions of Cascade volcanoes such as Mount Mazama (Crater Lake), Oregon (Bacon 1983), and Glacier Peak (Foit and others 1993; Mehringer and Foit 1990; Mehringer and others 1984), and Mount St. Helens, Washington (Crandell 1987, Mullineaux 1986, Yamaguchi and others 1990), cast long shadows downwind (fig. 1). Tephra of their individual eruptions may be distinguished and correlated by stratigraphic position, radiocarbon or tree-ring age, mineral suites, and glass chemistry. Mazama and Glacier Peak tephra appear in lake sediments in distant Montana (fig. 2). These two tephras are time stratigraphic markers important in correlating vegetation changes from the Cascades all the way to Glacier and Yellowstone National Parks (Carrara 1989, Whitlock 1993).

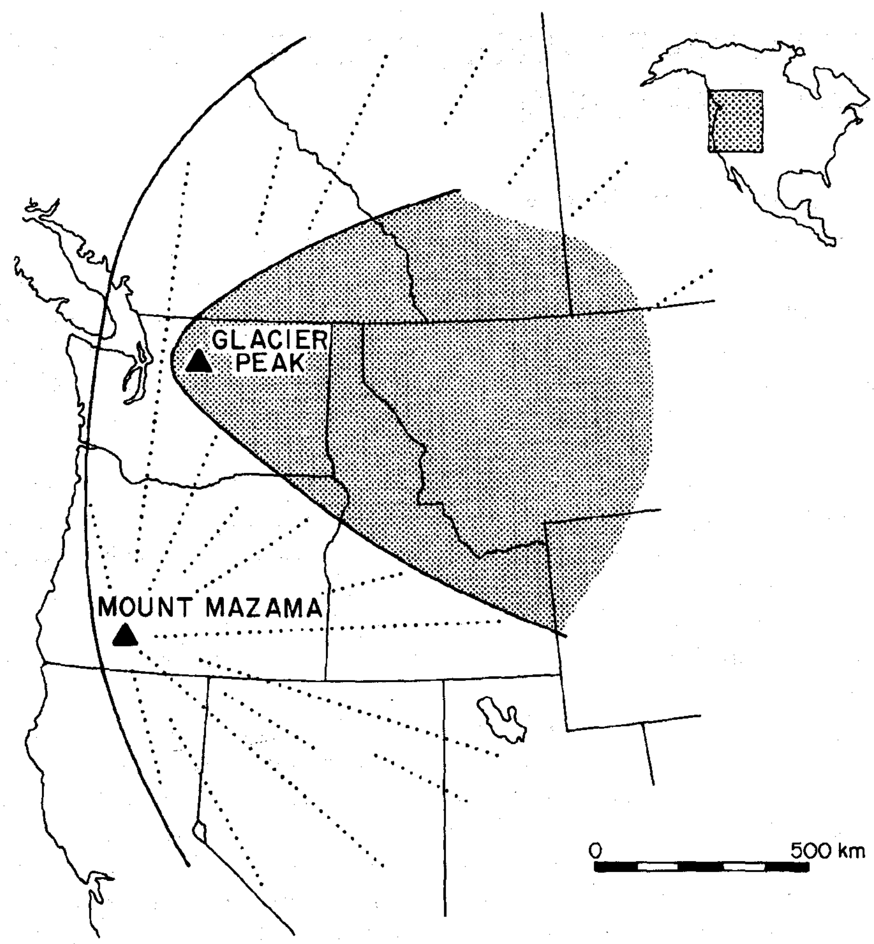

Figure 1. Distribution of Glacier Peak (11,250 B.P.) and Mazama (6850 B.P.) tephras (Blinman and others 1979).

Western Washington

Vegetation and climate-Because the eastside's climatic patterns are shaped over the Pacific Ocean and move eastward, primary features of climate-induced vegetation history are related on both sides of the Cascades. With one exception, published eastside late-Quaternary fossil-plant sequences are younger than 13,000 B.P. West of the Cascades, pollen records are old enough to be useful in evaluating full-glacial and interstadial conditions, and they frequently show more detail in the number of tree species and in the order of their arrivals or departures. In the Puget Trough, for instance, fossil sequences reveal vegetation of the coldest episodes south of continental glaciers, as well as the northward progress of developing postglacial forests. By contrast, eastside sites are scattered and forest is discontinuous at low to middle elevations (Franklin and Dyrness 1973, fig. 27). On the east side, causes of latitudinal or elevational differences in species's ranges or associations must be evaluated by details of specific, often geographically and ecologically isolated, data and by recognizing common patterns in fossil records from vastly different present plant communities.

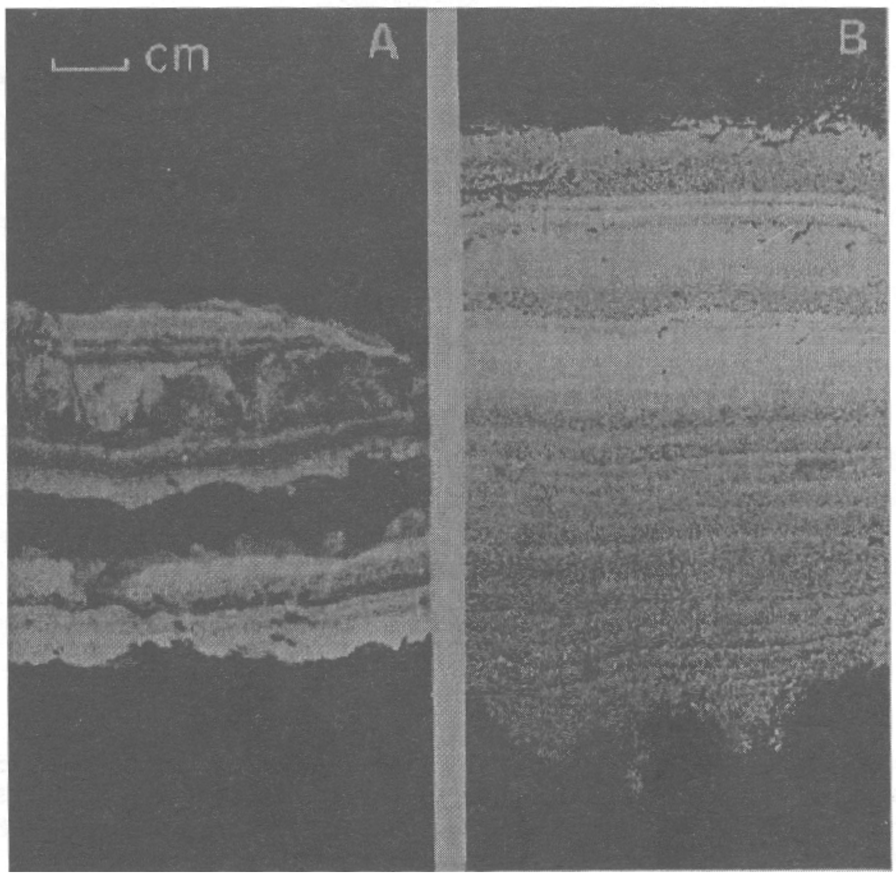

Figure 2. Glacier Peak (A) and Mazama (B) tephras from Lost Trail Pass Bog, Montana.

The following brief description highlights the main features of western Washington's late-Quaternary vegetation history to provide a broader chronologic and paleoclimatic context for discussion. The emphasis follows Whitlock (1992), who reviewed and explained the fossil records by reference to recent climatic models (COHMAP Members 1988; Thompson and others, in press).

During the last glaciation (20,000-14,000 B.P.), continental ice sheets cooled the middle latitudes, and winter storm tracks shifted south, leaving the Northwest cold and dry. Even the western Olympic Peninsula lowlands sported vegetation resembling today's cool, maritime, subalpine parkland of the Olympic Mountains. In the lowlands, sparse trees included spruce (*Picea* spp.), pines (*Pinus* spp.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and western hemlock (*T. heterophylla* (Raf.) Sarg.). Treeless, alpinelike communities occupied glacial margins and exposed sites. With a warming sea surface after 15,000 B.P., an ameliorated coastal climate enhanced the success of spruce, alder (*Alnus* spp.), and western hemlock.

Dominance of grass (Gramineae), sedge (Cyperaceae), and sagebrush (*Artemisia* spp.) pollen with macrofossils of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) suggest that the Puget Trough lowlands sustained open alpine parklands (fig. 3). Precipitation was much reduced, and mean annual temperatures were perhaps 5-7° C cooler than today. The most likely modern analog is found east of the Cascades in the alpine of the northern Rocky Mountains.

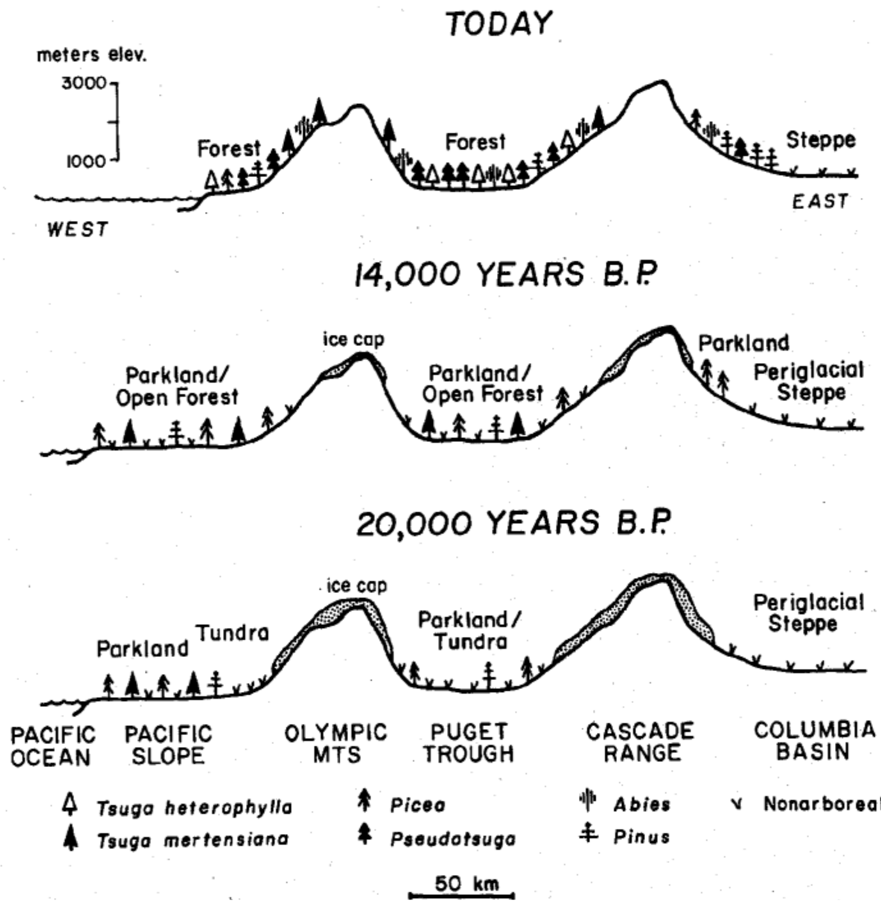

Figure 3. Schematic transect across southwestern Washington shows distribution of ice and dominant vegetation today, at 20,000 B.P. during the height of mountain ice caps (Evens Creek Stadel, and at 14,000 B.P. (Vashon Stade) during the maximum advance of Cordilleran glaciers into the Puget Trough north of this fransect (after Barnosky 1984, Whitlock 1992).

Between 14,000-10,000 B.P., deglaciation and appearance of temperate taxa marked the transition from the late glacial to the Holocene. Precipitation increased and annual temperatures rose to near modern values by the end of this period. New species forming transitional communities without modern analogs filled the freshly deglaciated terrain of the Puget Trough. Lodgepole pine (*Pines contorta* var. *latifolia* Engelm.), the most successful invader, was soon joined by alders, spruce, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western hemlock. Just south of the ice sheet, temperate, low-elevation elements first mixed with, then succeeded montane species.

Early Holocene introduction of xerothermic communities began about 10,000 B.P., when greater summer radiation brought warmer, drier summers to the Northwest. Whitlock and Bartlein (1993) suggest that summer dry areas of today were even drier about 9000 B.P., and summer wet areas (for example, the Southwest United States watered by the Mexican monsoon) were wetter than today. Their notions for the

Northwest find support in record after record from both sides of the Cascades. For example, between 9500 and 5000 B.P., the fossil pollen sequences from the Olympic Peninsula and Puget Trough show more Douglas-fir and bracken fern (*Pteridium aquilinum* (L.) Kuhn.) than today. Also, local prairies expanded, and sediments of this period contain abundant charcoal that attests to the increased importance of wildfires. In the southern Puget Trough, Washington, the late glacial forest gave way to open forest or savannah, similar to the historic vegetation of the Willamette Valley, Oregon.

After about 5400 B.P., increasing precipitation and rising water tables are again apparent on both sides of the Cascades. In western Washington, mesophytic taxa such as western redcedar (*Thuja plicata* Donn ex D. Don), western white pine (*Pinus monticola* Dougl. ex D. Don), and western hemlock assumed more importance, prairies became smaller, and modern plant associations began to emerge.

The highlights of western Washington's vegetation history for the last 20,000 years (Whitlock 1992) give a general idea of major climatic episodes and their influences (fig. 3). These generalities, however, often come from detailed data illustrating the continual short, sharp climatic shifts that produced rapid changes in the Northwest's vegetation directly (for example, through soil moisture) or indirectly (through fire and disease).

The Eastside Story

Fossil records of late-Quaternary vegetation east of the Cascades have been the subject of sporadic study since the 1930s, when Henry P. Hansen (1947) pioneered pollen analysis in Washington and Oregon. His studies showed that the Northwest's vegetation had been dynamic throughout the late-Quaternary in response to climate, volcanic eruptions, and fire. Instability and change were the norm. Over the past decade, several reviewers have compiled what is known about the late-Quaternary fossil pollen and plant macrofossils of the region and have discussed the chronologies and causes of vegetation change in the interior Northwest and adjacent areas (Barnosky 1985; Barnosky and others 1987; Chatters, in press; Heusser 1985; Mehringer 1985; Whitlock 1992).

Familiar eastside plant associations in steppe, woodland, montane and moist maritime forests, and alpine areas consist of species that have responded independently to the varying intensities of numerous glacial-interglacial cycles. In each cycle, brief warmth punctuated long, cold intervals, and plants responded to the vagaries of climate, dispersal potential, competition, selection, soils, topography, volcanic eruptions, fire, chance-and, more recently, ever increasing numbers of people. With few exceptions, details of past species distributions and associations are poorly understood in this region. Evidence is mounting, however, for the general features of late-Quaternary vegetation history (fig. 4), for their chronology, and for their causes.

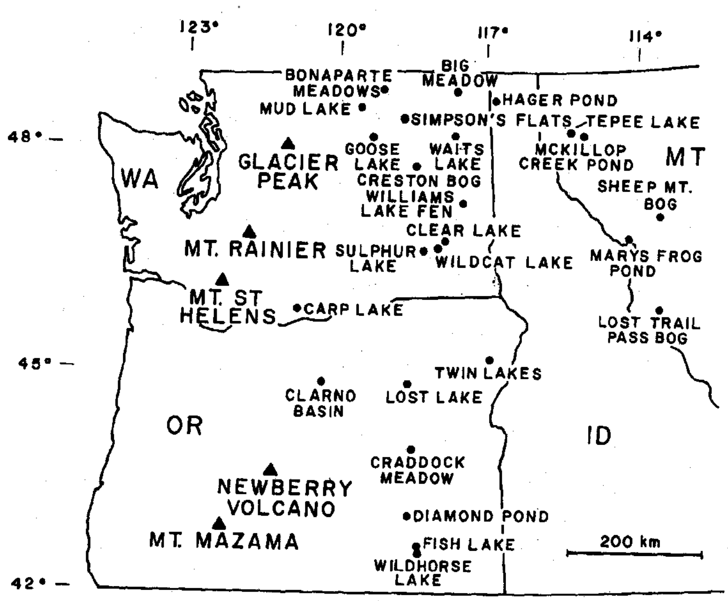

Figure 4. Important eastside study sites for fossil pollen and woodrat middens.

Steppe, eastern Washington-Although the northwestern United States is noted for its remarkably diverse conifer forests, steppe covers more area than all forest types east of the Cascades in Washington and Oregon (Franklin and Dyrness 1973, fig. 27). Grassy communities extend upward from shadscale associates in the hot, dry interior basins, through sagebrush and western juniper (*Juniperus occidentalis* Hook.) woodlands, ponderosa parklands, the lush Palouse grasslands of eastern Washington, and mountain grasslands of southeastern Oregon. Between 20,000 and 4000 years ago, steppe was even more widespread. In fact, fossil pollen or woodrat (*Neotoma* spp.) midden macrofossils from the Great Basin (Thompson 1990, Wigand and Nowak 1992) to southeastern Idaho (Beiswenger 1991) to eastern Washington (Barnosky 1985) and Oregon (Mehringer 1985) attest to expansion of steppe under cold continental conditions coincident with the last glaciation and continued importance of steppe with high temperatures of the early and mid-Holocene.

From 20,000 to 12,000 B.P., south of continental ice and below the mountain glaciers, cold steppe typified much of the northwestern interior of the United States. Carp Lake, southwestern Columbia Basin, Washington, holds sediments spanning parts of the past 33,000 years (Barnosky 1985). Sagebrush and grass pollen dominate this record. Slightly more conifer pollen before 23,000 B.P. suggests temperate steppe, but full-glacial temperatures too cold for trees apparently produced cold sagebrush steppe. According to Whitlock (1992), this sequence indicates colder and drier conditions from 23,000 to 10,000 B.P., with the lower tree line higher than today.

All other fossil pollen localities from eastern Washington are younger than Carp Lake because they lay in the path of glaciers or scabland floods until after 13,000 B.P. Through the oldest date to < 13,000 B.P., without exception, they show initial dominance of sagebrush and grass pollen. Sites now well within areas dominated by conifers continue to show large values of sagebrush, grass, and chenopod pollen until some time between the fall of Mazama tephra (6850 B.P.) and about 4000 B.P. For the pre-Mazama period, the most detailed analyses come from Williams Lake Fen.

At 635 m, Williams Lake Fen is located in a flood-formed plunge pool between Badger and Williams Lakes, 20 km south of Cheney, Washington. Its present position is within communities dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) where it meets *Artemisia tripartita-Festuca* and *Festuca-Rosa* communities that spread to the west and south (Daubenmire 1970). Initial coring and analyses established the site's potential and indicated grass and sagebrush dominance for most of the Holocene. Ponderosa pine was not important here until after 4000 B.P. (Nickmann 1979).

Recently, larger and deeper cores and additional analyses established details of late-glacial tephrochronology and the sequence of vegetation that followed the last of the Lake Missoula floodwaters through the Cheney-Palouse scablands. These cores (Mehringer, unpub.), dating from about 12,700 B.P., bottomed in flood gravels at 10.83-m sediment depth. They hold two layers of Mazama tephra separated by 9 cm of lake deposits and five late glacial tephra-one from an unknown source (the 10,600 B.P. "Tawny Ash"), two from Glacier Peak (11,250 B.P.), and. two (one above and one below the Glacier Peak tephra) from Mount St. Helens (Foit and others 1993). Selected ratios and percentages illustrate the fossil pollen sequence and suggest trends in past vegetation and climate.

Selected curves of 64 analyses of pre-10,000 B.P. sediments from Williams Lake Fen reveal details of events related, through climate, to fluctuating lake level, fire frequency, and vegetation. Large values in pollen curves of two kinds of lake-edge plants, sedge and waterlily (Nymphaceae) (fig. 5), indicate shallow water nearer the coring site. Their largest pre-Mazama values center on 9.85-m depth, corresponding to large charcoal concentrations. Three trends are evident before 10,000 BY (figs. 5, 6, 7).

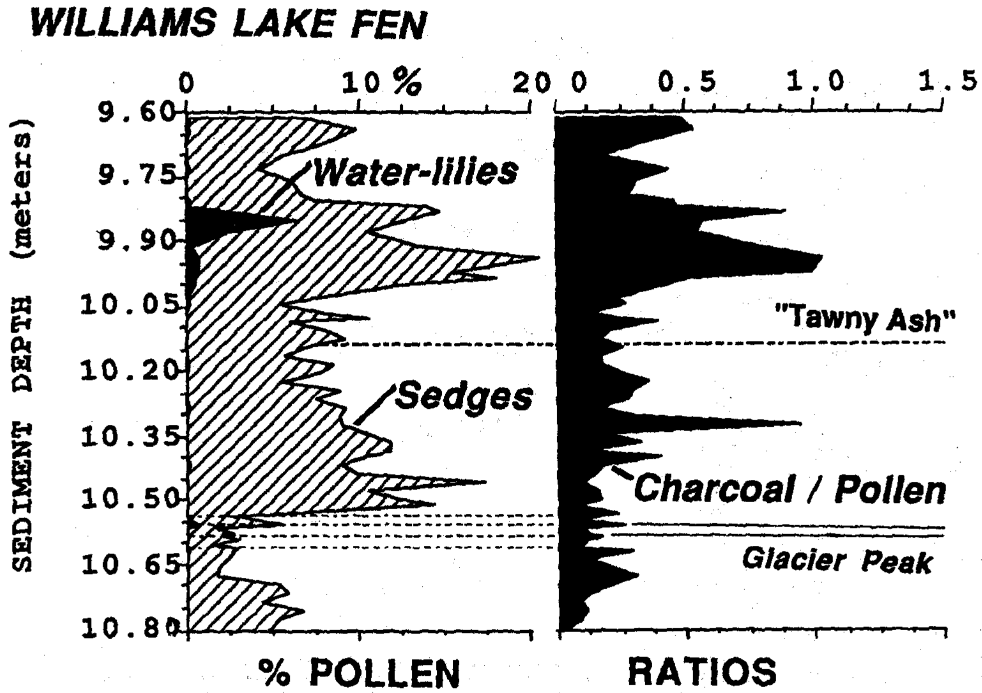

Figure 5. Percentages of pollen types showing correspondence between shallow-water indicators and charcoal abundance.

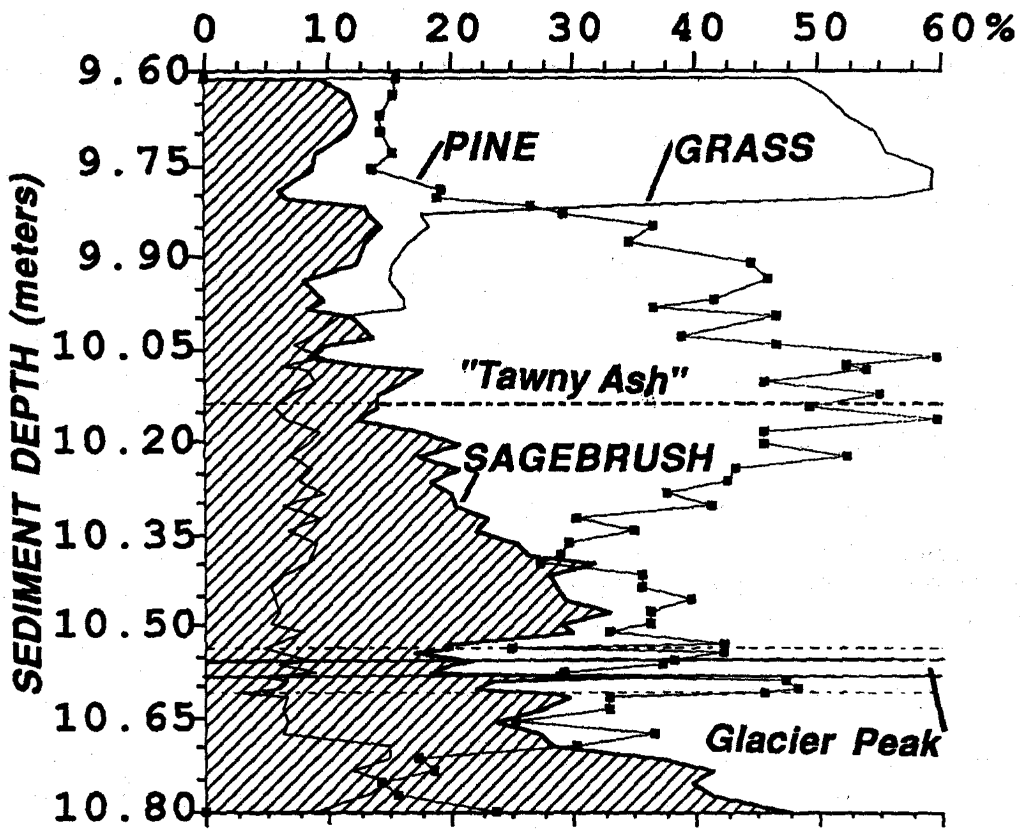

Figure 6. Percentages of sagebrush, grass, and pine pollen at Williams Lake Fen dating from about 12,700 after the last Missoula flood to about 10,000 B.P. after the decline of the late-glacial pine pollen event. "Tawny Ash" dates to 10,600 B.P.

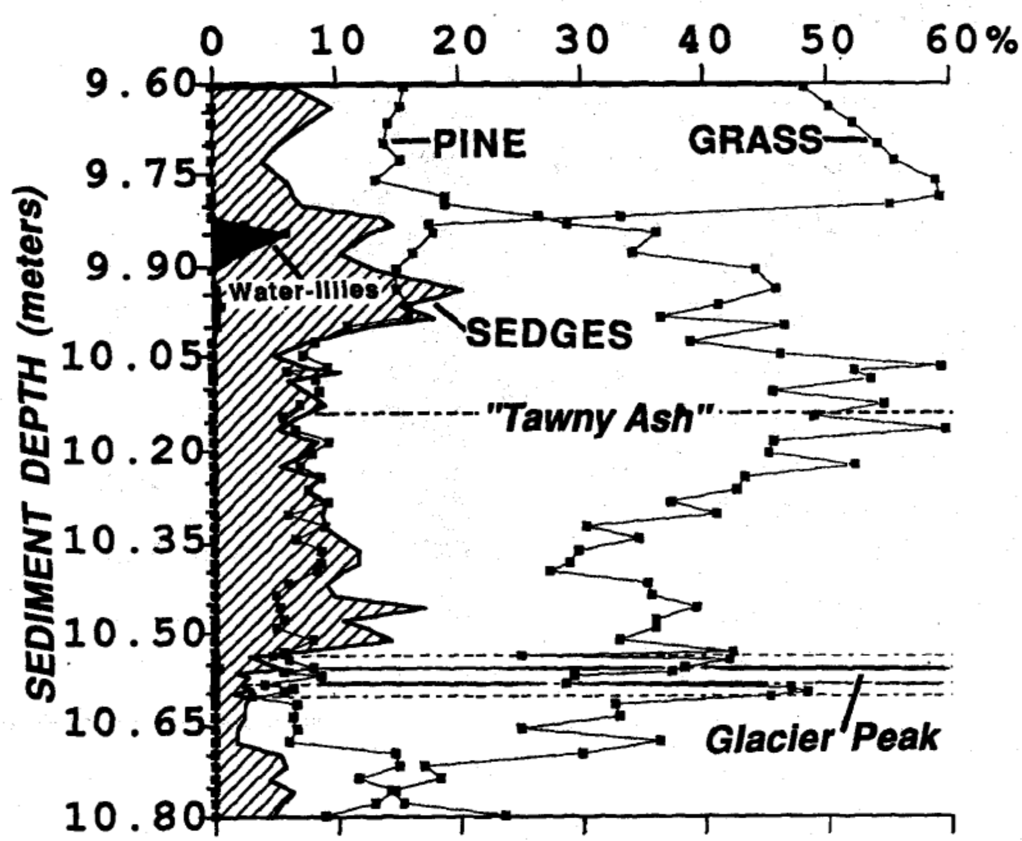

Figure 7. Percentages of water-lily and sedge pollen (shallow water-indicators) at Williams Lake Fen, compared with the grass and pine pollen curves. "Tawny Ash" dates to 10,600 B.P.

- Smallest pollen influx, largest percentages of spruce and birch pollen, and primary importance of sagebrush pollen suggest cold continental conditions from about 12,700 to 12,000 B.P.
- From about 12,000 to 11,000 B.P., grass and sagebrush pollen vary but pine pollen generally increases.
- The period from 11,000 to 10,000 B.P. shows marked fluctuations and the largest conifer pollen values (perhaps indicating a Younger Dryas-like oscillation) (Engstrom and others 1990, Zhisheng and others 1993).

After the second Glacier Peak ashfall, declining sagebrush and grass counts, and large pine pollen counts, indicated significant and rapid expansion of conifers, followed by their catastrophic decline (from 60 to 14 percent of total terrestrial pollen) and grass dominance (50 to 60 percent). The pine pollen peak centered on 10,600 B.P. result from more than one invader because it includes both haploxylon (white pines such as limber (*P. flexilis* James) and whitebark (*P. albicaulis* Englem.) and diploxylon types (such as lodgepole and ponderosa pines), as well as continued small amounts of spruce and fir pollen.

Perhaps a reliable snow pack, sufficient to protect young conifers and shorten the period of low late summer and fall soil moisture, encouraged rapid expansion of mixed conifers at lower elevations in the eastern Cascade foothills and on favorable sites throughout eastern Washington. Whatever the reason, climatic conditions that had brought success to conifers after the fall of Glacier Peak tephra changed suddenly.

Pollen of aquatic plants shows that shrinking lakes accompanied diminishing conifers. For example, between 9.8 and 10 m (centered on 9.85 m), indicators of shallow, warm water first appear in abundance. These indicators include the only pre-Mazama concentrations of water-shield (*Brasenia* sp.) pollen, the largest percentages of sedge and cat-tail (*Typha* spp.) pollen, and waterlily (*Nuphar* sp.) pollen and leaf hairs. Large charcoal values indicate increased fire frequencies or intensities.

By about 10,000 B.P., grassland must have dominated more of eastern Washington than it does today. At Williams Lake Fen, grasslands apparently persisted for the next 3000 years, with few differences by comparison with the preceding 3000 years. Slight increases in pollen percentages of saltbushes (*Atriplex* spp.) and (*Sarcobatus* spp.), sagebrushes, and other composites (compositae), however, indicate probable upwind expansion of more xeric steppe and newly exposed margins of shrinking lakes and ponds before the eruption of Mount Mazama.

The shift from conifer to grass pollen dominance at Williams Lake Fen about 10,200 B.P. is perhaps the most striking change recorded in this region's record of postglacial vegetation. At Wildcat Lake (Mehringer, unpub.) and Goose Lake (Nickmann and Leopold 1985), the shift from conifer to grass pollen dominance was similarly dated and as clearly revealed by close sampling. Hebda (1982) saw the same pattern in the southern interior of British Columbia where he reconstructed the post glacial vegetation sequence, emphasizing grassland, as follows:

- ☐ 13,000 to 12,000 B.P., open pioneer treeless vegetation;
- ☐ 12,000 to 10,000 B.P., mixed conifer forest invaded, established and declined;
- ☐ 10,000 to 8000 B.P., xeric grassland maximum;
- ☐ 8000 to 4500 B.P., mesic grassland, extent partially reduced by Douglas-fir and ponderosa pine; and
- ☐ 4500 to 3000 B.P., minimum grassland, maximum forest expansion into former grassland, and beginning of recent conditions of climate and vegetation.

From study of Wildcat Lake cores, Davis and others (1977) described effects of historic disturbance reflected in the changing pollen of aquatic, weedy, and exotic species, and response of algae to erosion and organic enrichment. Blinman and others (1979) described details of the Mazama tephra sequence. Since then, Wildcat Lake was cored again through 5 m of water to a sediment depth of 27.39 m (Mehringer, unpub.). Like Williams Lake Fen, the basal date is about 12,700 B.P., and Glacier Peak tephras allow exact correlation. Unlike sites farther from eastern Washington's arid core, however, Wildcat Lake has remained in steppe since at least 10,000 B.P. Today it lies within the *Agropyron-Festuca* grassland bounded on the west by the warmer and drier *Artemisia-Festuca* and on the east by the more mesic *Festuca-Rosa* zone (Daubenmire 1970).

Ternary plots (fig. 8) of grasses, sagebrushes, and saltbushes separate various steppe communities, as judged from plots of their fossil pollen over the last 5700 years. The same technique is helpful in distinguishing fossil pollen assemblages from Wildcat Lake (fig. 9) and, together with other data, lead to the following conclusions (fig. 10):

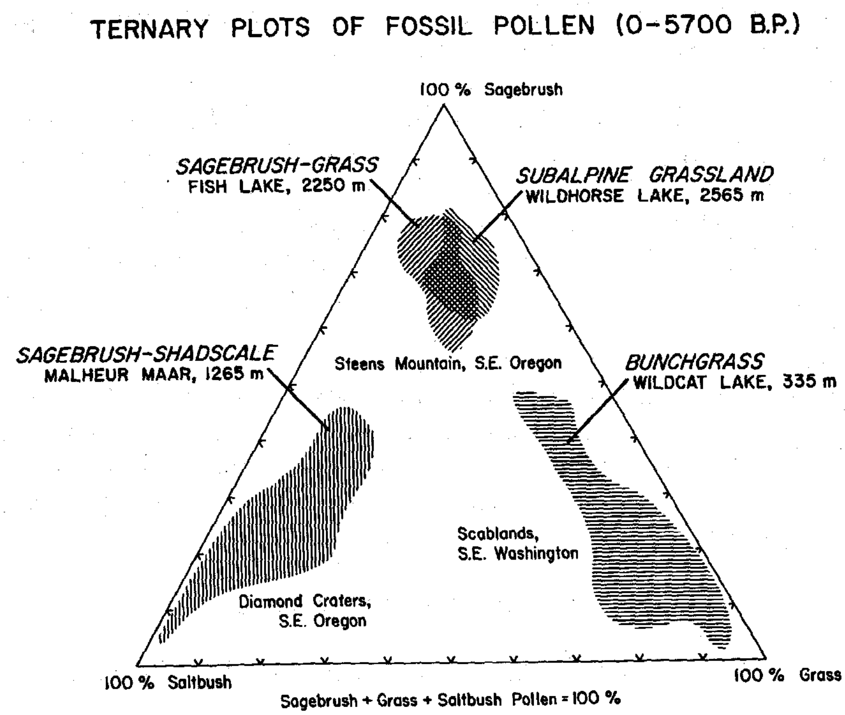

Figure 8. Ternary plots of fossil pollen from four steppe communities in eastern Oregon and Washington. Relative abundances of saltbushes (including *Sarcobatus*), sagebrushes, and grasses distinguish steppe associations that most often produce monotonous Holocene pollen profiles dominated by nonarboreal pollen and by pine pollen transported long distances (Mehringer 1985).

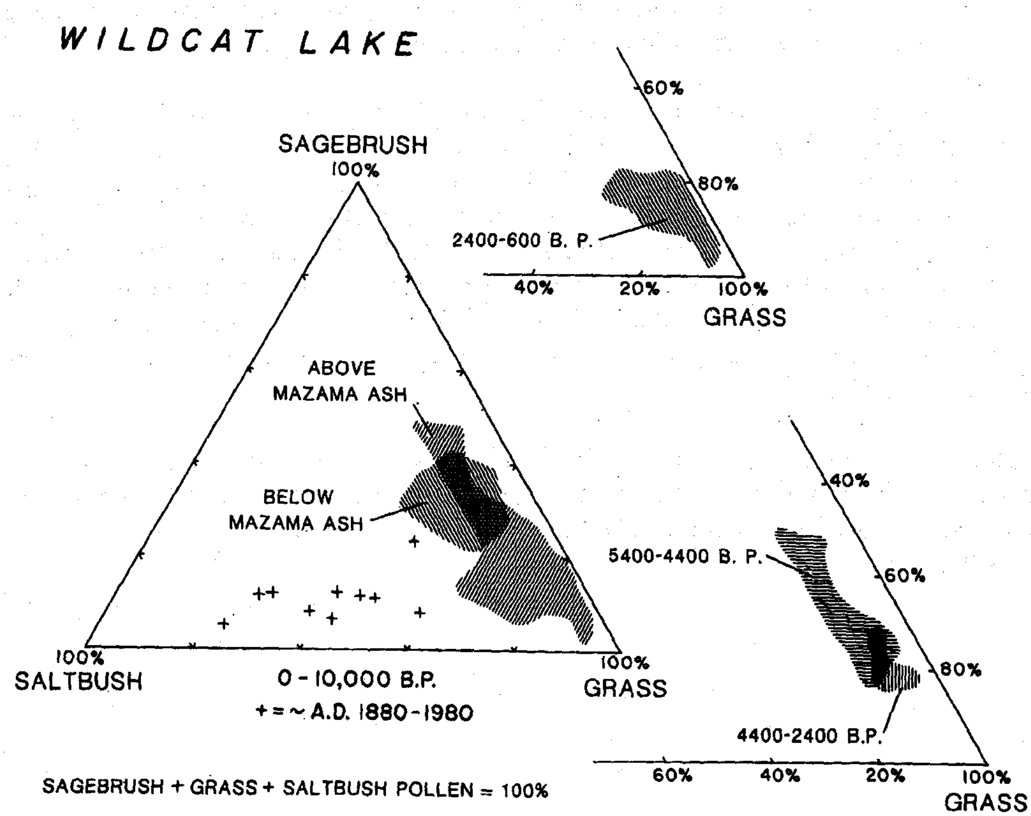

Figure 9. Ternary plots of pollen from saltbushes, sagebrushes, and grasses from selected periods of the last 9000 radiocarbon years from Wildcat Lake, Washington: Note that the largest grass values occur within the last 2400 years and that samples of the past 100 years (+) are distinctive (Mehringer 1985).

- ☐ Pre-Manama samples (9000 to 7000 B.P.) fall within a cluster in which both grass and sage-brush pollen are important. Sagebrush pollen values place these samples in big sagebrush (*Artemisia tridentata* Nutt.) communities to the west.
- ☐ Sagebrush communities, established locally before eruption of Mount Manama, expanded where soils permitted; sagebrush reached a maximum eastward position > 50 km east of Wildcat Lake before 5400 B.P.
- ☐ Sagebrush gradually gave way to grass between 4400 B.P. and 2400 B.P.
- ☐ The relatively large grass pollen values of the last 9000 years are not reached until into the last 2400 years.

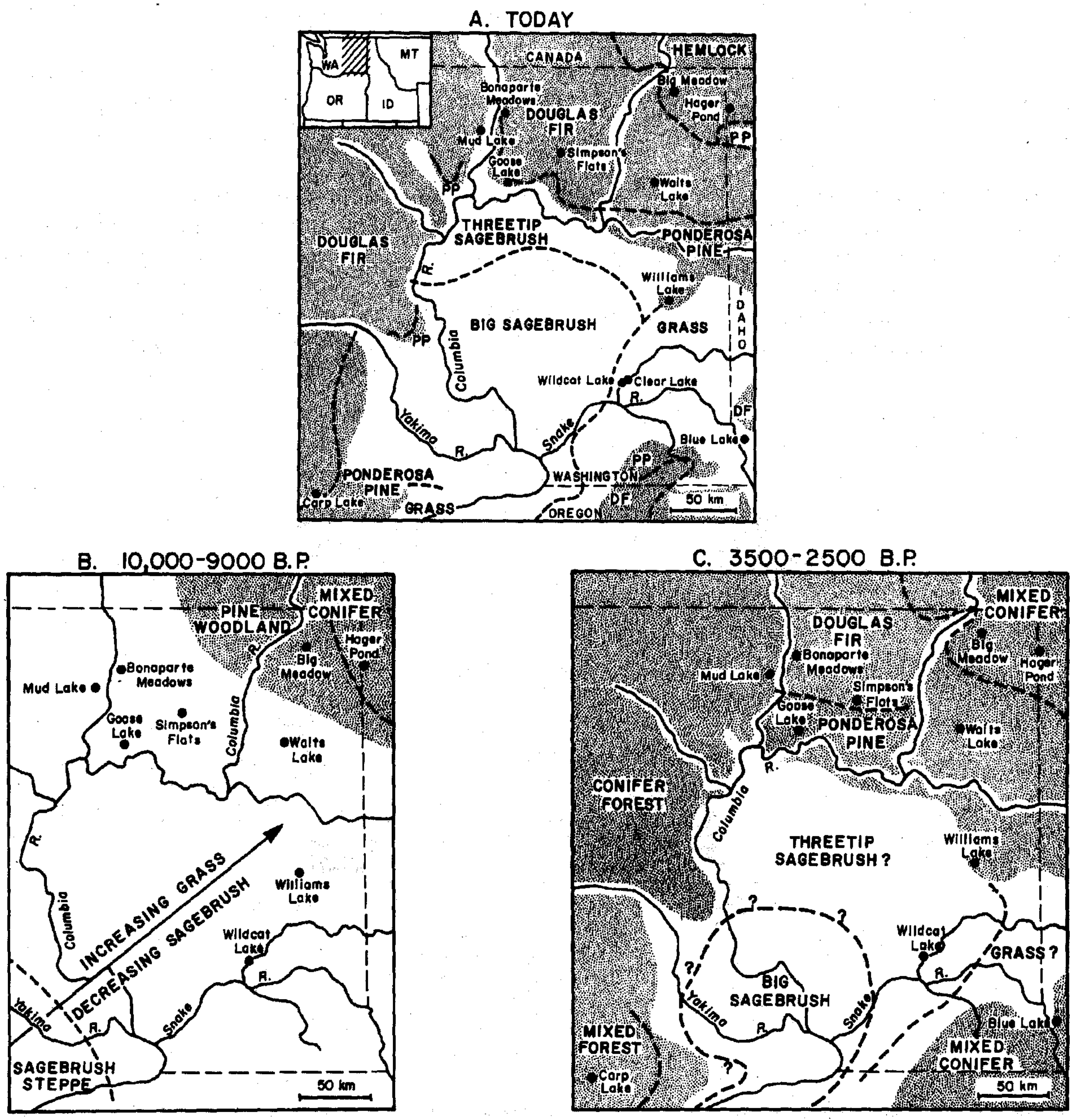

Figure 10. Today's steppe-woodland border and estimates of its position 10,000 to 9000 B. P., when steppe replaced conifer woodlands and forest, and 3500 to 2500 B.P., when conifer woodlands probably advanced into steppe all along eastern Washington's steppe-woodland ecotone (after Chatters, in press; Chatters and others, in press).

Steppe, eastern Oregon-Steens Mountain, southeastern Oregon, is unusual in lacking a montane coniferous forest zone (McKenzie 1982) and is, therefore, ideal for study of changing steppe vegetation. There, as elsewhere at lower elevations from the northern Great Basin to the Columbia Basin, various amounts of pollen produced by grasses, saltbushes, and sagebrushes are the primary clues to relative abundance of major steppe genera as influenced by climate (fig. 8).

Sites on Steens Mountain also show a long history of treeless vegetation with changing abundance of grass and sagebrush. At Fish Lake, sagebrush steppe followed retreating glaciers to 2300 m by 12,000 B.P., where it now persists. There; late glacial pollen spectra dominated by sagebrush and grass are distinguished from those of the Holocene by larger values of juniper (probably *J. communis* L.) and pine pollen suggesting an early, but short-lived, downwind source.

Cores from Fish and Wildhorse lakes in sagebrush and subalpine steppe, and from Diamond Pond on the sagebrush-shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.) desert ecotone, are precisely correlated by six volcanic ashes deposited over the last 6850 radiocarbon years. Fossil pollen exhibits a general three-part division of Holocene vegetational change with differences in the timing of specific events at each site. These differences most probably resulted from effects of temperature and precipitation at various elevations.

Greater abundance of sagebrush pollen in relation to grass pollen indicates relatively low effective moisture at Fish Lake (2250 m) between about 8700 and 4700 B.P. (fig. 11). The mid-Holocene episode of sagebrush pollen abundance began 1500 years earlier than the temperature-controlled upward expansion of sagebrush to Wildhorse Lake (2565 m) about 7200 B.P. Also, it ended at least 1000 years before grass again assumed dominance at Wildhorse Lake (about 3800 B.P.; fig. 11), marking the end of this prolonged but variable period of relatively higher temperatures and reduced snowpack (Mehringer 1987)..

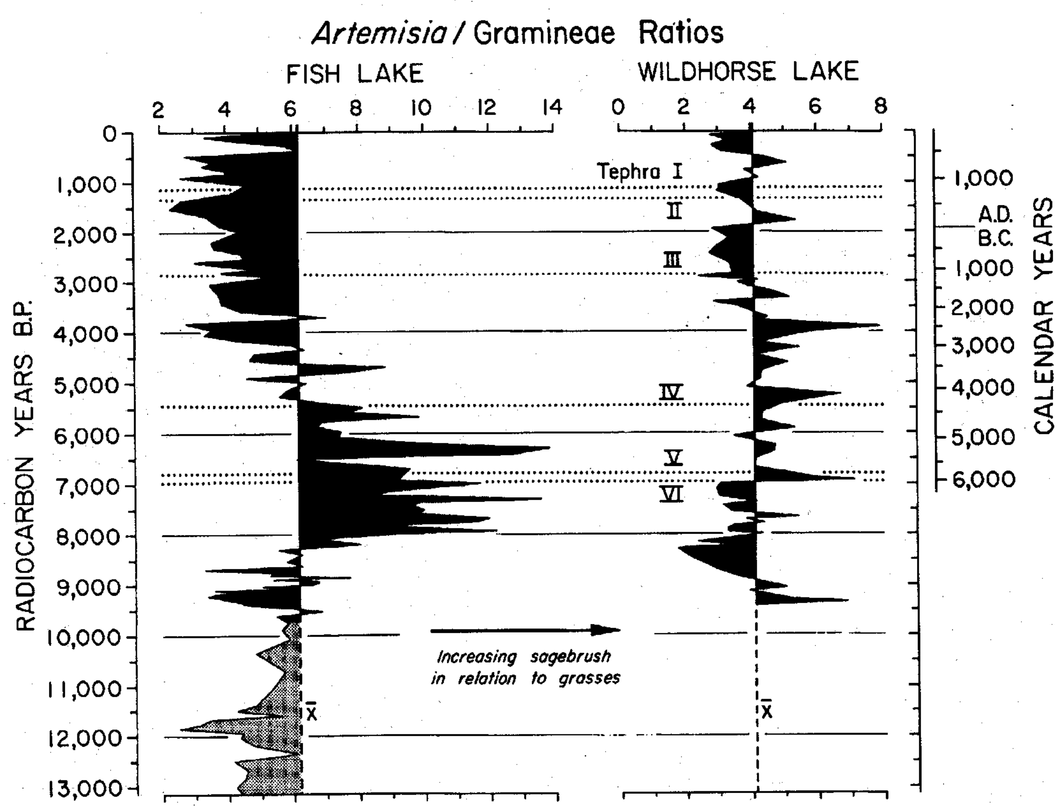

Figure 11. Ratios of sagebrush to grass pollen plotted about their means of the last 9700 and 9300 years B.P. Increase in sagebrush in relation to grass at Fish Lake (2250 m) indicates less effective moisture. The same variations at Wildhorse Lake, 315 m higher, at the current upper elevational limit of sagebrush, suggests up-slope advance of sagebrush because of warmer conditions with fewer snow patches lasting into summer (Mehringer 1985).

About the same time (4000 B.P.) at Diamond Pond (Malheur Maar, 1265 m), juniper and grass pollen percentages increased, with declining values of chenopod in relation to sagebrush pollen. Radiocarbondated macrofossils of western juniper from woodrat middens in lava tubes confirm that sagebrush and juniper grasslands replaced xeric shadscale vegetation as suggested by the pollen sequence.

In summary, according to the studies reviewed here, cold steppe dominated the eastside during the last glacial period. After 12,000 B.P., wasting glaciers in the north and shrinking pluvial lakes in the south witnessed a brief conifer expansion, but by 10,000 B.P. all sites now in steppe or ponderosa pine, and some in Douglas-fir mixed forest supported grass and sagebrush. In eastern Washington, the forest fringe had apparently retreated 50 to 100 km in the north and east; it would not approach its present lower elevational limits again until after 4400 B.P. In the Steens Mountains region of southeastern Oregon, steppe vegetation persisted at all elevations, but underwent punctuated differences in importance of grass, sagebrush, and juniper, as well as charcoal that reflects the importance of fire. Here, no evidence suggests that western juniper woodlands were present, much less regionally important, until after 4400 B.P.

Juniper woodland-Studies of radiocarbon-dated plant macrofossils from ancient woodrat middens are revealing the responses of desert shrubs and forest trees to late-Quaternary climatic variation to a detail never achieved solely through fossil pollen. In combination, the two complementary methods give greater resolution than either alone (Mehringer and Wigand 1990).

Unfortunately, except in the most xeric sites, the eastside's climate is not conducive to preservation of woodrat middens because the hardened, dehydrated, and crystallized woodrat urine (amberat) that inhibits decay and cements the mass of plant remains is water soluble; even in protected locations, it may dissolve with seasonally high humidity. At lower elevations in dry caves and rockshelters, however, woodrat middens may persist for at least a few hundred years as-far north as the dry interior of south central British Columbia. There, Hebda and others (1990) recovered Rocky Mountain juniper (*J. scopulorum* Sarg.) twigs, needles of ponderosa pine and Douglas-fir, and pollen and macrofossils of associated shrubs and herbs from two middens dating to 700 and 1150 B.P. The fossils represent species growing locally today. To the south in the northern Great Basin, woodrat middens 10,000 to 20,000 years old are not unusual; some have been dated to > 30,000 B.P. (Thompson 1990, Wigand and Nowak 1992).

At Diamond Craters (BLM Outstanding Natural Area) in southeastern Oregon, and Lava Beds National Monument in northeastern California, plant remains from woodrat middens in lava tubes and rock shelters give a 5000-year perspective on the spectacular historic success of western juniper, despite programs for its eradication (Mehringer and Wigand 1987, 1990). Notions that today's western juniper woodlands are "unnatural" and artificially induced by cattle grazing and fire suppression must be modified in light of recent information from pollen and macrofossils that reveal late-Holocene expanses of juniper most probably exceeding current coverage. The range and abundance of juniper has changed through the late Holocene (figs. 12 and 13). At Diamond Craters, the combination of closely sampled cores from Diamond Pond (Malheur Maar) and woodrat middens in nearby rimrock reveal the reasons for the changing importance of juniper and associated phenomena.

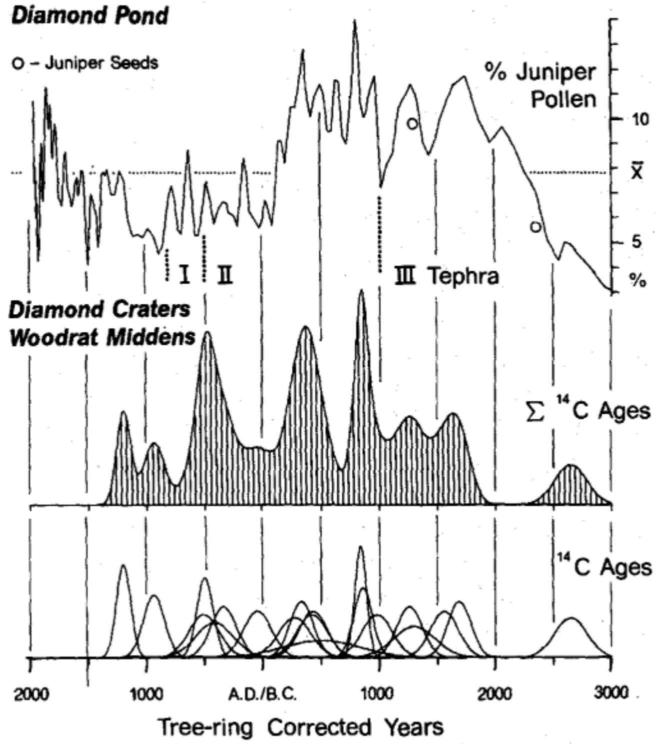

Figure 12. Smoothed percentages of Diamond Pond juniper pollen (fig. 13) and tree-ring-corrected woodrat midden dates, each plotted as a normal distribution with a probability of one; width at the base of each date is three standard deviations. Note that the clusters of midden ages correspond to the larger juniper pollen values from Diamond Pond sediments (Mehringer and Wigand 1990).

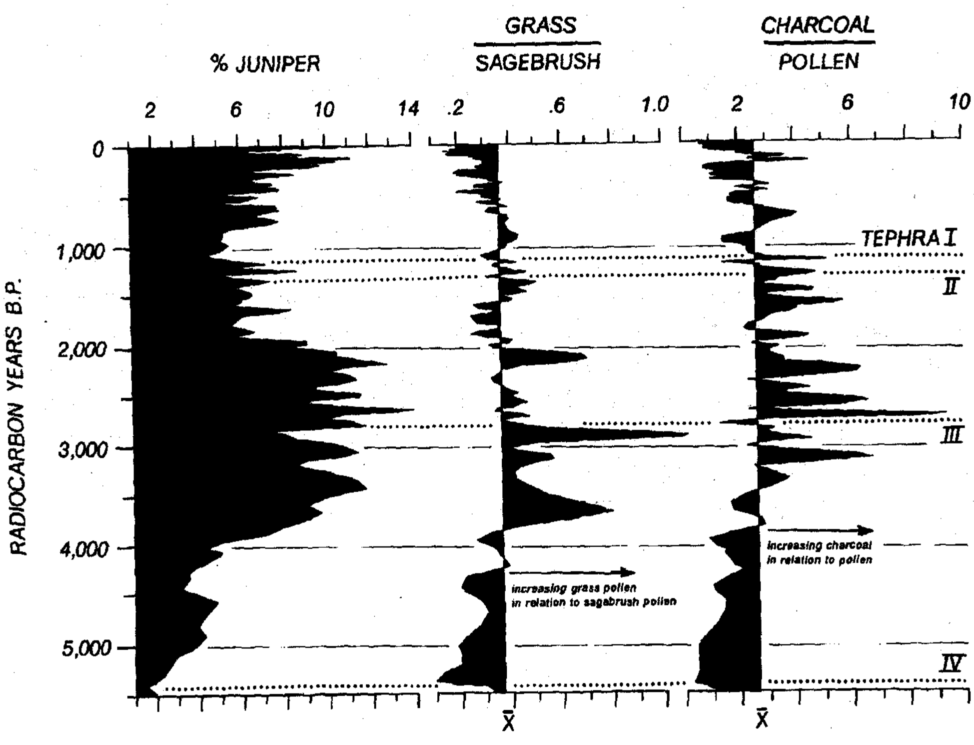

Figure 13. Smoothed juniper pollen percentages and ratios from the Diamond Pond core are plotted about the mean of the average values for each 500-year interval since 5500 B.P. Note correspondence in relative increase in juniper pollen, of grass in relation to sagebrush pollen, and of charcoal in relation to total terrestrial pollen beginning about 4000 B.P. Expansion of juniper woodland, increase in grass, and decline of sagebrush suggested by this diagram are confirmed by macrofossils from woodrat middens (Mehringer and Wigand 1990).

Both macrofossils (Wigand 1987) and pollen of pond weeds (*Potamogeton* spp., *Ruppia marigima* L., *Ceratophyllum demersum* L.), pond edge species such as cattails and sedges, and differing abundances and types of acid-resistant algae reveal periods of varying water depths and quality, and pond size. Deep, fresher water indicators are associated with relatively more grass in relation to sagebrush pollen and more sagebrush in relation to saltbush pollen. Juniper pollen is most abundant in these same samples. Because the water table is controlled by recharge and evaporation, episodes of deeper water suggest periods of more effective moisture. During these periods juniper expanded its range and sagebrush steppe held more grass.

Confirmation of striking changes in the late-Holocene history of juniper woodlands comes from macrofossils in woodrat middens whose ages correspond to large juniper pollen values between about 3800 and 2200 B.P., with several lesser peaks between 2000 and 700 years ago, and again in the late A.D. 1700s and mid-1900s (fig. 12). These middens hold plant assemblages that record the fluctuating lower elevational border of western juniper onto present, barren basalt flows and into communities now dominated by shadscale desert species. Additionally, at a site in the nearby Catlow Valley, where western juniper is common today, a 6100-year-B.P. woodrat midden dating from a xeric interval lacks juniper macrofossils (Mehringer and Wigand 1990). On Steens Mountain, the upper elevational limit of western juniper near Fish Lake has remained unimpeded by competition from other coniferous trees throughout the Holocene. Yet the Fish Lake pollen record does not show western juniper's expansion near its upper elevational limit corresponding to xeric episodes and decline near its lower limit.

According to studies of climate response functions from tree rings, mild winters with ample precipitation and cool springs favor wide annual rings in western juniper (Earle and Fritts 1986, Fritts and Xiangding 1986). The fossil record from Diamond Pond (fig. 13) reveals a relation among the largest juniper pollen percentages and the charcoal to pollen and grass to sagebrush ratios. Algae, plant microfossils, and pollen indicate deeper water during the same period. The woodrat midden fossils and the fossil pollen sequence from Diamond Craters show that juniper's lower elevational limits and abundance changed often over the last 5000 years. On a scale of centuries, juniper increased at times when water tables were higher, grass was most abundant, and fires that favored grass discouraged sagebrush. In the short term, expansion of juniper woodland seems to have been set back by drought and was sometimes ended by catastrophic fires.

Plant macrofossils from woodrat middens from the Pine Creek Drainage of the Clarno Basin, northcentral Oregon, also show the history of western juniper in sagebrush steppe. Croft (1989) concluded that the historic expansion of juniper woodlands is not unique and that western juniper, along with bitterbrush (*Purshia tridentata* (Pursh) DC.), was probably more common than now between about 4700 and 4200 B.P. Otherwise, over the last 5000 years, shrubs, such as big sagebrush and shadscale, and grasses varied primarily in relative abundances.

In eastern Oregon, the record of woodlands is short, either because woodland was not important much before 4000 B.P. or because the fossil record is incomplete. Though western juniper abounds there today, the oldest (6100 B.P.) Holocene woodrat midden from Catlow Valley, Oregon, does not contain western juniper. But western juniper is present at Lava Beds National Monument, northeastern California, by 5200 B.P. and represented by a single seed in pond sediments at Diamond Craters, Oregon, at 4-800 B.P. (Mehringer and Wigand 1987). Just to the south, however, in northwestern Nevada, many more, older, woodrat middens show a long history of shifting distributions of desert scrub, steppe, and woodland.

Study of 96 dated fossil-plant assemblages from 24 woodrat midden localities in northwestern Nevada gave evidence for the 30,000-year presence of Utah juniper (*J. osteosperma* (Torn) Little) and the arrival of pinyon pine (*Pinus monophylla* Torr. & Frem.) only 1700 to 1000 years ago. Wigand and Nowak (1992) suggest the following sequence of changing vegetation and climate for the region along the western arm of Pluvial Lake Lahontan:

- About 30,000 years ago, during a cold and dry period, Utah juniper woodland had a sagebrush and shadscale understory.

- After 24,500 B.P., increased moisture encouraged spread of whitebark pine to as low as 1380 m (1300 m below and 10 km from its present nearest locality in the Sierra Nevada). The increased moisture also promoted sagebrush-dominated, moist, open slopes that now support shadscale.
- By 21,500 B.P., with onset of a cool, dry glacial maximum climate, whitebark pine and Utah juniper gave way to sagebrush-dominated steppe and desert scrub communities.
- Sagebrush steppe expanded with warmer and wetter conditions of the late glacial period.
- After 10,000 B.P., much warmer and drier conditions favored shadscale communities at the expense of sagebrush steppe and juniper woodlands.
- After 4000 B.P., under cooler and more mesic conditions, sagebrush steppe and juniper woodlands regained importance.
- Ponderosa pine arrived in the region only 2000 years ago.
- Macrofossils of pinyon pine finally appeared in woodrat middens between 1700 and 1000 B.P.

Forests-Pollen records from present forests east of the Cascades consistently reveal that the first invading conifers flourished on what had been glacier or lake-covered terrain, flood tracts, or frozen ground supporting cold steppe during the last full-glacial episode. In some places, these conifers persisted; in others, they gave way to grasses and steppe shrubs that remain to the present day or, after a few thousand years and changing climate, were in turn overrun by forests that burned repeatedly but held their ground.

The fossil pollen localities most important in deciphering forest history east of the Cascades are reviewed below. These few records come pitifully short of detailing forest history. They do, however, reveal the broad sweep of changing forest vegetation in response to climate. They also expose specific topical and geographical areas of near total ignorance. For example, despite a few pollen diagrams from the region, the full-glacial fate and Holocene history of northern Idaho's moist maritime hemlock and cedar forestsunrecorded in fossil pollen sequences before 2500 B.P-remain a puzzle. Likewise, late-Quaternary vegetation of the Blue Mountain region of northeast Oregon and adjacent Washington (including the Wallowa, Ochoco, Strawberry-Aldrich, Greenhorn, and Elkhorn ranges) remains unknown for lack of study.

A combination of related factors-including fire suppression, some logging practices, and insect infestations-have left the forests of the Blue Mountains teetering on the edge of an ecological disaster. If appropriate fossil pollen and plant macrofossil data were available, these conditions could be evaluated in terms of natural, longterm disturbances. Even without this urgency, any study of eastside forest history should, perhaps, emphasize forests of the Blue Mountains because of their extent and diversity (Johnson and Clausnitzer 1992). The only two published pollen records from this entire region come from a few exploratory samples collected by Henry P. Hansen (1943) from Anthony Lakes, which offer little information in a modern context, and, from the Silves Valley (Craddock Meadow, 1630 m), which span most of the Holocene. At Craddock Meadow only 23 samples were analyzed, and pollen was poorly preserved. Ponderosa pine, western juniper, and big sagebrush (*A. tridentata* Nutt.) interfinger in Craddock Meadows area today, yet sagebrush was the dominant pollen from about 9000 B.P. until 2000 years or so after the Manama ashfall. Only then did pine pollen values to 60 percent suggest presence of ponderosa pine. Two nearby woodrat middens, dating to 1280 (juniper twigs) and 300 B.P., held species now present at the site (Reid and others 1989).

Cursory examination of cores from two other sites indicate the potential for detailing eastside forest history for northeastern Oregon. Cores from Twin Lakes in the Wallowa Mountains and Lost Lake near Dale, Oregon, show well-preserved pollen and macrofossils in post-Manama sediments (Mehringer unpub.). For instance, Lost Lake, in mixed Douglas-fir, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) forest, holds abundant charred Douglas-fir cones and needles in redeposited Manama tephra. Pollen samples from 3000-year-old sediment show mountain hemlock pollen values indicating a nearby source at that time, whereas younger tephra blankets a layer of western larch needles (*Larix occidentalis* Nutt.). Larch grows nearby today, but the nearest mountain hemlock are about 110 km to the northeast in the Wallowa Mountains (Johnson and Simon 19$7).

In the north, Mack and others (1978a, 1978b, 1978c, 1978d; 1979; 1983) studied several sites, from the San Pod to Priest River valleys of northeastern Washington, northern Idaho, and into adjacent Montana (fig. 14). These sites, along with Williams Lake Fen and Goose Lake, show the local sequence of forest history and also suggest regional trends. Some of these trends could have been anticipated from the discussion of the history of eastern Washington's steppe. They include:

- ☐ Sediments dating to at least 12,000 B.P. show an initial treeless episode dominated by pollen of sagebrush and grass. Spruce, fir, and lodgepole and other pines arrived before the fall of Glacier Peak tephra (11,250 B.P.).
- ☐ Mixed conifers, sometimes with birch (*Betula* spp.), dominate for the next 1000 years or so.
- ☐ By 10,000 B.P., grass or sagebrush began to assume dominance at lower elevations. To the east in northern Idaho and adjacent Montana, larch and Douglas-fir, along with diploxylon pine pollen (lodgepole or ponderosa), and small but persistent percentages of grass and sagebrush pollen indicate predominance of widespread steppe and dry interior forests.
- ☐ By 4000 B.P., as sagebrush steppe retreated toward eastern Washington's arid central core, the forest fringe (ponderosa and lodgepole pine, and larch or Douglas-fir) had begun to advance west and south, and perhaps downsiope from the Cascades as well. Spruce and fir pollen increased at sites within the former forested areas.
- ☐ Between 2500 and 1000 B.P., fossil counterparts of modern forest were apparent at most sites, and eastern Washington's grasslands finally began to achieve their historic importance.

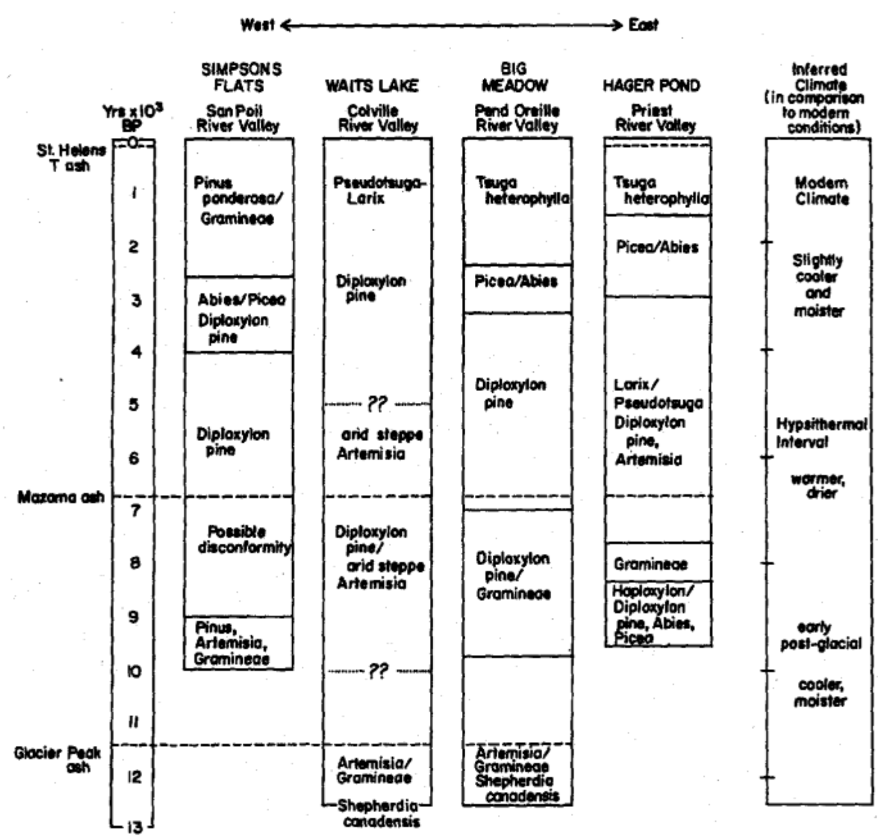

Figure 14. Summary of vegetation dominants and inferred climatic changes for sites in northeastern Washington and northern Idaho since recession of the last ice sheet (from Mack and others 1978d).

To the east, at elevations above 1900 m in the Bitterroot Mountains (Lost Trail Pass, Montana: Mehringer and others 1977a, b) and smaller ranges (Sheep Mountain Bog, Montana: Hemphill 1983, Mehringer 1985, Mehringer and others 1984), coniferous forests dominated throughout the Holocene. Timing and direction of changing vegetation suggest that forest species were reacting similarly to the climatic patterns that influenced the vegetation of eastern Washington.

Sheep Mountain Bog (1920 m), 18 km northeast of Missoula, Montana, lies at the upper limit of ponderosa pine and larch on south-facing slopes. Mixed forests with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce surround the bog. According to fossil conifer needles and cones (Mehringer, unpub.), Douglas-fir has grown near this site since at least 10,000 B.P. Its largest pollen frequencies occur between 9700 and 4000 B.P., along with pollen and macrofossils of lodgepole pine and pollen of ninebark (*Physocarpus* sp.); all of which suggest a dry mid-Holocene forest. Haploxylon and diploxylon pine pollens are represented by macrofossils of whitebark and lodgepole pines. Haploxylon pine pollen (whitebark) is most abundant, along with macrofossils and pollen of spruce and fir, only between 11,000 and 10,000 B.P. This abundance may reflect the short-lived cooling of the Younger Dryas episode described for Williams Lake Fen. The importance of Douglas-fir diminished relative to spruce and fir pollen, which showed marked increases after 4000 B.P.

Before the fall of Glacier Peak ash, subalpine conifers began to fill higher elevations of the Bitterroot Range near Lost Trail Pass Bog (2152 m), where they grow today. Then, before the fall of Mazama ash (about 6850 B.P.), grass and sagebrush pollen percentages, along with pollen of the warmth-requiring Douglas-fir and lodgepole pine replaced the more cold-tolerant whitebark pine. Upslope migration and persistence of Douglas-fir marks a period of undoubted warming, yet an unbroken sedimentary record indicates that the small pond at Lost Trail Pass did not go dry.

About 4000 B.P., Douglas-fir lost dominance to whitebark and lodgepole pines, perhaps for the first time in 5000 years, and retreated to warmer downslope positions. Since that time and especially after 1750 B.P., the vegetation was apparently similar to the present, with at least one unusually cool (and wet?) climatic episode around 3600 B.P. This later event is perhaps the same one noted elsewhere (for example, at Blue Lake near Lewiston, Idaho; Carp and Wildcat Lakes, Washington).

Blue Lake, Idaho (1035 m), is now surrounded by Douglas-fir and ponderosa pine; varying abundances of the pollen and macrofossils of these two trees suggest important variations in effective moisture over the past 4300 years. According to Smith (1983), a relatively warm, moist interval, dominated by Douglas-fir, from 4300 to 4000 B.P. preceded a cooler period from 4000 to 3000 B.P., with mixed Douglas-fir, lodgepole, and ponderosa pine. Then, conifer pollen decreased from 3000 to 1700 B.P., and dry, open, ponderosa pine parkland persisted until 1000 B.P., when vegetation similar to present day’s emerged.

Volcanic Ash (Tephra) and Charcoal

Late-Quaternary volcanic eruptions, wild fires, and fires set by the prehistoric inhabitants no doubt influenced vegetation history. Where influences were extreme, the ecological effects of volcanic activity are obvious. But immediate effects and the long-term consequences of any prehistoric catastrophe-even one as severe as the eruption of Mount Mazama (Crater Lake, Oregon)-are not always discernible: No one can say exactly how most vegetation of the northwestern United States would be different if Mount Mazama, Mount St. Helens, or Glacier Peak had been inactive in the last 20,000 years, nor in what ways the magnitude and timing of their eruptions determined or altered the course of Holocene vegetational “development.” Certainly, pumice soils of east-central Oregon favor lodgepole pine. For the Yellowstone National Park region, Whitlock (1993) also ascribes differing vegetational histories to volcanic soils. There, over the last 5000 years, mixed forests of pine, spruce, and fir developed on andesitic and nonvolcanic soils, and closed lodgepole pine forests persisted on rhyolotic soils.

Effects of an ashfall on terrestrial or aquatic ecosystems depend on thickness of primary and secondary tephra, season and duration of the ashfall, and time separating recurrent eruptions. Therefore, estimates of the depositional chronology of ashfalls is essential to evaluating their influences (Blinman and others 1979, Mehringer and others 1977b). Sagebrush pollen from Mazama tephra at Lost Trail Pass, Montana (fig. 2), suggested an autumn ashfall. A graded bed of clean tephra with little pollen and lack of seasonal indicators implies that Glacier Peak tephra fell at Sheep Mountain Bog, Montana, when the lake was ice free and probably in late summer (Mehringer and others 1984).

Varying charcoal accumulation rates, pollen-to-charcoal ratios, and washed-in charcoal layers may reveal the history of fire in forest and steppe (fig. 13; MacDonald and others 1991). The observation that charcoal was unusually abundant over the past 2000 years or so near Lost Trail Pass, Bitterroot Mountains, Montana, led to three studies of late Holocene relations between reconstructed vegetation, charcoal layers, and charcoal and pollen abundance in lake sediments. Three widely separated sites showed the same broad chronological patterns of changing charcoal abundance over at least the past 7000 years or more (Mehringer 1985, table 3). All sites showed the largest charcoal-to-pollen ratios during the last 1000 years. Perhaps this superabundance of charcoal is related to increasing populations of Indians, who used fire as a management tool (Barrett and Arno 1982, Gruell 1985). Leiberg (1900, p. 314-316) estimated that Indians burned 2,270,000 acres (9183 km) during the last 200 years before their populations plummeted as a result of small pox, measles, and conflicts.

At Blue Lake, near Lewiston, Idaho, severe fires, resulting in distinctive bands of.washed-in charcoal, burned through Douglas-fir forests about once every hundred years between 4300 and 4000 B.P. Only two severe fires in mixed conifer forests left charcoal layers between 4000 and 3100 B.P., but such fires were nearly twice as common between 3100 and 1700 B.P. From 1700 to 1000 B.P., severe fires averaged only one in 175 years. Light surface fires, leaving no charcoal layers in the-lake sediments but producing abundant microscopic charcoal, characterized the last 700 years (Smith 1983).

Fire frequency, as evidenced by the charcoal-to-pollen ratio at Sheep Mountain Bog, Montana, declined gradually between 7000 and 2000 B.P. and then increased to produce a superabundance of microscopic charcoal during the past 1000 years. These peaks of charcoal in bog sediments proved comparable with tree fire-scar studies and historic records (Hemphill.1983). A remarkable record of early and middle Holocene fires comes from deposits of Sheep Mountain Bog.

The sedimentary sequence at Sheep Mountain Bog began about 12,500 B.P., with till left by the wasting glacier that had carved the > 12-m-deep depression. From that time, the depression held a lake that accumulated primary and redeposited Glacier Peak and Mazama tephra, and distinct layers of charcoal. These layers were graded beds and usually formed couplets. Sand, coarse silt, and charcoal made.up the lower black layer of each couplet, and the upper layer consisted of gray wood ash and clayey silt. In,all, 167 layers (most of them couplets) were measured with a dissecting microscope (fig: 15). Between 10,600 and 4000 B.P., erosion after fire accounted for at least 23.5 percent of sediments deposited in the basin.

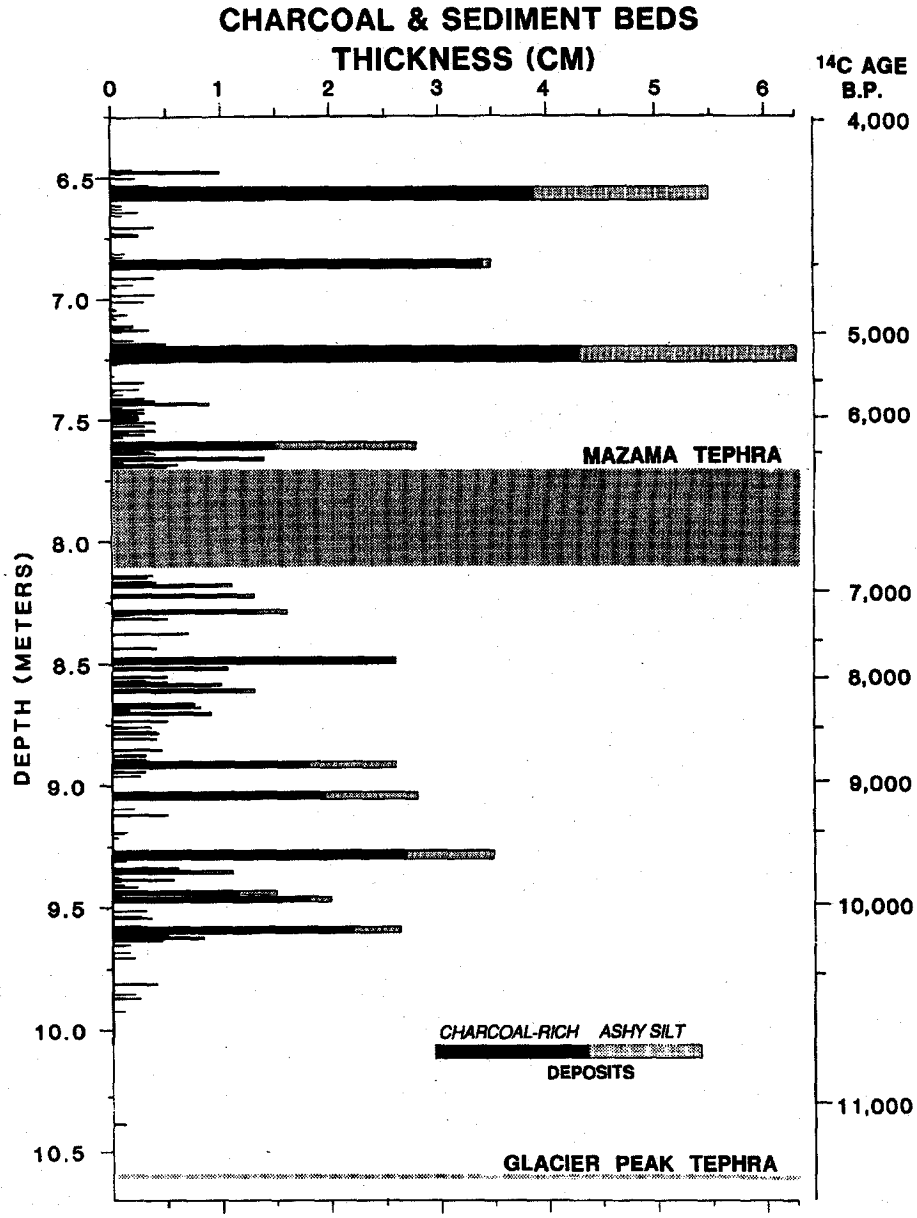

Figure 15. Widths of black charcoal-rich sands and silt layers overlain by gray, ashy silt and clay layers containing fine charcoal and ash. These couplets, and occasional single charcoal-rich layers, resulted from wash-in after fire and, therefore, afford a 6000-year record of the number and intensity of fires in the basin of Sheep Mountain Bog (Mehringer, unpub).

The charcoal, ash, and sediment layers resulted from erosion into the lake after fire and, therefore, afford a record of fires in the basin. The thickest layers most likely result from severe erosion after high-intensity, duff-destroying fires, and the thinner layers represent low-intensity fires. By 4000 B.P., a filtering fringe of vegetation surrounded the gradually filling pond, and slopewash deposits no longer reached the coring site. Distribution of the measured layers show no single “natural” fire regime in the 6400 years represented by charcoal layers; three patterns are evident:

- ☐ Many small fires (around 6000 B.P.);
- ☐ Small fires with occasional large fires (around 8000 B.P.); and
- ☐ Few small fires followed by potential stand-replacing fires (around 5400-4200 B.P.).

The first charcoal layer was deposited about 11,150 B.P., while lodgepole pine dominated scattered woodlands. Four narrow (0.5-2.5 mm) laminae form the first cluster of charcoal layers about 10,600 B.P. At this time, the site supported scattered whitebark pine with spruce and fir; sagebrush occupied openings.

Between 10,200 and 9600 B.P., the number and intensity of fires suggest a different climatic regime. By the end of this period, lodgepole pine and Douglas-fir largely replaced whitebark pine, spruce, and fir. This first period of abundant charcoal at Sheep Mountain Bog is also the period of demise of conifer woodlands in east-central Washington and the largest pre-Mazama charcoal values at Williams Lake Fen (fig. 5). The number of fires increased around 8000 B.P., when pollen frequencies show the largest values of Douglas-fir and smaller values of pine pollen, primarily lodgepole pine.

From 5400 to 4200 B.P., many, very small fires burned, and, judging by thickness of the charcoal layers, the three largest fires burned. At Sheep Mountain Bog, this period saw increasing percentages of pine, spruce, and fir pollen and decreasing Douglas-fir pollen. Perhaps fewer low-intensity fires, such as those that marked the preceding 1000 years; or perhaps more ground cover supported occasional light fires, but inhibited slope wash. In either case, during this 1200-year period, the basin of Sheep Mountain Bog apparently experienced three conflagrations unlike fires of the earlier Holocene and any of the last 1000 years or more (Hemphill 1983).

THE PAST AS KEY TO THE PRESENT - AND FUTURE

In a human life span or two, eastside communities may seem predictable. On this scale, vegetation history can be explained by observed succession in the enduring harmony of climax communities. The idealized stable cycles, always returning to the natural state, are unfortunately just a few frames in a continuous movie (Graham 1988). They are illusions of forest and steppe primeval-the pristine vegetation of the imagination.

Effects of cows, plows, and alien weeds have sped up the movie, but still leave room for short-term predictability, with no necessary appreciation for the longer view. The specter of sudden global warming and fates of ecosystems (Franklin and others 1991) are, however, another matter. Short-term observations provide few analogs for the magnitude and extent of past and potential vegetation change.

Two principles emerge from paleo-vegetation studies here and elsewhere in North America: change is continual and change is unpredictable. Although change may be imperceptible in the center of mixed montane forest or steppe, sensitive sites on the fringes often show that plants, even long-lived trees, respond rapidly to disturbance. For example, buried needles, cones, and whole logs of spruce and alpine fir above tree line in the Canadian Rockies show upslope advances to > 110 m above present tree line between 9000 and 5000 B.P, and again near 1000 B.P. (Luckman 1990). These warm (+0.5-1.5° C), temperature-controlled responses at the tree line affect only a small area of vegetation. In eastern Washington and Oregon, even slight changes at the lower forest border have a great influence on total areas of vegetation types.

The eastside's steppe-conifer ecotone has been in flux over the past 12,000 years. In eastern Oregon, historical and past successes of western juniper are impressive because a small increase in effective moisture and downward displacement of western juniper brings wide expanses of woodlands. The same is true for the steppe-ponderosa pine border in eastern Washington (fig. 10). Change is perpetuated not only by plant responses to climate, but by disturbances that accompany climatic change-fire is the most obvious of these disturbances.

At Williams Lake Fen, falling water tables and fire brought an end to the scabland's late-glacial woodlands and the beginning of expansive steppe (figs. 5, 7, 10). The record of pollen and charcoal from Diamond Pond, Oregon, shows a different sequence, but a similar effect-trees were lost to fire. There, in short drought periods during generally favorable times (2000-4000 B.P.), fuel in grasses carried fires that set back juniper woodlands when they had become dense enough to carry some fires themselves. If vegetation changes lag behind climatic changes (Franklin and others 1991), then-in the long view-vegetation is often out of equilibrium with climate and subject to rapid change through disturbances such as disease and fire.

The second principle, unpredictability, is best illustrated by unfamiliar late-glacial and Holocene assemblages of both plants and animals. These assemblages suggest that individuals, rather than communities or vegetation zones, react to climatic change and that fossil assemblages and modern communities are loosely organized collections of individually distributed species. With disturbances, species may be redistributed along different environmental gradients and at different rates, and may reassemble in unpredictable ways (Graham and Grimm 1990). In short, present communities are not necessarily good guides to the past, nor to the future. In Quaternary vegetation, surprises are the rule (Franklin and others 1991).

By studying today's communities, without reference to the fossil record, we could not have known that the eastside's familiar broad distributions of woodland and steppe did not take shape until after 4000 B.P., that northern Idaho's hemlock and cedar forests were even younger, or that a few centuries ago and many times during the last 4000 years, juniper woodland's expanse exceeded that of its historic spread. The remarkably rapid demise of the scabland's, late-glacial woodlands shows the process and pace of total replacement, and the potential magnitude of future vegetation change with rapid global warming of 4 to 5° C (Overpeck and others 1991).

Two primary areas need considerable study before eastside forest history can be understood. The first is the historical process by which moist, maritime forest communities of northern Idaho and adjacent Washington and Montana became so successful in apparently less than 3000 years (Mack and others 1978a). When did hemlock, cedar, and associates typifying present habitat types arrive (Cooper and others 1991)? When did they become abundant, and what role did stand-replacing fires and succession have in their initial success and regeneration (Moeur 1992)? These questions are just a few that might be answered by macrofossils and pollen from the lakes and bogs of this region.

The second, and perhaps most important, area is the Blue Mountains of northeastern Oregon and adjacent Washington. Here, near total ignorance about vegetation history leaves room for imagination. With the vision of Janus and fossil plant records, scientists may unravel the past and thereby achieve a wise view of future eastside ecosystems .

DESCRIPTION OF EASTSIDE VEGETATION

The vegetation on the landscapes of the intermountain Pacific Northwest (east of the Cascade Range and west of the Rocky Mountains in Washington and Oregon) is influenced by climate, landforms, soils, and relief. Climates of either maritime or continental derivation provide the temperature and moisture required by the individual plant species that make up the communities across the landscape. The landscape is highly varied on the east side of the Cascade Range. Therefore, the variation in kinds of plant communities found across the inland Pacific Northwest is also highly varied.

Climax plant communities on the eastside can be divided into forests, grasslands, shrublands, and wet- . lands. Our description of eastside vegetation follows the classification work by taxonomic plant ecologists over the past 25 years (Daubenmire and Daubenmire 1968, Daubenmire 1970, Hall 1973, Hopkins 1979a, 1979b, Williams and Lillybridge 1983, Clausnitzer and Zamora 1987; Johnson and Simon 1987, Kovalchik 1987, Volland 1988, Williams and others 1990; Williams and Smith 1991; Johnson and Clausnitzer 1992).

Forests

Subalpine fir zone-The highest mountain elevations contain the harshest temperature extremes for forest vegetation. Subalpine fir is capable of persisting in the cold, wet or cold, dry environments at high elevations. Desiccating winds also provide a limiting factor to species and type of community. Three primary series where coniferous trees form the climax dominant plant layer are the subalpine fir, mountain hemlock, and whitebark pine series:

- Subalpine fir series-All forest stands are dominated at climax by subalpine fir or Engelmann spruce. Spruce is longer lived and is co-climax in many late seral stands, especially on moist sites and cold-air pockets. Subalpine fir is dominant when sites are too cold for other shade-tolerant species to reproduce. Lodgepole pine is the principal seral fire species associated when stand-replacing fires have occurred. Douglas-fir and western larch are important seral species on warmer, drier sites-especially on southerly slopes at higher elevations or at the lower slope elevations adjacent to the grand fir zone
- The following plants are important members of climax communities with subalpine fir, spruce, or both in the eastside forests: twisted stalk (*Streptopus amplexifolius* (L.) DC.), false bugbane (*Trautvetteria caroliniensis* (Walt.) Vail), queenscup beadlily (*Clintonia uniflora* (Schult.) Kunth.), bunchberry (*Cornus canadensis* L.), twinflower (*Linnaea borealis* L.), false huckle-berry (*Menziesia ferruginea* Smith), Cascades rhododendron (*Rhododendron albiflorum* Hook.), grouse huckleberry (*Vaccinium scoparium* Leiberg), big huckleberry (*V. membranaceum* Dougl.), dwarf blueberry (*V. caespitosum* Michx.), delicious blueberry (*V. deliciosum* Piper), red mountainheath (*Phyllodoce empetriformis* (Sw.) D. Don), bearberry (*Arctostaphylos* spp.), Hitchcock’s woodrush (*Luzula hitchcockii* Hamet-Ahti), pinegrass (*Calamagrostis rubescens* Buckl.), elk sedge (*Carex geyeri* Boott), skunkleaved polemonium (*Polemonium pulcherrimum* Hook.), and beargrass (*Xerophyllum tenax* (Pursh) Nutt.).
- Mountain hemlock series-Mountain hemlock communities are limited to northerly aspects below ridgetops where deep snowpacks and cold temperatures persist throughout the year. Two huckleberries, big huckleberry and grouse huckleberry, form climax communities with mountain hemlock in northeastern Oregon. Hitchcock’s woodrush occurs in climax communities with mountain hemlock in northeastern Washington.
- Whitebark pine series-High winds, severe desiccation, ice pruning, and snowfall create open stands, clumped stands, and krummholz communities at the upper limits of tree growth. Climax communities are dominated by fleeceflower (*Polygonum phytolaccaefolium* Meisno), Drummond’s rush (*Juncus drummondii* E. Meyer), and skunkleaved polemonium.

Grand fir zone-The most extensive environmental zone in the eastside is characterized by cool, moist or dry to warm, moist growing conditions where grand fir is the climax dominant tree species. The relation of moisture to temperature, coupled with ash or ash-influenced soils, provides for ideal coniferous tree growth and productivity. The grand fir series is normally bounded by subalpine fir at upper elevations and Douglas-fir climax vegetation on lower slopes. The principal seral tree species are lodgepole pine, western larch, Douglas-fir, and ponderosa pine.

Cool, moist environments provide grand fir climax communities with false bugbane, queenscup beadlily, Pacific yew (*Taxus brevifolia* Nutt.), Rocky Mountain maple (*Acer glabrum* Torr.), twinflower, and big huckleberry. Cool, dry environments provide grand fir climax communities with grouse huckleberry, dwarf blueberry, ninebark (*Physocarpus malvaceus* (Greene) Kuntze), Columbia brome (*Bromus vulgaris* (Hook.) Shear), pinegrass, and elk sedge. The warm, moist maritime climate provides climax communities of grand fir with oakfern (*Gymnocarpium dryopterus* (L.) Newm.), sword fern (*Polystichum munitum* (Kaulf.) Presl.), and ginger (*Asarum caudatum* Lindl.).

Douglas-fir zone-Douglas-fir is climax on sites that are more mesic than climax ponderosa pine sites; sites too dry for subalpine fir or grand fir. Tree species that may be seral to Douglas-fir are ponderosa pine, western larch, and lodgepole pine. Midsummer drought is a limiting factor to establishment by some shrub and herbaceous species. Cool, moist environments provide Douglas-fir climax communities containing Rocky Mountain maple, ninebark, big huckleberry, dwarf blueberry, mountain snowberry (*Symphoricarpos* *oreophilus* Gray) and common snowberry (*S. albus* (L.) Blake). Warm, dry environments provide Douglas-fir climax communities containing birchleaf spiraea (*Spiraea betulifolia* Pall.), oceanspray (*Holodiscus discolor* (Pursh) Maxim.), bearberry, western fescue (*Festuca occidentalis* Hook.), pinegrass, and elk sedge.

Ponderosa pine zone-Ponderosa pine is widely distributed throughout eastern Oregon and Washington but is climax on the warmest, driest forest sites. It is a major seral species in Douglas-fir and grand fir series communities but forms a climax community near the limits of tree growth imposed by drought. Of the tree-dominated vegetation on the east side, only western juniper woodlands occur on warmer, drier sites than climax ponderosa pine communities. Ponderosa pine climax communities occur on coarse, sandy soils and where fissures in the underlying bedrock permit the tree to tap deep moisture sources. Other trees often associated with climax ponderosa pine communities are western juniper, quaking aspen (*Populus tremuloides* Michx.), lodgepole pine, and Oregon white oak (*Quercus garryana* Dougl. ex Hook.).

Principal climax communities are formed with the following shrubs: mountain-mahogany (*Cercocarpus ledifolius* Nutt.), bitter-brush, mountain snowberry, common snowberry, and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana*). Oregon white oak is associated with ponderosa pine in north-central Oregon and south-central Washington (Topik and others 1988). Principal climax communities are formed with the following herbaceous species in eastern Oregon and Washington: pinegrass, elk sedge, Wheeler's bluegrass (*Poa nervosa* var. *wheeleri* (Vasey) Hitchc.), Idaho fescue (*Festuca idahoensis* Elmer), and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith).

Western juniper zone-Toward the Great Basin, with its cold desert and continental climate, ponderosa pine is incapable of survival. The western juniper occupies an environmental zone between the pine and the shrub-steppe of the Great Basin. Western juniper forms climax communities with mountain mahogany, bitter-brush, big sagebrush, elk sedge, and the two principal bunchgrasses-bluebunch wheatgrass and Idaho fescue.

Shrublands

The shrublands of the eastside can be separated into two kinds-climax and seral. Shrublands may be seral in forest successional pathways. Climax shrublands are communities where a shrub species is the dominant life form on sites where conditions will not support a forest community. The climax shrub communities of the eastside provide diversity to the landscape as part of a vegetation mosaic. Shrublands are often found intermediate between forests and grasslands, and between scablands and wetlands. Climax shrublands can be grouped artificially as follows: mesic shrublands, where ninebark and common snowberry occur with rhizomatous sedges and grasses, and sagebrush shrublands where the most mesic species (mountain big sagebrush) forms communities with mountain snowberry, elk sedge, and Idaho fescue; where low sagebrush (*Artemisia arbuscula* Nutt.) forms communities with Idaho fescue and Sandberg's bluegrass (*Poa sandbergii* Vasey); and where stiff sagebrush (*A. rigida* (Mutt.) Gray) forms a community with Sandberg's bluegrass.

The driest and hottest habitats with shrubland communities are found in the deep canyons of the eastside. Here, smooth sumac (*Rhus glabra* L.), netleaf hackberry (*Celtis reticulata* Torr.), and green-bush (*Glossopetalon nevadensis* Gray) form communities with bluebunch wheatgrass. Other common shrublands that form climax communities are bitter-brush and mountain-mahogany.

Grasslands

The climax grasslands in eastside Oregon and Washington are dominated by bunchgrasses on sites that are incapable of supporting forest or shrubland communities. They constitute a fairly high percentage of the landscape in canyonlands and on lower montane ridges. The grasslands can be separated into five groupings as follows:

Subalpine grasslands-Green fescue (*Festuca viridula* Vasey) occurs principally in the Wallowa Mountains of northeastern Oregon at elevations above 7000 feet. It occurs with sedges, rushes, and forbs. Idaho fescue and elk sedge are found on subalpine summits of the Blue Mountains in communities with various subalpine forbs. Disturbance from overgrazing has resulted in subalpine forbfields and grasslands at higher elevations, where the two fescues have been replaced by needlegrasses (*Stipa* spp.), lupines (*Lupinus* spp.), and phloxes (*Phlox* spp.).

Mesic grasslands-Idaho fescue forms climax communities at upper canyon elevations, on favorable aspects at lower elevations, and on deeper soils of the ridges where moisture is retained longer into the summer drought period. Principal plants associated with fescue in these communities are prairie junegrass (*Koelaria cristata* Pers.), bluebunch wheatgrass, and Hood's sedge (*Carex hoodii* Boott).

Xeric grasslands-Bluebunch wheatgrass dominates in these drier, warmer habitats. Many different climax communities occur in the eastside grasslands, often associated with Sandberg's bluegrass.

Scablands

Scablands occur where soil depth is less than 10 inches and an impervious bedrock limits establishment of deeper rooted plants. Occupying these sites is a vegetation unique to the harsh environmental extremes caused by freezing and thawing, and saturated soils in the spring followed by hot, desiccated soils in the summer. Onespike oatgrass (*Danthonia unispicata* (L.) Beauv.) and Sandberg's bluegrass are climax on these scablands. The deep canyons provide specialized habitats for grasslands occupied by sand dropseed (*Sporobolus cryptandrus* (Torn) Gray), red threeawn (*Aristida longiseta* Steud.), and giant wild rye (*Elymus cinereus* Scribn. & Merr.).

DISTURBANCE AS A NATURAL EVENT IN EASTSIDE ECOSYSTEMS

The vegetation of eastside Washington and Oregon has a long history of natural disturbance. Unlike other ecosystems where stability is measured in centuries, eastside ecosystems are considered stable when the period between modifying events is decades. Eastside vegetation, as a reflection of climate and topography, is comprised of plants with reproductive mechanisms capable of withstanding relatively frequent, severe disturbances.

The principal disturbance processes have provided vegetation opportunities for adaptation to periodic disturbances of varying severity. The primary disturbance processes affecting plant communities of the eastside are fire, grazing and browsing by ungulates, insect outbreaks and disease epidemics, windthrow, flooding, and erosion (mass wasting).

The Disturbance Paradigm of Forest Ecosystem Development

The ubiquity of natural disturbances became better appreciated as modern communication and transportation allowed the human population to see the size and extent of natural disturbances. The hurricane of New England that affected 600,000 acres of forest was not unlike similar hurricanes of 1815. Hurricanes Hugo and Camille were also not unusual, because similar ones occurred in 1972, 1969, 1965, and 1955 (Oliver and Larson 1990). The Yellowstone fires of 1988, which burned 1,408,000 acres, were similar to the Entiat fire of north-central Washington, which destroyed over 200,000 acres of forests in 1970, and to the fires in the Colville, Washington area of the 1920s, which also destroyed hundreds of thousands of acres.

The importance of disturbances has become more appreciated now that biologists recognize that forests do not immediately return through a single pathway of forest change (succession) to a single, stable condition (climax) after a disturbance. Instead, both natural and human disturbances have long-term influences on the appearance and composition of forests.

Forests consist of tree species not coevolved to grow with each other in mutualistic support. In fact, many species currently found together have not been together for many tree generations. The short life span (and often shorter memory) of people relative to tree life spans (hundreds of years) gives the mistaken impression of stability and constancy of the forests.

Fire as a Rejuvenating Event

Throughout the presettlement period, fire was an integral part of the maintenance and function for the majority of eastside ecosystems. The seasonal cycling of fire through the landscape was as regular as the incidence of late summer lightning occurrence in the canyonlands and mountains of this region. The periodicity of fire in certain plant communities has been determined by investigators for many forested plant associations (see review by Agee 1993) and has been estimated for several key grassland plant associations (Volland and Dell 1981). Depending on the composition of the community, its structural configuration, and the buildup of dead plant biomass, fire resulted in burns of various intensities and extension across the landscape. The shorter the return interval between fire events, the less dramatic would be the result of the fire on plant composition. With infrequent return intervals, stands tended to burn hotter and be replaced by a vegetation often different in composition, structure, and age from what it replaced.

The variation of landform and climatic patterns have combined to provide a rich mosaic of plant communities across the eastside. As annual lightning storms would play across this landscape, a patchwork quilt of various-sized patches, textures, and kinds of vegetation would result. This mosaic would be as resilient and dynamic as the annual play of storm-induced fire. The probability of fire in any given place would be a function of chance, the position on the landscape relative to storm-building geographic features, and the vulnerability of the plant community to fire.

The period since settlement and subsequent growth of industry by Euro-Americans has seen the curtailment of fire as a periodic modifying event in the vast majority of eastside plant communities. Over the past 130 years-and even more dramatically in the past 60 years-vegetation has changed from stands dominated by seral fire-adapted species to stands and communities where fire-susceptible species predominate and form “unhealthy” stand configurations. The classic example has been the widespread disappearance of open, parklike stands of ponderosa pine with the ingrowth of grand fir as a result of fire exclusion. Likewise, in grand fir plant associations where ponderosa pine is not seral to grand fir, fire has not been allowed to perform its natural role of stand-replacement burning. The poor vigor of these stands has contributed to the incidence of increased outbreaks of insects and epidemic diseases that have further increased the probability of large-scale fires with greater stand-replacing capacity.

A given fire can burn with high or low intensity, depending on topography, weather, stand structure, and fuels. Fires usually burn hotter and kill more living trees if they burn upslope. They also burn hot where stand development or a previous disturbance has created a great amount of fuel, especially during dry, warm, and windy weather. Fires burn with low intensity during cool, damp weather or where they travel through areas of low fuels. Fires can predispose a stand to other disturbances. Low-intensity fires can weaken the trees by scorching the crowns, and making the trees susceptible to insect and pathogen attacks.

Fires of high intensity give competitive advantage to light-seeded tree species such as lodgepole pine and larch and to sprouting species such as grasses and forbs. True firs, which often regenerate from heavy seeds or from advance regeneration, are generally not favored. Low-intensity fires favor tree species, such as ponderosa pine, larch, and-to a lesser extent-Douglas-fir, that can endure fire. True firs are not favored by low-intensity fires.

Grazing and Browsing as Modifying Activities

Many centuries ago, eastern Oregon and Washington were probably subjected to grazing and browsing by many North American mammals that became extinct about 10,000 years ago (Martin 1967). Few elk were present in eastern Oregon and Washington from 1800 until about 1930 (Shay 1954, Thwaites 1905).

The relatively dry, warm summers and cold, moist winters of the eastside region have promoted open forest, forest interspersed with shrublands, grasslands, and a high percentage of nonforest vegetation. Bunchgrass vegetation as well as the rhizomatous sedges and grasses of the eastside plant communities are well adapted and stimulated by disturbance from grazing animals. Under controlled and managed conditions, these plant abundances in the community are enhanced by selective grazing by ungulates. As a result, this vegetation has provided an ideal habitat for ungulate species that depend on grains, grasslike plants, and shrubs for sustenance. Historically, a wide variety of ungulates occurred in eastern Washington and Oregon across the presettlement landscape. Early trappers speak of deer, elk, mountain sheep, antelope, and even bison in the valleys and canyonlands of the region (Evans 1991). These animals had wide ranging mobility, and coupled with their preferential use of the vegetation, caused moderate to light effects on vegetation. Natural predators, then more varied and numerous, helped keep ungulates in balance. As Euro-Americans settled the eastside region, many predators were displaced from their natural rangelands. As the domestic livestock industry gained prominence-first sheep at the turn of the century, then cattle in the 1930s and 1940s-the effect on native vegetation of too many animals too early in the season and for too long during the season became apparent.

Thresholds beyond which vegetation could not rebound were regularly surpassed by overgrazing on many rangelands of the east side. Accounts of ridgetops white with hundreds of sheep and dust lingering in the sky from cattle being driven across stock driveways are found in written accounts by the early administrators of the public domain (Tucker and Hall 1985). Significant upland areas on the eastside landscape have lost the capacity to support the native vegetation where livestock and wild ungulates once competed for fescues and other bunchgrasses. Streamside vegetation was also vulnerable because these areas were relatively isolated across landscapes of dry hills, canyons, and mountainous areas. Many meadows and stringers of grasses were irreversibly modified by the overuse of rangelands in the late 1800s and early 1900s. .

Just as curtailing fire has brought a response by the vegetation to restore ecosystem balance, the lack of grazing animals in the bunchgrass ecosystem, coupled with the lack of frequent fire, has resulted in grassland decadence. The annual grazing of standing biomass by selective animals achieves a certain balance to the bunchgrass community by invigorating grazed plants and promoting dissemination and germination of the grasses. Grazing as a modifying activity has been generally perceived as negative as a result of the overuse by animals over too long a period of time. Highly productive sites have retrogressed to earlier seral stages and species richness has declined.

Insects and Diseases as Modifying Agents

Vegetation is not stable. Environmental factors influence eastside vegetation, which changes in response to disturbances within and among stands. When periods of stability are too extended for a vegetation that naturally receives periodic disturbances, instability is heightened. For example, if fire is not allowed to cause charge, native insects, diseases, or both will. Lodgepole pine forests are historically replaced and rejuvenated by stand-replacing fires. In the Blue Mountains, lodgepoles live about 90 to 125 years, but in the early 1970s, foresters were surprised by.wholesale tree mortality from mountain pine beetle damage. This shift from low beetle populations to outbreaks in eastside lodgepole pine forests was an ecosystem response to the lack of stand-replacement fires that recycle lodgepole pine stands before they become susceptible to bark beetles. In essence, the stands were over-aged, the trees were destined to die, and the beetle caused their mortality because fire (or harvest) did not. Lodgepole pine forests were not harvested because other forest products of greater economic value were being sought by industry.

Insect outbreaks have been reported since the late 1800s in eastern Oregon and Washington. The pine butterfly (*Neophasia menapia* Felder & Felder), the western spruce budworm (*Choristoneura occidentalis* Freeman), the Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)), the western pine beetle (*Dendroctonus brevicomis* Le Conte), and the mountain pine beetle (*D. ponderosae* Hopkins) have all had major outbreaks; such outbreaks of native insects have probably always occurred in eastern Oregon and Washington when weather and stand structures were favorable to them. These outbreaks probably increased fuel loads and led to fires as well.

Many insects are host specific; consequently, insect outbreaks tend to favor the development of nonhost species. In mixed species stands, both nonhost species and young trees, which grow into newly available space, are favored. The young trees are often shade-tolerant true firs, which are highly susceptible to insects and diseases. Insect attacks often create snags which are favored by insectivorous birds. The dead stems also contribute to available fuels.

Glaciation

For tens of thousands of years, the continental glacier covered extreme northern Washington, and valley glaciers covered parts of the Cascades of eastern Oregon and Washington until about 12,000 years B.P. Since then, valley glaciers have advanced and retreated at different times, generally in response to climatic fluctuations. The cool period-the "little ice age" of about 1400 to 1850 A.D.-was a time of valley glacier advance. Since about 1850, these glaciers have generally been retreating (Lamb 1977).

Glaciers remove all vegetation in their paths, although trees and other vegetation sometimes remain on hills above valley glaciers. Retreating glaciers leave slopes of mixed rocks, sand, and little silt. Valleys where glacial meltwaters run often contain soils with high concentrations of boulders, gravels, and sands; the valleys are relatively unproductive for tens of thousands of years. Lakes form and ice dams break as glaciers retreat, resulting in floods of different magnitudes. Dry lake-bed areas of silts and clays are left in the wake.

The main effect of the glaciers in eastside landscapes was to establish a soil pattern of various productive sites on which species with differing competitive advantages grow.

Other Modifying Events

Although much less recognized than fire, grazing, insects, and diseases, other natural processes windthrow, flooding, and erosion-influence the composition, structure, and age of vegetation on the landscape. Occasional windstorms reach high velocities and topple many trees, but winds also create small pockets of blowdown that leave canopy gaps where plants that need sun can grow. Root diseases, snow loading, and ice breakage often interact with wind in modifying stands.

Winds-Windstorms often break or uproot trees where the wind is channeled by local topography, and severe windstorms can overturn trees across large areas. Trees in overcrowded stands snap off or break at their root collars in windstorms or uproot, if they are on shallow soils. Trees blown over by winds create conditions that favor other disturbances such as insects and fires. Where only some trees blow over, the partial shade of remaining trees promotes shade-tolerant species such as true firs. Windstorms generally favor advance regeneration of true fir species in eastern Oregon and Washington. Windstorms create downed, woody material that favors some wildlife species, but it can also form barriers to the movement of large animals.

Floods and soil mass movements-Flooding, an annual feature of wetland ecosystems, is a natural, creative, and nurturing event to many wetlands communities. The infusion of new microsites for colonization and the delivery of nutrient-charged substrates ensures that these riverine or riparian communities will continue.

Erosion can produce changes beyond nature's abilities to rectify them. Erosion is part of an ongoing, sculpting process that provides landform patterns by deposition and mass-wasting activities. New landforms are continually created by rotational slumping, landslides, avalanches, and other debris-depositing events. The new landscape segments and patches enhance diversity and ecosystem health.

Floods and mass movement are considered undesirable because they silt reservoirs, displace river channels, undermine roads, and destroy property and human lives. But control of flooding and mass movement have also reduced the input of sediments into streams, creating scoured stream channels free of sand and silt and of less use for many fish species. Floods and mass movements wash sediments into streams and stream channels, replenishing the gravel, sand, and silt in the stream and adding it to the floodplain soils. The riparian and aquatic animal and plant species that withstand siltation are given a competitive advantage, and other plants and animals are killed. Fish species are affected positively or negatively, depending on the frequency and time of year the sediment is added.

Climate Change-Within the last 1.000 years, the climate became cooler, then warmer (fig. 16). Recent warming between about 1850 and 1940 led to stress among species that had begun growing under cooler climates at the warmer and drier extreme of their natural ranges (lower elevations and latitudes). Beginning in the 1930s (Franklin and others 1971), this natural warming also increased the upper latitudes and elevations at which species can grow, causing trees previously found at lower elevations to invade alpine meadows.

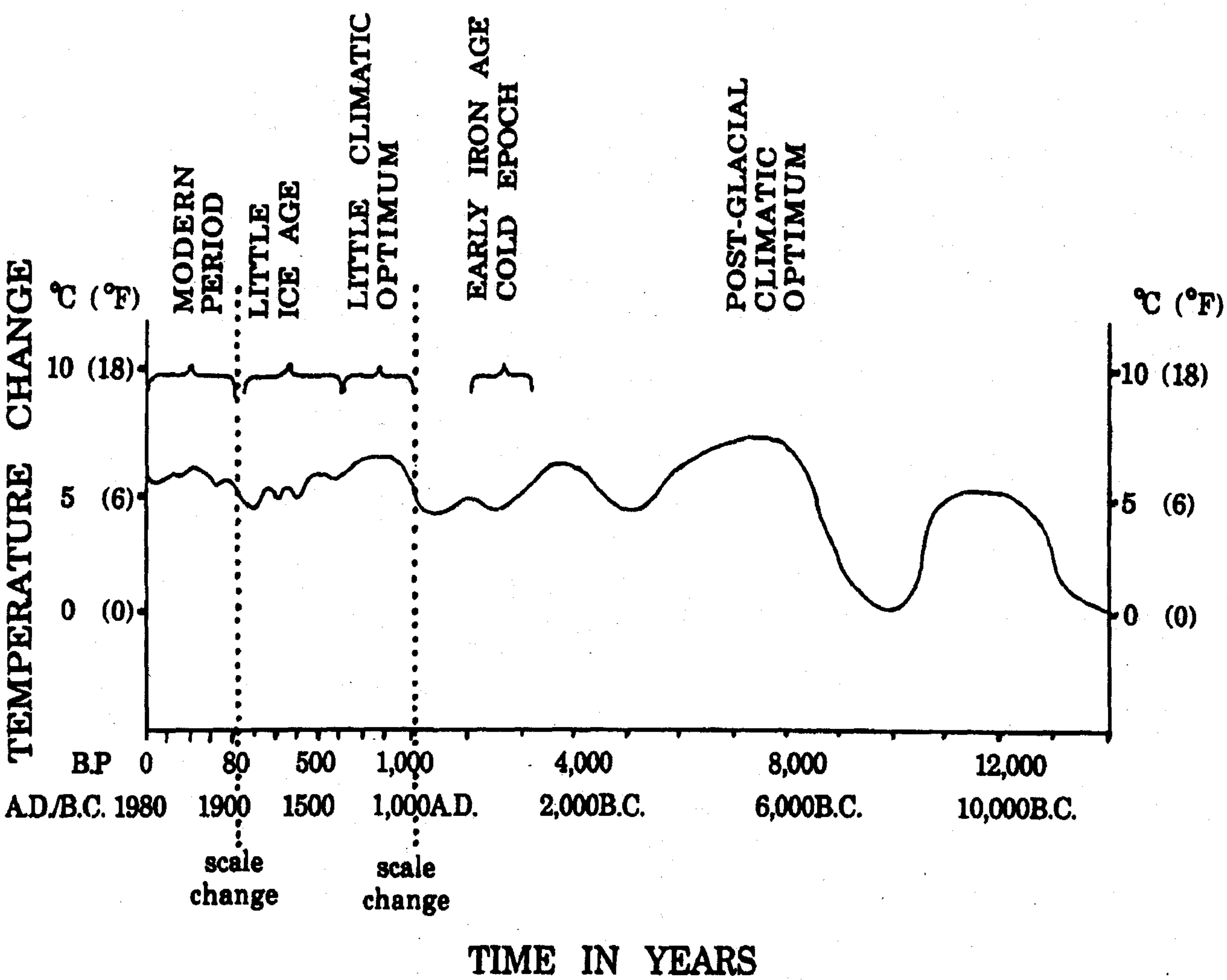

Figure 16. Average temperature variation in the northern hemisphere since the last glaciation (from Lamb 1977). Global climatic conditions have not been stable and have altered growing space and the species that are most competitive on a site (Oliver and Larson 1990).

MANAGEMENT-INDUCED DISTURBANCES

The natural disturbance regimes generally provide beneficial responses to the eastside vegetation. Plants that comprised eastside ecosystems have generally adapted to the effects of fire, grazing, and other disturbances. The long-term consequences of natural disturbances tend to enhance biological diversity.

The activities of human (especially Euro-American) occupation and industry modified to the natural order in ways both complementary and detrimental to eastside ecosystems. The effects of stand scale treatments are often additive over time and space and therefore influence ecosystems at the landscape and watershed scales.

Harvesting

Western expansion repeated the treatment of forests by Euro-Americans as they crossed the continent to the Pacific Northwest (Billington 1967). The eastside forests were exploited along major valleys and around centers of population as industrial growth consumed forest products from the 1860s to the 1920s. Public lands provided commodities for a new western-based society. In the 1930s, 1940s, and 1950s, forest practices were essentially along streamcourses and roads built for extractive activities. Silvicultural practices were usually selective or for salvage and represented conservative use of timber resources.

Starting in the 1960s, and coming to fruition in the 1970s, changes in forest management philosophy and practices dramatically accelerated the volume of timber products being removed from the forests of the eastside. The active curtailment of fire for more than 50 years had allowed the ingrowth of fire seral and climax tree species to overstock forest stands that had received periodic underburning or stand-replacement fire. As a novel practice for the eastside, the large-scale removal of slower growing, older trees was promoted by intensive thinnings of small-dimension trees, as a way of reducing stocking and encouraging rapid wood-fiber growth on the residual trees. The first clearcuts were performed in many areas of the eastside region during the 1970s, where stand replacement was deemed necessary for sanitation and rejuvenation of a thriftier forest. Also, total tree-overstory removals became a common practice to harvest ponderosa pine trees that had ceased to grow at increments acceptable to silvicultural guidelines for site capability and to allow better growth of residual trees. Thus, many acres of parklike ponderosa pine forests, which had become dense from grand fir, Douglas-fir, and pine saplings and pole-sized trees as a result of fire exclusion, were now converted from pine dominance, through management practices, to greater dominance of firs.

For the most part, fire was not employed as a silvicultural tool during this period. If stocking was not adequate from the ingrowth under the older trees, nursery stock was planted. Seedbearing trees were generally removed for wood instead of being left to provide future progeny. Without fire as a promoter of seedbeds for pine seedlings, these sites became more conducive to fir. In the 1980s, with stocking still too high for thrifty, vigorous trees and with forest composition different from what it had been, the populations of insects, both defoliators and bark beetles began to rise.

Today, with many acres of severely diseased and defoliated trees throughout the eastside forests, the public has questioned the management of both public and private forests. Professional land managers and specialists have joined with natural-resource scientists to determine how to improve forest health (Gast and others 1991). After several years of intensive study and communication, several initiatives have emerged to improve the forests.

Management has shifted from even-aged and single species stands to uneven-aged management promoting seral fire species (ponderosa pine, Douglas-fir, and western larch). A concerted effort is being made to reintroduce fire into the forest ecosystem with prescribed natural fire and planned ignitions. Management focus has shifted from the stand to the landscape scale. And land management agencies have championed assessing and managing ecosystems rather than forest commodities and benefits (Overbay 1992, Robertson

1992). This ecosystem focus has diminished the emphasis on extractive activities and heightened the awareness of how sensitive various ecosystems are to management activities.

Part of the work of the 1990s and beyond the turn of the century will be restoration and rehabilitation of landscapes and ecosystems. Some of the disturbances created in this accelerated extractive period were too severe for the sites and have caused successional shifts that took the vegetation beyond thresholds to stages where later seral vegetation cannot return, either because basic habitat elements (soil, water) or plant disseminules have been lost.

Overgrazing

Perhaps livestock grazing has caused the greatest degree and extent of disturbance on the east side. The mobility of the various ungulates across western rangelands has affected virtually all segments of the landscape to some extent. The effect has been greatest along watercourses, in basin meadows, and on ridgetops, where stock driveways and bedding grounds were used season after season for many years. The degrading of native vegetation in these areas has been so complete that thresholds were passed, leaving disclimactic vegetation. This “new” vegetation is usually either simpler biologically than the native flora, or composed of invasive, less desirable or noxious plants.

Examples of communities resulting from overgrazing sites that can support communities of climax Idaho fescue (Idaho fescue plant associations) are now devoid of any bunchgrasses. Severely overgrazed ridgetops where fescue once dominated are now growing much simplified communities. Deeper soils carry dense stands of cluster tarweed (*Madia glomerata* Hook) which inhibits germination and establishment of other plants by exuding resins (Carnahan and Hull 1962, Hull 1971). Shallower soils on these sites may contain noxious populations of gumweed (*Grindelia* spp.), pussytoes (*Antennaria* spp.), or knotweeds (*Polygonum* spp.).

Meadows have been severely affected to the extent that investigating ecologists often have no clues to predict what the native vegetation might have been. Examples of invasive communities that have overtaken eastside wetlands are terraces dominated by Kentucky bluegrass (*Poa pratensis* L.), big sagebrush flats, and annual brome (*Bromus* spp.) grasslands. Incising the fluvial channel to greater depths as a secondary result of the overgrazing activities has reduced the availability of moisture to the meadow vegetation and permitted invasion by more xeric plants.

Native American and Euro-American Fire Setting

Although the extent and intensity of fires before Euro-American settlement is unknown, accounts by fur traders, explorers, missionaries, and early immigrants say that fires were actively set throughout the eastside forests and grasslands to improve rangelands for livestock and to help in hunting game (Evans 1991). The early settlers also used fire to clear land and promote nonforest vegetation, irretrievably altering the principal valleys where the combination of settlements and agricultural pursuits rapidly replaced the native vegetation.

The settling of the West gradually reduced the influence of fire in periodically modifying vegetation. With the diminishing of the Native American presence and life style and as meadows and grasslands were converted to farmlands, fire gradually declined. Because the young settlements were at risk to wildfire, prevention was politically stimulated. Fire was not recognized as an integral part of the natural cycle in the intermountain Pacific Northwest landscape.

Other Induced Disturbances

Mining, railroad logging networks, roadbuilding, dams, and agriculture all combined to dramatically alter the eastside landscape. Where these activities were conducted-in streambottoms, along river terraces, and on the most fertile lands of the region-native plant communities have generally been replaced by exotic or invasive communities.

THE ECOLOGICAL ROLE OF DISTURBANCE

The Steady-State Paradigm of Ecosystem Development

Disturbances have long been recognized in forest ecosystems; however, their significance was not appreciated as long as scientists maintained the view that forests consisted of stable, coevolved tree species that develop through succession toward a steady-state of specific climax species and structures (Oliver 1992a).

Belief in this steady-state forest has led scientists and others to assume that undisturbed forest structure or development pattern is natural and therefore conducive to sustaining biodiversity and sustainability. The steady-state paradigm of forest development has prevailed at different times in the thinking of foresters, conservationists, ecologists, and politicians for some parts of the past century. The paradigm has led to the management policy of stopping all fires, to the ecological theories of disturbances destroying a steadystate ecosystem, to the conservation policies of reducing clearcuts and trying to stop stream siltation events, and to the political assumption that stopping all human activities in the forests will mitigate the loss of endangered species.

The steady-state paradigm for forest ecosystems has lost credit among plant ecologists during the past two decades (Oliver and Larson 1990, Pickett and White 1985, Stevens 1990); however, it is still assumed to be true among those who learned earlier ecological theories and have not kept abreast of the science. Ecosystem management requires that management, laws, and organizational systems be based on accurate concepts of dynamic forests where the role of disturbances-both natural and human-are appreciated.

Competition as the Primary Interaction Among Tree Species

The primary interaction among tree individuals and species is competition. Under various circumstances, different species gain competitive advantage and are able to survive and dominate a forest landscape. The same area may be dominated at one time by grasses and shrubs, at another time by ponderosa pine trees, and at another time by grand fir trees. Some plant and animal species survive primarily during the first few decades after a disturbance, and others survive primarily in forests with no or minor disturbances. Old forests have no inherent desirability, stability, or naturalness; nor is a single forest structure or domination by certain groups of species more inherently natural than others. As in all areas, forests observed in eastern Oregon and Washington in the short time of recorded history are simply the result of those species present and most competitive in the conditions during this period.

The Concept of “Growing Space”

Trees compete for such growth factors as sunlight, moisture, nutrients, and soil oxygen, which we refer to simplistically as “growing space” (Oliver and Larson 1990). Plants establish and grow where their basic environmental needs are met. When they grow together, they compete for the same or similar growing space.

The growing space of an area fluctuates so regularly day by day and seasonally that plants have adapted their diurnal and annual cycles to it. When plants have grown in an area until their roots have completely occupied the soil or their foliage is blocking all available sunlight, the growing space is said to be filled. After the space is filled, one plant can only increase its growing space by taking it from another plant through competition.

Factors Influencing Species Domination

The plants that have the most growing space at a given time and place appear to dominate the area. Various tree, shrub, and herbaceous species are able to dominate the growing space because they survive in an area and have competitive advantages under specific species, climate, soil, and, disturbance regimes. The regimes are discussed on the next page:

☐ Species presence. Species are constantly migrating into and out of a region. A species has the opportunity to dominate an area at a given time only when a species is present in a region and can survive under the specific soil, climate, and disturbance regime existing at that time.

☐ Climate. Each species has a range of climatic conditions under which it can grow. These climatic conditions usually restrict each species to a combination of latitude and elevation zones (fig. 17). A species usually grows most vigorously near the middle of its suitable range of climatic conditions. A species is most sensitive to the climate when it is initiating and undergoing intense competition shortly after a disturbance (as will be discussed later.) The climate of the Pacific Northwest (and elsewhere) has fluctuated, and continues to fluctuate, at shorter intervals than the lifespan of trees (fig. 16); consequently,. a species' presence at a specific location is partly indicative of the climate when the species became established.

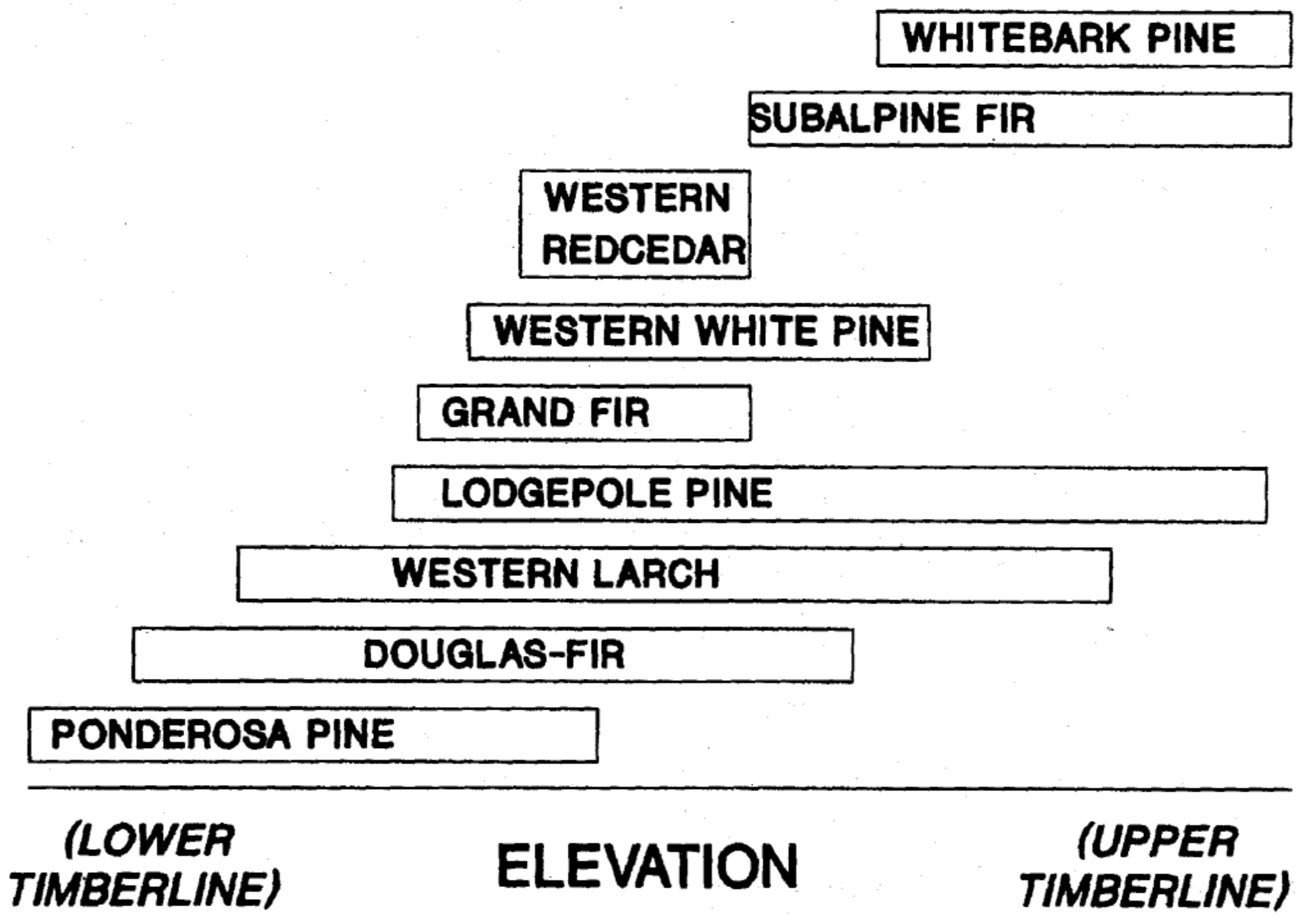

Figure 17. Distribution of tree species along a gradient of elevation (also indicating climate) in the northern Rocky Mountains (after Adams 1980).

If the climate changes enough to be outside the species' range of tolerance while it is growing in an area, the species may become weakened and susceptible to various insects and diseases. Insect and disease buildups in certain places in eastern Oregon and Washington may be the result of the changing climate. Because climate has changed and will always change for natural (and some human-caused) reasons, weakened trees will always exist at the extreme ranges of species.

☐ Soil. Nearly all species grow most vigorously in moist, well-drained soils within their climatic range; however, certain species are able to compete well on dry or poorly drained soils. For example, grand fir grows extremely vigorously on moist, well-drained soils and outcompetes other species there under most conditions (fig. 18).

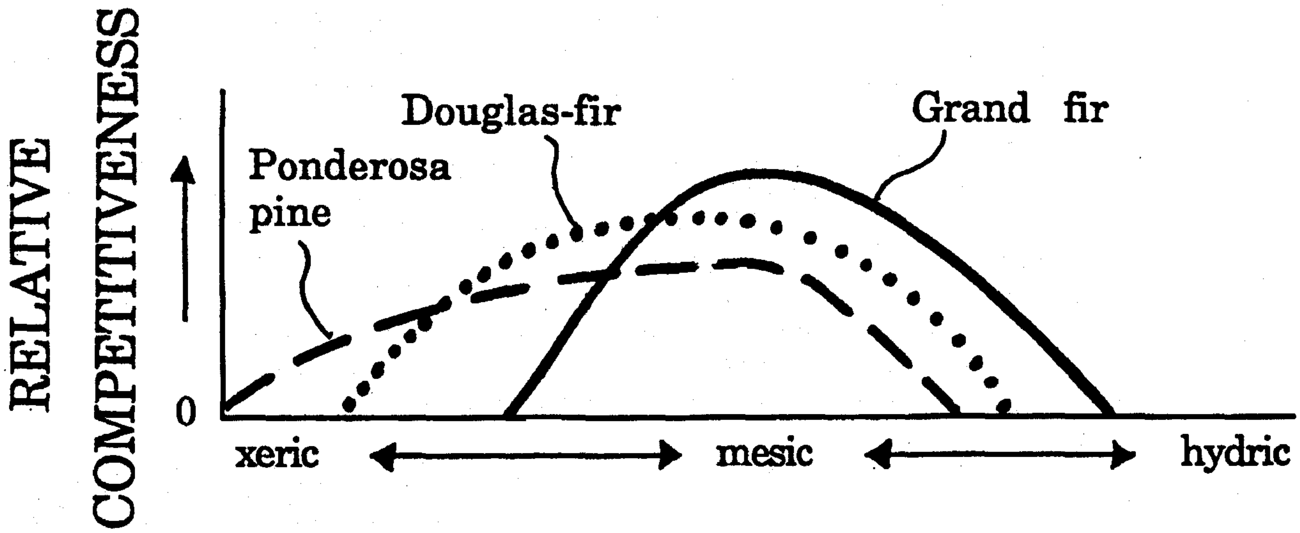

Figure 18. Most tree species grow best within a relatively narrow range of moist, well drained (mesic) soils; however, some species can tolerate more extremes of dry (xeric) and wet (hydric) soils and outgrow other species. Consequently, tree species dominate and are found where they compete successfully, not where they grow best (after Oliver and Larson 1990).

At the other extreme is lodgepole pine, which also grows best on moist, well-drained soils but generally cannot compete very well on sites with grand fir or other tree species. It can outcompete most other species on extremely dry soils or soils with frosts; therefore, it is usually found on these soils-not where it can grow best, but where it can compete successfully.

If a species can compete in soils poorer than those where it usually outcompetes other species, it exists in a stressed condition that renders it susceptible to insects and diseases. Some species have gained a competitive advantage on poor sites, and so became susceptible to insects; insect outbreaks and disease epidemics have always been present in portions of the forests.

- ☐ Disturbances. Various natural and human disturbances affect forests (White 1979, White and Pickett 1985). Fires, windstorms, floods, insect attacks, diseases, soil slumping, avalanches, volcanic activity, and grazing and browsing have been common to eastern Oregon and Washington before recent (1840s and later) population increases. Settlement of the region changed the frequency of these natural disturbances and added farming, increased grazing and browsing, timber harvest, and mining.

Disturbances and Growing Space

Disturbances eliminate some or all plants from an area. Disturbances to forests are usually not so severe as to damage the soil; by killing some plants, they open growing space to other plants (Oliver and Larson 1990). Plant species may gain a competitive advantage after a disturbance in one of two ways: they may endure the disturbance (while their competitors cannot) and thus grow into the released growing space immediately after the disturbance, or they may germinate or otherwise initiate after the disturbance and thus occupy the growing space before competitor individuals and other species. Specific details of the type of disturbance gives one species or another a competitive advantage.

Type of Disturbance and Species' Ability to Endure it

If the disturbance is not too severe, certain species are able to endure it (Oliver and Larson 1990). For example, thick-barked ponderosa pine trees and, to a lesser extent, Douglas-fir trees, are better able to endure ground fires, except at the seedling stage, than are thin-barked true firs (grand and subalpine).

Aspen trees generally endure floods and siltation better than other species by adding adventitious roots up their stems. Certain shrubs and herbs avoid damage from grazing and browsing by being unpalatable or thorny. Insects and diseases are generally somewhat host specific; consequently, the resistant species will gain a competitive advantage when a certain type of insect outbreak or disease epidemic occurs. Ashfall from volcanic eruptions tends to affect true fir species more than it does Douglas-fir trees. More recently, selective harvesting, a frequent silvicultural practice in eastern Oregon and Washington, tended to leave (and therefore favor) species of low timber value-true firs, for example.

Type of Disturbance and Regeneration Mechanisms

Disturbances that do not allow a species to endure may give the species a competitive advantage in the long run. Different species regenerate by one or several of a variety of mechanisms, and each mechanism gives the species a competitive advantage after certain types of disturbances. For example, landslides, erosion, very heavy grazing, and farming-which destroy root systems, stumps, and buried seeds-give the competitive advantage to species that regenerate from light seeds because they enter the area rapidly after the disturbances. Less severe disturbances, such as fairly intense fires, give the advantage to species that can regenerate from buried, dormant seeds, root sprouts, rhizomes, and tubers. Slightly less severe disturbances, such as cool fires or light grazing, give the competitive advantage to species that regenerate from stump sprouts, tubers, and stolons; even less severe disturbances, such as windstorms and avalanches (in the run-out zone), give the competitive advantage to advance regeneration. (Advance regeneration consists of understory individuals that germinate in a relatively closed forest and grow little for the ensuing decades; for example, some fir advance regeneration can be less than 2 feet tall and over 50 years old. On removal of the overstory, however, advance regeneration can often grow rapidly and dominate, providing it is not destroyed in the disturbance that removes the overstory.)

Disturbance Frequency and Forest Growth

Disturbances range from very frequent to very infrequent, depending on the predisposition of the stands and conditions surrounding the disturbance agent. The stand’s development pattern can sometimes set up another disturbance, thus influencing the disturbance frequency and type. The frequency of a disturbance can sometimes be indirectly related to the intensity of the disturbance. Different disturbances can also interact within a stand, with one disturbance either increasing the probability of another disturbance, or compensating for its absence.

Fire, disease, insects, wind, and grazing disturbances can be greatly affected by the condition of the stand. For example, a stand is often susceptible to an intense fire soon after a fire or other disturbance has killed many trees and the dead stems and twigs have dried. If the stand does not burn then, it becomes more susceptible after density-dependent mortality has created dry fuel (the stem-exclusion stage, to be discussed later). If the stand does not burn then, it sometimes becomes less susceptible as this mortality slows and a green understory develops. Stands are often susceptible to diseases, insects, and wind when they have grown very densely and the trees have become crowded as they increased in height. This crowding reduces diameter growth and physiological resistance, which makes the trees susceptible to buckling or blowing over in windstorms as well as to attacks by insects and diseases. A stand of tree seedlings is more susceptible to damage from grazing and browsing soon after a disturbance that has resulted in many forage plants growing within reach of grazing and browsing animals. Once the trees in a stand have grown more than 5 or 6 feet tall and have killed shorter shrubs and herbs through shading, the site is of less value for grazing and browsing animals for many years.

The frequency of some disturbances can be indirectly related to their severity, if the underlying factors affecting disturbance severity increase with time. For example, the severity of fires, soil slumping, wind events, and insect outbreaks is somewhat directly related to the time since the last similar disturbance. Where fires are absent for a long time, a large amount of fuel can accumulate; then, the burn would be extremely hot. Similarly, a stand’s susceptibility to insects can increase with time. Insect outbreaks are greater when small, frequent outbreaks have not reduced the amount of susceptible trees. The tendency for soil slumping is especially high near stream channels, with the size of each slump increasing as the time since the last slump increases.

On the other hand, the magnitude of floods, grazing, and volcanic activity is not directly related to their frequency. Floods are primarily related to rainfall, snowfall, and winter warming periods. Grazing is related to the number of animals, sometimes a direct (rather than indirect) relation to the amount of previous grazing. Volcanic activities are geologic events and are generally independent of previous activities.

Disturbances may result in stands that are either more or less susceptible to other disturbances. For example, windstorms and insect outbreaks and disease epidemics make stands more susceptible to fires. Similarly, fires sometimes make stands more susceptible to insect outbreaks. Under extreme conditions, fires or harvesting can make a hillside more susceptible to soil slumping, although the slumping would occur eventually anyway. Harvesting can make floods more extreme, although very extreme floods occur independently of forest harvest conditions.

Some disturbances make stands less susceptible to other disturbances. For example, appropriately implemented forest harvesting can make stands less susceptible to fire, insects, diseases, and windthrow as well as flood events. Fires can make stands less susceptible to insects, diseases, and windstorms.

Disturbance Size

In the recent history of eastern Oregon and Washington, disturbances have ranged from less than an acre to several hundreds of thousands of acres. Size and location of a disturbance partly depend on the type of disturbance and partly on soils and topography, stand structures, weather, and other conditions.

Certain types of disturbances occur in predictable areas. Floods generally occur in low-lying areas and avalanches on high mountains. Windstorms often are more frequent where mountains channel winds. Insect outbreaks occur where certain soils; in combination with specific stand structures, create stressed trees. Fires vary in intensity with topography and stand structure. Areas of intense grazing vary with species, animal populations, and stand structure. Most domestic and wild species graze over a range of elevations-at high elevation areas in late summer and lower elevations in spring, autumn, and winter.

The extent of a disturbed area is, therefore, influenced by the area’s topography and stand structures. A large, contiguous area of similar stand structures will allow a disturbance to cover a large area. Similarly, once a single disturbance has covered a large area, it will promote similar species and lead to similar stand structures, which can again become susceptible to a single, large disturbance. In this way, disturbances of a given size can be somewhat maintained once a pattern is begun.

STAND DEVELOPMENT PATTERNS AND PROCESSES AFTER DISTURBANCES

Relay and Initial Floristics Patterns of Development

Two theories on successional patterns of development are called “relay floristics” and “initial floristics” (Egler 1954). Forest (or other vegetation) regrowth after disturbances has often been assumed to follow a pattern of some early (pioneer) species invading soon after the disturbance and creating microenvironments favorable for other species to invade later. These late-arriving species then create favorable conditions for still other species to invade, until one or several species are able to create conditions that maintain themselves in a “climax” condition. This pattern of sequential invasion has been referred to as relay floristics.

Instead, a pattern of initial floristics generally occurs, where those plants that gain a competitive advantage soon after the disturbance continue to dominate the stand for many years. Consequently, the same area may be dominated for long periods by grasses, shrubs, or any of several tree species or combinations of species, depending on which gained the initial advantage (Drury and Nisbet 1973, Oliver and Larson 1990).

Development After Disturbance

Disturbances create a range of conditions in eastern Oregon and Washington forests. At one extreme, a disturbance can be stand-replacing (or major); all previous trees are destroyed and new trees develop with no influence from trees that grew there before the disturbance. A disturbance can also leave various amounts of older trees in a stand. Disturbances that do not destroy all previous trees are referred to as partial (or minor) disturbances (Oliver 1981).

Forest development in eastern Oregon and Washington will be described for two types: development after stand-replacing disturbances and development after partial disturbances, although a gradient exists between these two types of forests. Stand structures change dramatically after both stand-replacement and partial disturbances (fig. 19). Many variations of these stages are possible and each stage can be subdivided (Oliver 1992b).

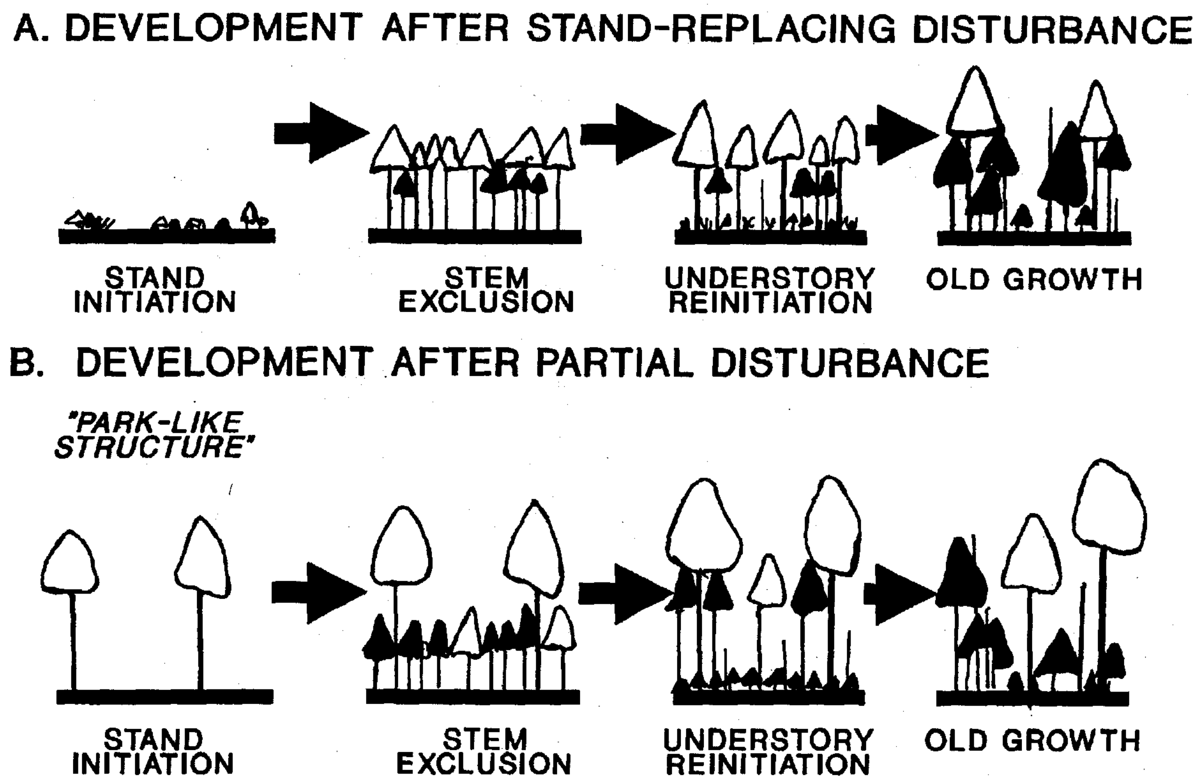

Figure 19. Stands in eastern Oregon and Washington developed after both stand-replacing disturbances and partial disturbances. Stands change through a variety of structures as they grow after a disturbance. Each structure is suitable for some animal species and not others. White tree crowns represent shade-intolerant species (such as pines and larches); dark crowns represent more shade-tolerant species (such as grand fir and Douglas-fir).

Forest Development After Stand-Replacing Disturbances

Some examples of stand-replacing disturbances are intense fires, windstorms, clearcut harvesting, clearing for farming, floods, and siltation events (Oliver 1981, Oliver and Larson 1990). Reburns or fires that follow windstorms, insect outbreaks or disease epidemics, or partial cutting operations can be especially hot fires and often are stand-replacing disturbances.

Stand-initiation stage-After a stand-replacing disturbance, the growing space becomes available and a variety of species initiate from regeneration mechanisms favored by the preceding type of disturbance. The initiating stems expand and occupy the growing space above and below ground. This stage often contains the most numerous species of plants and animals.

Many plants flourish during this stage because none have gained a competitive advantage and excluded the others. Many animals are also present because a great variety of vegetation species and structures are accessible from the ground. Stands in this stage are generally suitable for grazing and browsing species and their predators. The lynx partly depends on this stage because it preys on the rabbits that feed on the low herbs and shrubs. Stands in this stage are resistant to most disturbances except grazing and fires. The stand-initiation stage can last for many decades on poor soils where plant species invade and dominate very slowly. Individuals that initiate after the same disturbance are referred to as being in the same cohort (Oliver and Larson 1990). (Cohort is used here instead of age-class because of the possibly varied and wide age range the trees may have.)

Stem-exclusion stage-Eventually, the growing space is completely occupied by the plants. The more competitive plants both exclude others from invading and take over the growing space of the less competitive plants. Forest stands often lack vegetation near the forest floor because vigorous tall trees have outcompeted smaller shrubs and herbs for light. Where two or more tree species compete, one will often grow taller than the other and cause the shorter one to grow very slowly in a lower layer or stratum (fig. 20). As the taller trees continue to grow vigorously in full sunlight, the differences in sizes between trees in the two strata become more pronounced. The small size of trees in the lower stratum trees has led scientists to mistakenly assume they are younger, and either that relay-floristics succession is occurring or that a second, partial disturbance has occurred in the stand. This stratification pattern has been observed in several species mixtures common to eastern Washington and eastern Oregon.

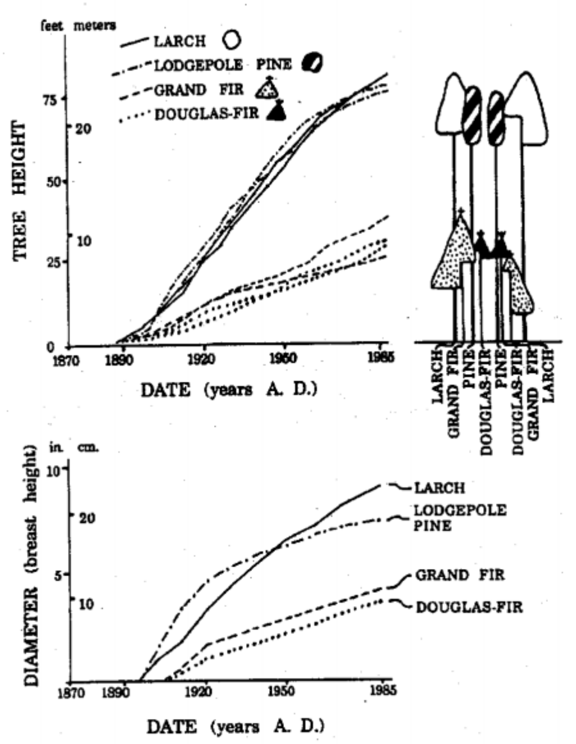

Figure 20. Development of a mixed-species stand in the eastern Washington Cascades after a fire in about 1885. Faster early growth rates allowed larches and lodgepole pines to outgrow and suppress growth of Douglas-firs and grand firs. The stratified (layered) appearance and differences in size have led ecologists to assume incorrectly that the smaller trees are younger and developing as a steadystate, climax component in the stand (Oliver and Larson 1990, from Cobb 1988).

This stage is usually least diverse for plant and animal life. Some trees become suppressed as others gain the competitive advantage. The suppressed trees, slow in diameter growth, become susceptible to insects, winds, and diseases, and often-die. Stands in this stage are quite susceptible to fires because of the dry, dead, and suppressed trees and lack of moist, living vegetation on the forest floor. They are even more susceptible to fires if they have had wind, insect, or disease outbreaks. If trees in this stage are overcrowded because of their initial invasion pattern, they may never grow large in diameter. The stem exclusion stage can last for many decades, provided the stand is not destroyed by a disturbance.

Understory reinitiation stage-If the stand is not completely destroyed by a disturbance, the overstory trees eventually lose their ability to dominate the site completely through crown abrasion and other mechanisms (Oliver and Larson 1990). Shrubs and trees that invade the understory grow very slowly in height for many years and form advance regeneration. This stage contains a greater variety of plant and animal species than the stem exclusion stage, but fewer than the stand-initiation stage. Stands at this stage can be used for hiding cover, thermal cover, and foraging; they are often less susceptible to fires than those in the stem-exclusion stage. Provided it is not destroyed by disturbances, this stage can last for several hundred years.

Old-growth stage-Barring large partial or stand-replacement disturbances, the forest continues to grow until eventually the overstory trees die. As they die, understory trees formerly existing as advance regeneration often grow to the overstory. The result is a structure with many layers of foliage, a diversity of tree sizes, and large standing and downed woody material. This structure is not always attained where stands develop without disturbances, however.

Stands in the old-growth stage often become susceptible to diseases, insects, and windthrow. A diversity of plants and animals usually live in forests during this stage-often as much diversity as in the stand-initiation stage. These species, however, are usually different from those living in the stand-initiation stage.

Forest Development After Partial Disturbance

Examples of partial disturbances are fires, windstorms, and harvesting other than clearcutting (Oliver and Larson 1990). After partial disturbances, patches of growing space are released, and the newly invading cohort undergoes changes similar to the stages described after “stand-replacement” disturbances. The invading individuals, however, compete both with other invading plants of the same cohort and with trees of older cohorts that survived the disturbance. As in stand-replacement disturbances, the type of partial disturbance helps determine which species first gain the competitive advantage.

Soon after the partial disturbance (and especially if the disturbance destroys much of the previous cohort), a large variety of plant and animal species and greater structural diversity are found than in the standinitiation stage of single cohort stands. Stands of this structure, once common at lower forest elevations in eastern Oregon and Washington, were kept open by the partial disturbance of repeated small fires and grazing. The older cohorts were primarily fire-resistant ponderosa pine and Douglas-fir trees. These parklike stands are very resistant to disturbances other than ground fires.

During the initial growth of the younger cohort, it excludes many shrub and herb species. As it grows taller, the initial diversity of plant and animal species is lost. The older cohort or cohorts shade the newly invading plants, giving an advantage to shade-tolerant species in the younger cohorts. True fir species (and to some extent Douglas-fir trees) are generally the shade-tolerant species in eastern Oregon and Washington. On droughty sites, these trees can reduce the vigor of overstory Douglas-fir and ponderosa pine trees, increasing their susceptibility to insects and diseases. The younger cohort of true firs are also very susceptible to insects, diseases, and mistletoes. As they grow, they also create large amounts of dry biomass which make the stands susceptible to stand-replacing disturbances.

As the older and younger cohorts grow, they often resemble stands in the old-growth stage and contain the old-growth structural features. They contain many species common to stands with many strata, mistletoe, hollow trees, and logs.

FOREST PATTERNS COMMON IN EASTERN OREGON AND WASHINGTON

Forests of all structures (fig. 19) can be found in eastern Oregon and Washington. Because of the disturbance history, however, some structures are more plentiful and others less plentiful than they have probably been during the past 100 years.

Fewer stands have parklike structure at low and middle elevations now than in the past because the exclusion of fires has allowed these stands to grow to the stem-exclusion structures. These stands have become susceptible to stand-replacing insect, disease, and fire disturbances or a combination of them.

Probably fewer stands are in the understory re-initiation and old-growth stages at middle elevations than in the past. In addition, stands in the old-growth stage probably have smaller, less vigorous trees in the older cohorts. These changes are because past harvesting practices have promoted true fir species and retained nonvigorous, often diseased or scarred trees. These stands are now susceptible to stand-replacing disturbances from insects, disease; fire, or all three.

Probably slightly fewer stands at the upper elevations are in the understory re-initiation stage, and more in the parklike stage at present because recent shelterwood harvesting has favored this structure. The parklike structure is resistant to many disturbances and, where the older cohorts do not cast too much shade, should grow to vigorous stands in the older stages.

Many more stands are probably in the stem-exclusion structure at all elevations because of stands regrowing after the large fires and the abandonment of grazing between 1890 and 1940. In addition, regeneration practices were to plant trees close together during the 1950s and 1960s. Many stands in the stem-exclusion stage are overly dense and becoming susceptible to fires, windthrow, and insects. Because the trees are overcrowded, they probably will not grow to large diameters.

LANDSCAPE PATTERN, STAND STRUCTURE, AND WILDLIFE

The interactions of disturbances, topography, and climatic regions tend to create stands across a landscape of relatively uniform growth potential, species composition, disturbance history, and structures. A landscape area is comprised of stands that form a mosaic of structures. The pattern to the mosaic of structures then dictates which species survive and how they migrate among areas as well as how fires, insect outbreaks, and similar disturbance agents move across the landscape.

Direct and indirect evidence suggests that before the active settlement period, a relatively small landscape area, such as 15,000 acres, did not contain a balance of the stand structures in figure 19. Large fires, insect outbreaks, grazing, timber harvesting, and other disturbances covered many such landscape units, which created many stands with similar structures. Such large disturbances did not, however, affect all stands in all landscapes. The disturbance missed some area-for various topographic and other reasons characteristic of the disturbance. These missed areas contain stand structures distinctly different from the predominant ones.

Immediately after a large disturbance, the landscape probably consisted of a matrix of most stands in the stand-initiation stage, with isolated pockets of stands with the other structures (Camp and others 1993). Shortly after the disturbances, species that occupied this structure proliferated and, expanded, with suitable genetic mixing within landscapes to maintain a diverse genetic base. As the stands grew, open structures suitable for these species were reduced; the species diminished through death, emigration, and low germination rates.

As the matrix of most stands grew to the stem-exclusion stage, species that required the stand-initiation stage became restricted to relatively small, isolated open areas. As the matrix grew older, species that had previously been restricted to closed forest structures expanded into the matrix, increased in number, and genetically mixed with individuals in previously isolated parts of the landscape. Disturbances and regrowth continually changed the structures in the matrix somewhat randomly. Over large areas, however, all structures and populations were maintained.

Across the landscape, therefore, populations that require a variety of structures predominate at different times and then become reduced and confined to small areas as unfavorable stand structures predominated. This fluctuating pattern allowed many species with conflicting requirements to avoid becoming endangered through permanently fragmented landscapes.

Eastern Oregon and Washington now contain relatively few open and parklike structures; species such as the goshawk and lynx that use them are relatively few and endangered. At the same time, the many old-growth structures provide habitat for the spotted owl. The proportions of structures will change again as they always have; however, whether they change randomly through natural disturbances, which may not create refugia, or through controlled disturbances that maintain and control areas of refuge depends on how successfully ecosystem management can be implemented.

SUCCESSION

Vegetational succession is the unidirectional change in species proportions of a stand or the complete replacement of one community by another (Daubenmire 1968). It is the process of species establishment, development, and replacement within a community. Primary succession is the change that occurs on a surface recently bared by physiographic processes such as lava flows, glacial retreat, and erosion (Daubenmire 1968). After colonization and vegetational development of such sites, subsequent disturbance initiates a sequence of vegetation change defined as secondary succession. In secondary successional seres, change is initiated by disturbance agents (such as fire, insects, wind, flooding, logging) that affect preexisting vegetation.

Smith (1982), Franklin (1982), and Farrell (1991) have suggested that succession is a complex process with a multitude of mechanisms and patterns yet to be analyzed and described. A view of succession has emerged that is driven by life histories of individual species, autecological attributes, and by chance elements (Franklin 1982, West and others 1982). A strictly deterministic model of the natural process has evolved to a model in which elements of uncertainty drive both biotic and abiotic interactions (Christensen 1988).

Connell and Slatyer (1977) described three successional models dependent on species interactions during establishment and development of postdisturbance populations: the tolerance model-early successional species interaction with mid-and late-successional species is minimal with no effect on the establishment of later colonists; the facilitation model-early successional species interact with later ones and hasten their establishment; inhibition model-early successional species interact with later successional species and slow their establishment (Farrell 1991). Along this interaction gradient, specific mechanisms of successional change should be identified and described to promote understanding of inland Northwest ecosystem dynamics.

Successional pathways depict the probable course of community development within a framework of defined community types for a disturbance regime. If the natural disturbance regime is altered in type, frequency, duration, intensity, scale, or reliability (Rykiel 1979) or management effects on ecosystem components are modified through technological evolution, the successional sere may also change. Altered abiotic and biotic interactions may lead to different expressions of individual plant species responses and the identification of different successional pathways. Predictability of ecosystem responses may suffer unless new interaction data are incorporated into a more complete model of successional change.

Knowledge of plant succession is the foundation of sound vegetation management where the primary goal is to retard, arrest, or accelerate the natural forces of vegetation change. Detailed descriptions of the target plant communities, their probable developmental pathways, and site-specific habitat factors (that is, soils, geology, slope, aspect, elevation) can assist in identifying alternatives for management objectives and vegetation units.

Steele (1984) and Arno and others (1985) proposed approaches to classify succession of intermountain and northern Rocky Mountain forest vegetation, respectively. Clausnitzer (1992) described a successional classification of grand fir plant associations of northeastern Oregon and southeastern Washington. These efforts describe the temporal variation in plant association structure and composition and promote the understanding of western forest ecosystem dynamics.

Steele and Geier-Hayes (1987, 1989, 1992) presented dominant plant species responses to disturbance agents such as scarification and broadcast burning, common to forest regeneration activities. Arno and others (1985) described community responses within a framework of similar disturbance factors, including wildfire. The Northern Forest Fire Laboratory created a database of species' autecological characteristics, including fire response, for many tree, shrub, grass, and forb species of the intermountain West. The latter effort should be broadened to include information for more Pacific Northwest species' responses to varied disturbance regimes.

Community responses to a single disturbance have often been studied, but variations of community responses to several disturbance regimes should also be analyzed. The elements of a regime (type, frequency, duration, intensity, scale, and reliability) would vary the interaction of these elements across community types. Compositional and structural changes are the interaction of the disturbance regime with the plant community components at the time of disturbances. Describing this interaction at the scale of successional classification is appropriate.

LANDSCAPE ECOLOGY

A landscape is a heterogenous land area with a cluster of interacting ecosystems as repeated components throughout. The study of three landscape attributes, structure, function, and change, are the foundation of landscape ecology (Forman and Godron 1986). Landscape development is driven by five factors linked directly and indirectly to one another. Climate is the major controlling factor of landscape pattern. Soils, geomorphic processes, animals, and vegetation are all linked to each other and climate. Disturbance, interacting with these abiotic and biotic factors, produces landscape heterogeneity (Forman and Godron 1986).

Landscapes have three structural elements: a matrix, patches, and corridors. In forested landscapes, the matrix is defined as the most contiguous vegetation type. Patches are homogeneous (in structure and composition) areas of vegetation that differ from adjacent vegetation. Corridors are vegetation units that provide connectivity of similar patches through a different matrix or patch aggregation (Diaz and Apostol 1992).

The successional classifications of Steele, Arno, and Clausnitzer can be used as a framework for landscape element identification. The matrix, patches, and corridors would become dynamic ecosystem elements with predictable developmental pathways within a plant association framework. At the ecosystem scale of biodiversity, a successional classification provides compositional, structural, and functional knowledge for resource managers.

Landscape patterns in the inland Northwest have evolved in a heterogenous environment with a variety of disturbance regimes. Human activity has affected this natural landscape, often to a high degree. Completed studies of the region's ecosystems should be supplemented with investigations of disturbance agents and regimes operating at different scales in the landscape to provide better understanding of ecosystem dynamics at the landscape scale.

To illustrate the use of successional classification in understanding ecosystem responses to both natural and human-induced disturbances, examples of the Blue Mountain grand fir series follow. A brief description of classification concepts precedes discussion of applications within an ecosystem framework.

The classification concepts presented by Steele (1984) have been applied in developing the successional classification for grand fir plant associations of southeastern Washington and northeastern Oregon (Johnson and Clausnitzer 1992, Johnson and Simon 1987). The plant associations are first separated into component layers of trees, shrubs, and herbs in recognition of the developmental independence of these layers. This independence is related to differential susceptibility to disturbance and differential rates of recovery in the tree overstory and shrub-herb understories. Within this successional framework, classification diagrams, keys, and association tables are displayed to represent the layer groups and layer types defined for each component layer.

Each layer group has a diagnostic seral indicator species present at 5 percent or greater abundance. For example, in the tree layer of the grand fir/Pacific yew/queencup beadlily plant association, five layer groups are defined. Each layer group is named for a seral indicator-western larch (LAOC), ponderosa pine (PIPO), Douglas-fir (PSME), Engelmann spruce (PIEN), or grand fir (ABGR). The species near the base of the classification diagram (fig. 21) have less successional amplitude than those near the top; that is, these species are found during the early stages only, but the climax species may be found during all stages. The western larch layer group is the earliest successional tree layer and includes stands with western larch at 5 percent or greater canopy coverage. Time is depicted as a vertical axis in the diagram.

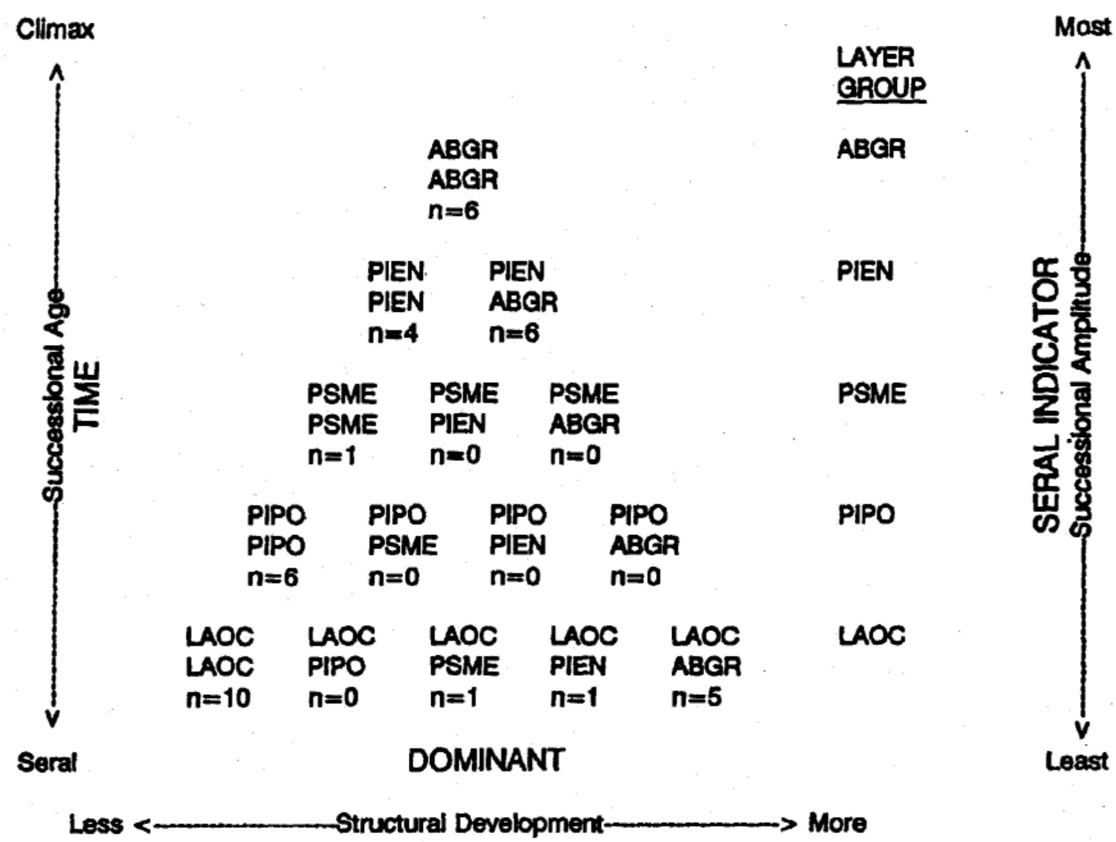

Figure 21. Successional classification of the tree layer in the grand fir/Pacific yew/queencup beadlily plant association.

Layer type is a classification unit in which a particular plant species dominates a portion of the layer group. The LAOC layer group has five layer types (fig. 21). These separate layer types depict stands dominated by western larch, ponderosa pine, Douglas-fir, Engelmann spruce, or grand fir; they represent structural and compositional development along the successional gradient within a layer group. The nomenclature for this unit combines the seral indicator species and the dominant species. For example, LAOC-ABGR would include all stands within this plant association in which western larch occurs at 5 percent or greater canopy coverage and grand fir dominates the tree layer.

Plant associations of the grand fir series are resilient and recover relatively quickly after light or moderate disturbance. High-intensity disturbances have slower recovery rates if combined with forest stand conditions of dense overstory and depauperate understory.

Two fire severities have been identified for the Blue Mountains of Oregon and Washington: underburning, and conflagration fire (Hall, unpublished). Where the mean fire return interval has been 10 years in forested stands, fire-resistant species dominate both the overstory and understory. Ponderosa pine is the dominant tree, and pinegrass or elk sedge is abundant in the understory. The conflagration fire has a return interval of 50 to 300 years. Lodgepole pine and western larch are dominant pioneer species in this regime. Understory shrubs and herbs are surviving members of the preburn plant community or they are early successional species reproducing from windblown seed or persistent seed stored in the soil.

Grand fir plant communities are uniquely affected by insect pests and pathogens. Susceptibility of individual stands to a particular pest depends on existing stand structure, composition, and environmental stress. Low populations of pests can cause the mortality of trees, either singly or in small groups. Outbreaks usually operate at another scale in the landscape and can result in tree mortality over large acreages. Historically, the mountain pine beetle, Douglas-fir tussock moth, and western spruce budworm have severely affected stands of lodgepole pine, grand fir, and Douglas-fir. These disturbance agents interact with forest stand composition and structure to retard, arrest, or accelerate vegetation development. For example, mountain pine beetle could either recycle a mature lodgepole pine community in the absence of other tree species or accelerate succession, if a vigorous seedling and sapling understory of grand fir were present in the stand.

Logging effects to forested plant communities are related to the season of disturbance by the specific activity (machine scarification, broadcast burning, pile and burn). The intermountain West has a truncated disturbance regime because logging has not been a historical disturbance factor in the same frequency as fire. Nonetheless, machine scarification has affected species establishment, survival, and growth in various ways. In grand fir plant associations, for example, huckleberry species are susceptible to this type of disturbance. More information is needed concerning community and species responses to these types of disturbance regimes.

Unlike the frequency of logging a site once every 120 years, the effects of grazing are related to the continuous or recurrent removal of biomass by ungulates. This disturbance regime should be studied in grand fir successional stages of the intermountain West. Vegetation changes within and outside of exclosures could compare effects of grazing on recovery rates, direction of vegetation development, productivity, and composition.

The tree layer of the grand fir/Pacific yew/queencup beadlily plant association becomes increasingly susceptible to pests of grand fir as succession proceeds (fig. 21). The layer types show differential susceptibility (fig. 22). Elevated portions represent types susceptible to western spruce budworm outbreaks. For any individual pest, highly susceptible layer types could be identified and subsequent management designed to reduce negative effects.

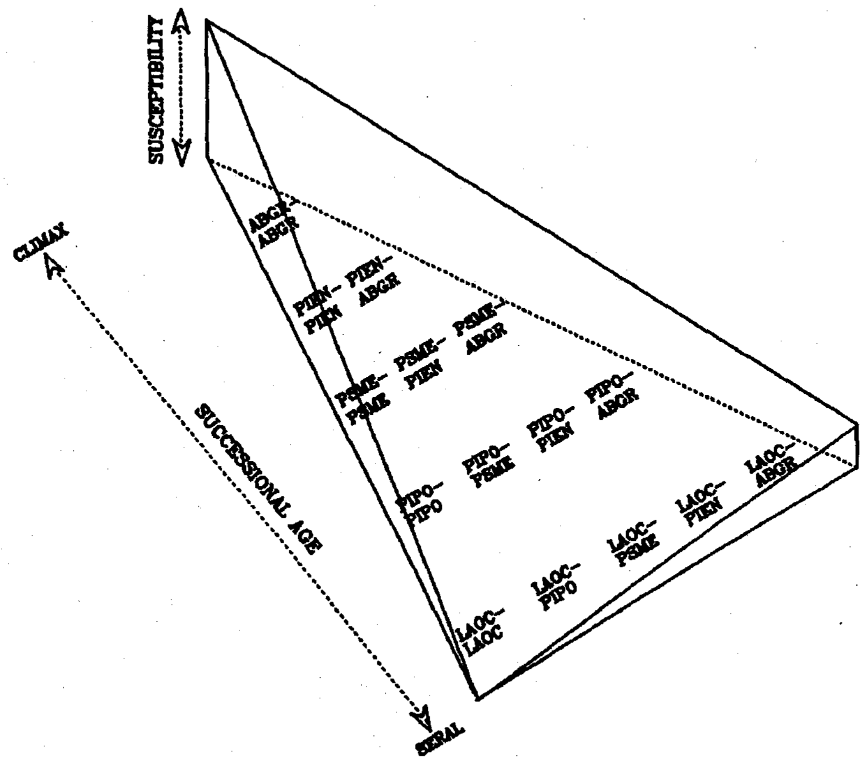

Figure 22. Western spruce budworm susceptibility plane for tree-layer types in the grand fir/Pacific yew/queencup beadlily plant association.

A successional trend of tree-leaf-area index in a grand fir plant association (fig. 23) illustrates a hypothesis of biotic and abiotic interactions about thresholds beyond which an ecosystem seemingly unravels. As succession proceeded, leaf-area index increased because both shade-tolerant and shade-intolerant trees established and grew. Periodic burning historically reduced leaf-area index, and it fluctuated within the range of natural variability (A and B). After fire suppression was initiated, leaf-area index increased to near the upper limit of natural variability. As climatic fluctuations led to lower soil moisture and subsequent water stress for trees, the upper limit for the range of natural variability shifted downward to reflect the lowered leaf area carrying capacity of the site. When leaf-area index exceeded the drought-induced threshold, -tree mortality became significant because it was directly linked to the abiotic environment. But secondary agents (the western spruce budworm) may cause significant mortality through linkages to the abiotic and biotic environments. Budworm populations may interact directly with the warmer, drier environment in addition to indirect linkages with predator and parasite populations. Further, the budworm may interact with stressed host trees through reproductive structures (male and female cones), which are more abundant on stressed trees. These feeding sites may be more favorable to budworm populations (Mattson and others 1991). This community can be self-regulating, as long as structure and function are preserved, but exceeding threshold values may lead to a different trajectory of ecosystem recovery and development. However qualitative this conceptual model appears, it nevertheless displays abiotic and biotic interactions at the ecosystem scale important to resource management decisions.

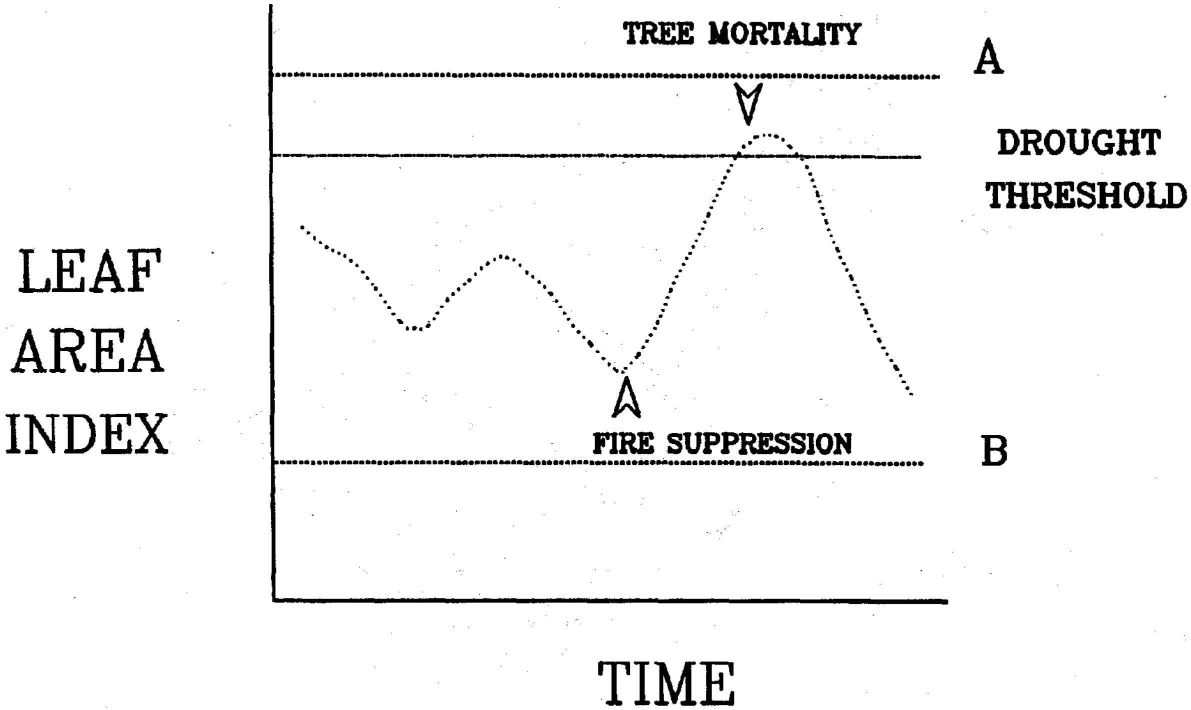

Figure 23. Leaf area index in a stressed ecosystem.

IDAHO FESCUE PLANT ASSOCIATIONS

The Relations Between Disturbances and Community Structure, Composition, and Distribution

The bunchgrass vegetation of the canyonlands in northeastern Oregon provide a mosaic on a contorted landscape that was sculpted over geologic time by mass-wasting after Pliocene flooding of the Snake River and its major tributaries (Baldwin 1964). The grassland soils are highly variable. Composition of bunchgrass community can vary dramatically based on soil depth below eroding rims or above buried basaltic flows. The aspect of bunchgrass sites also influences the kind of vegetation that can establish on them based on orientation to solar radiation and desiccating temperatures. The elevation of bunchgrass sites also determines temperature and moisture. Sites that can support the fescue plant association can occur between extremes of 1000 and 8000 ft elevation (Johnson and Simon 1987), but moisture availability is what allows fescue to persist at the lower elevations. Subsurface moisture emanating from the basaltic flows beneath the colluvium often determines whether moisture is sufficient to sustain fescue communities.

Of the three common bunchgrasses native to northeastern Oregon (Idaho fescue, bluebunch wheatgrass, and Sandberg's bluegrass), Idaho fescue requires more moisture and cooler temperatures (Daubenmire 1972). Therefore, where temperatures are warmer and soil moisture less, plant communities representing bluebunch wheatgrass plant associations can establish, but the more sensitive fescue communities cannot. Sandberg's bluegrass plant associations are found on shallow, dry, warm sites where soil depth and moisture are insufficient for the larger bunchgrasses.

The nine Idaho fescue plant associations described for northeastern Oregon (Johnson and Clausnitzer 1992, Johnson and Simon 1987) are distinguished by structure, composition and microhabitat; the associations reflect the environmental differences that influence their distribution across the varied relief of the canyons and ridges. At the most mesic end of the fescue continuum, Idaho fescue is associated with sedges. At the wetter end of the series are Idaho fescue-timber oatgrass (*Danthonia intermedia* Vasey)-sedge and Idaho fescue-Hood's sedge plant associations. Four plant associations were described where prairie junegrass was associated. These Idaho fescue-prairie junegrass communities were intermediate between the moister meadow steppe associations and the drier fescue associations of the series. The prairie junegrass association with fescue is typified by substrates with low surface colluvium and rock. Finally, three plant associations represent the most xeric of the Idaho fescue series (and therefore the most allied to the bluebunch wheatgrass series). These are the Idaho fescue-bluebunch wheatgrass associations that are differentiated by three distinct environments at the warmer, drier end of the series.

Natural Disturbances as Modifying Events in Community Structure, Composition, and Distribution

As with all vegetation in eastside communities, Idaho fescue bunchgrass communities rely on periodic disturbance to rejuvenate and maintain vigor and vitality of the associated plant composition. The following events are ongoing and cyclic within bunchgrass communities of Idaho fescue plant associations:

Soil and slope movement-The majority of these communities are on steep colluvial slopes or on gentle ridgetops. The steep colluvial slopes are in constant movement; "stable," late-seral bunchgrass communities move 3 to 5 ft downslope over 15 to 20 years on 40 to 60 percent slopes (as defined by realignment of fixed transects across slopes from anchor positions at rim outcrops) (Johnson, unpub. data). On the gentle slopes and ridgetops, fescue communities contain 10 to 15 percent bare ground in late seral stages, with up to 50 percent rock and gravel on the surface. These bare patches are prone to frost heaving in the early spring after late winter saturation and freezing-thawing of the soil mantle.

Fire-Fire ignitions by late summer and early fall thunderstorms historically burned across these bunchgrass slopes with a haphazard, interfingering extension based on daily temperatures, wind velocity and the microrelief of the slope. Fire was certainly not uniform in its effects on the vegetation. Some areas burned intensively where standing biomass was dense and grass crowns were dry. In others, the burns were rapid and left the crowns of the grasses alive and ready for new tillers and sprouts with the onset of fall moisture. Of the three primary bunchgrasses, fescue is considered the most sensitive to fire. When the most mesic fescue associations burn intensely, associated forbs are promoted and succession regresses to earlier stages where forbs dominate until the reemergence of bunchgrass dominance in later successional stages. Natural fire regimes tended to burn with 10-year periodicity in open forest stands of the southern Blue Mountains (Hall 1976). The fire interval for bunchgrass vegetation was probably as frequent, with minor effects to the plant composition. When fires burn across the fescue-bearing landscapes today (after decades of fire exclusion) the effect of the burns is greater because of the buildup of dry, dense litter in the bases of the grasses.

Grazing-The modification of climax fescue communities has been greatest where the grazing animal has had easiest access to the range. In northeast Oregon canyonlands, fescue provides grazers with an early succulent plant, preferred over the taller bluebunch wheatgrass plant by elk, cattle, and sheep. Because soils are often wet in the spring, early grazing on fescue tends not only to consume the foliage, but also to dislodge plants from the ground. Perhaps the greatest detrimental grazing practice, which has decreased the vigor of bunchgrass, has been use by ungulates.too early in the season and for too many seasons over time.

After continued pressure season after season, the stand of bunchgrass ultimately succumbs. As degradation continues in fescue communities, other plants tend to increase or invade-perennial forbs such as balsamroot (*Balsamorhiza sagittata* (Pursh), lupine (Mutt.)., field chickweed (*Cerastium arvense* L.); annual forbs such as deerhorn (*Clarkia pulchella* Pursh); and annual grasses such as cheatgrass (*Bromus tectorum* L.), rattlesnake brome (*B. brizaeformis* Fisch. & Mey.), and Japanese brome (*B. japonicus* Thunb.). Invading species are goatweed (*Hypericum perforatum* L.), Kentucky bluegrass, gumweed (*Grindelia* spp.), and tarweed (*Madia* spp.). Because grazing causes structural and compositional changes to the fescue community after overuse and abuse, the community dominated by bunchgrass in late-seral stages has forb-grass co-dominance in mid-seral stages and simpler communities dominated by either annual grasses or forbs in early seral stages.

Grazing, like fire, can be a stimulus to the bunchgrass plants and provide a natural, beneficial role to plant vitality and community stability. The key to maintaining and enhancing bunchgrass communities lies in timely grazing of the plants and the moderate use of the community: Studies have shown that early and repetitive grazing before seed set is injurious to the bunchgrass plant (Blaisdell and Pechanec 1949, Mueggler 1974, Pond 1960). Different classes of ungulates tend to graze the bunchgrass community preferentially, seeking different plant species within the community, which can benefit the vigor and vitality of the vegetation.

Management-Induced Disturbances of Idaho Fescue Grasslands

The climax fescue grasslands are a natural mosaic caused by topographic landform undulations, which in turn produce microclimates and promote differing grassland structures and compositions. Added to this diverse landscape are the superimposed modifications by past fires and by grazing pressures that have combined to form a variety of seral stages across the land. All of these effects are certainly not undesirable from an ecological perspective. Grasslands where lack of disturbance has resulted in late seral vegetation dominated by bunchgrasses to the virtual exclusion of other plants may provide the best forage for grass-eating ruminants. The greater diversity in plant species composition in mid-seral stages of fescue plant associations however, may provide the most balanced offering to all users of the grasslands (Thomas and Towell 1982). The early and very early seral stages of fescue grasslands that have increased from earlier use by land managers are the cause for concern to land managers today. Many sites capable of supporting Idaho fescue bunchgrass communities are so modified that they appear as bluebunch wheatgrass or Sandberg's bluegrass climax communities, or have been so thoroughly degraded that they contain no bunchgrass vegetation. Management for the next century must focus modern restorative techniques on these sites. Some of our grassland communities are so degraded that attempts at rehabilitation may be in vain. The principal problem beyond economics is the ability to protect restoration efforts from wild grazing animals long enough to establish the new community.

Introduction of Exotic Grasses

The grasslands of the northeastern Oregon area have had, repeated rangeland improvement seedings in an attempt to rectify the damage of the past. The majority of these seedings have failed because highly preferred grass species were planted, and the grazers have sought them out immediately after the seed germinated. Also, some exotic species not appropriate for the environment were seeded. Restoring the grasslands should rely on planting native species, especially those mid- and early-seral species naturally promoted by disturbances. The forbs and grasses dominating in early- and mid-seral stages are the most likely to respond and be maintained on a degraded site. To assure availability of seed for native plant restorative work, local nurseries must be developed to produce the necessary seed from local populations.

Alien Invasion and Naturalization

The fescue grasslands of northeastern Oregon have diminished. The gentle benches and ridgetops have been severely affected by the plow and grazing animals. Alien plants have become firmly established, with no chance for natural succession to native bunchgrass vegetation without intervention by land managers. Examples of invasion can be found in cluster tarweed monocultures growing on deep, fertile ridgetop soils in the complete absence of native vegetation. Other ridgetop locations may look like thin-soil scablands. Onespike oatgrass, a climax codominant of scablands, can be found on deep soils of such fescue sites. Severe overgrazing has all but eliminated deep soil bunchgrasses to favor the shallow-rooted bunchgrasses (such as onespike oatgrass) as moisture retention diminishes.

Perhaps the most degraded fescue sites are found on the structural benches of the Snake River, Imnaha River, and Grande Ronde River canyons. These gentle benches (less than 20-percent slope) contain deep, clayey soils with abundant moisture provided by the contact between two prominent basaltic formations. Springs and seepages are numerous. Homesteaders, early ranchers, sheepherders, and wild ungulates all converged on these benches for the lush vegetation and ease of movement in an otherwise up-and-down world.

Today, the bunchgrasses are absent-or nearly so. Kentucky bluegrass has become the primary invasive species to dominate these benches, but red three-awn, annual bromes (cheatgrass, Japanese brome, rattlesnake brome), and goatweed all may be found in large patches throughout these benchlands Uohnson and Simon 1987).

The presettlement vegetation cannot be brought back on these sites. Attempts to do so would require the impossible task of ridding the community of all naturalized aliens. Perhaps the most notorious of these is cheatgrass. Virtually all plant communities in the canyonlands contain this species, along with one or two other naturalized aliens. The task of rebuilding biological diversity through diversification of the plant community with earlier seral forbs and bunchgrasses is a goal to pursue

Sustaining Eastside Vegetation

The eastside landscape has been modified by disturbing agents and activities. Some of these modifications are natural to the ecosystems and are part of the process of ecosystem maintenance. Other modifications have been induced by human activities on the landscape, and Euro-Americans have had the greatest effect over the past century. The questions that land managers ask about maintaining or enhancing ecosystems is, “What can we do without surpassing the capacity of the sites to rebound from highly disturbed communities toward natural successional pathways?” And, at what point has a particular site, or complex of sites, been so severely affected as to be unable to respond to enhancing activities?

Variables that influence thresholds also determine the capacity of a site to develop a particular kind of plant community. Soil fertility, moisture, temperature variation, and presence of disseminules are the key factors influencing plant community development. As a degrading modification occurs on a site, any one or all of these factors may be negatively affected. For example, continued overgrazing of a late-seral bunchgrass community will increase the percentage of bare ground exposed to erosive wind and water. Grazing too early in the season may compact the soil through trampling. Moisture availability may be curtailed earlier than normal in the growing season with removal of standing herbage and subsequent loss of shading by growing foliage and litter (both of which have been removed by overuse). The lack of standing foliage and the loss of litter also cause the microsite to heat up and be too warm for plants that require cooler, moister conditions. Likewise, lichen and mosses between the rocks, gravel, and plants on the soil surface, are affected by the surficial disturbance by grazing animals. As the degree of disturbance increases, the micro-climate of the ground surface changes. Temperatures become lethal to mosses and lichens on the site. The severe effects of overgrazing on bunchgrass foliage results in the inability of the plants to produce viable seed. And the plants are too weakened to send out new tillers. The relation of moisture and temperature has changed so that the plant species is no longer sustainable on the site.

This scenario has occurred not only in bunchgrass communities, but also on sites supporting shrublands, forests, and wetlands. These sites are incapable of response, even when the degrading activity stops, and a “disclimax” is created by the degrading activities. To regain a resemblance of the original vegetation on the site, managers must intervene-at great expense in time, energy, and dollars.

The key to restoring these ecosystems is to understand the interactions of the component parts. To understand ecosystems requires the talents and wisdom of trained professionals, experienced technicians, and leadership of an interdisciplinary team of ecologists and other specialists. This team must understand that information is insufficient to make decisions correctly on behalf of all ecosystem components. They must also understand those processes the ecosystem requires to maintain itself, in light of the modifications being planned: Decisions must be conservative to avoid the risk of error that would take the system beyond its sustainable threshold.

Passive management is not the best choice after the long tenure of human management of the land. To improve degraded ecosystems and landscapes requires active use of tools and techniques still being developed. The key is to shift from functionalism to multifunctional projects performed on a large scale. Degraded landscapes and vegetation on the eastside cannot be improved without planning, conducting, and monitoring restoration projects at a landscape scale.

The State of the Landscape on the Eastside

After more than a century of active land management, the various ecosystems and included plant communities of the intermountain Pacific Northwest are in need of nurturing assistance from the human population. In comparison with other sectors of the United States and other countries in the World, this part of the planet is in relatively good shape. Entire provinces of the region have not been placed under intensive agriculture, nor have large segments of the forested landscape been converted to subsistence agricultural pursuits. Great numbers of plant and animal species have not been displaced to the point of extinction. And the human population has not yet overwhelmed the region so as to make quality of life unacceptable to the majority of its occupants.

This “sanctuary” will surely be found, however, and the pressures exerted by an expanding society will cause our vegetation, natural resources, landscapes, and ecosystems to be overexploited and forever modified. The time to act is now. The way to act is to focus on the landscape; to emulate the disturbances that have created and shaped its plant communities; to initiate projects on a large scale that use modifying events to enhance the combined plant communities of the included ecosystems; and to cease those destructive activities that do not replace elements required by the ecosystem.

CONCLUSIONS

People observe succession in a life span that is but a “few frames in a continuous movie.” people have envisioned idealized stable cycles and classified vegetation into artificial units based on their perceptions of how plants interact competitively over time. They have imagined the forest and steppe primeval as one of pristine vegetation. Paleo-vegetation studies have shown that vegetation has changed dramatically in composition and extent in the intermountain Pacific Northwest over the past 20,000 years. The forest and steppe plants have responded rapidly to environmental disturbance. Change is continual, change is unpredictable, and climatic shifts will continue to exert a large influence on the steppe-forest interface in the future.

Successional pathways depict the probable course of community development within a framework of defined community types for a disturbance regime. Altered abiotic and biotic interactions may lead to different responses by individual plant species and the identification of different successional pathways. Knowledge of plant succession is the foundation of a sound vegetation management program where the primary goal is to retard, arrest, or accelerate the natural forces of vegetation change. Many investigations have studied community responses to a single disturbance; now the variations of community responses to different disturbance regimes must be studied.

Both natural and human disturbances have long-term influence on the appearance and species compositions of eastside vegetation. The long-term consequences of natural disturbances are, for the most part, enhancing to biological diversity. The natural disturbances that resulted in the current vegetation need to be reintroduced. The scale of the modifying events and activities needs to shift from species and stand to the landscape scale. Activities that do not replace elements and processes needed for maintaining and enhancing the ecosystems must be curtailed. After more than a century of active land tenure and management by Euro-Americans, the various ecosystems of the eastside are in need of nurturing.

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GLOSSARY

Adventitious-Additional; occurring in unusual or abnormal positions, as adventitious roots or buds.

Alien (plant)-A species occurring in an area to which it is not native, i.e., one introduced very recently, and usually by man.

Alpine glacier-A mass of ice occupying a depression within or lying on mountainous terrain.

Andesitic-Pertaining to andesite, a gray to grayish-black, fine-grained volcanic rock.

B.P.-An abbreviation for Before Present. Used with radiocarbon age estimates. A.D. 1950 is the standard zero point. See tree-ring corrected and radiocarbon age.

Biodiversity (biological diversity)-The variety and variability among living organisms and the ecological complexes in which they occur.

Biomass-The sum total of living plants and animals above and below ground in an area at a given time.

Climax (community)-The stable community in an ecological succession which is able to reproduce itself indefinitely under existing environmental conditions in the absence of disturbance. The final stage of succession.

Climax (vegetation)-The pattern or complex of climax communities in a landscape corresponding to the pattern of environmental gradients or habitats.

Cohort-A group of trees regenerating after a single disturbance.

Colluvium (colluvial)-Unconsolidated earth material deposited on or at the base of steep slopes by mass wasting (direct gravitational action) and local unconcentrated runoff.

Colonization-The process of plant population establishment on a recently bared surface.

Competition-An interaction that occurs whenever two or more living organisms make demands of the ecosystem in excess of supply.

Continuum-An abstract concept to describe plant and vegetation distributions. Plant species have different environmental requirements. Since these environmental factors vary continuously in time and space, vegetation can be described as a continuous variable. Plant distributions form a continuum of variability, not discrete communities.

Continental ice sheets-Glaciers occupying a large part of a continent. See Cordilleran and Laurentide.

Cordilleran ice sheet-A continental ice sheet which formed along the northern Rocky Mountains and spread eastward during the last part of the Pleistocene some 75,000 to 10,000 years ago.

Couplets-A pair of sedimentary layers in lake deposits which represent related deposits. In the case of charcoal and ash deposits in a sediment core, the couplets represent the settling out of the heavier particles before the finer particles from a single fire event.

Coverage-The area of ground included in a vertical projection of individual plant canopies.

Deglaciation-The uncovering of an area from beneath glacier ice as the result of melting (wasting).

Depauperate-A stand with sparse ground covering vegetation due to 1) tree overstory density precluding sufficient light for understory plant growth, or 2) a deep restrictive litter of duff layer or, 3) a combination of limiting site factors.

Diploxylon-A subgenus of *Pinus* without conspicuous verrucae on the pollen grain distal membrane. Includes lodgepole and ponderosa pine.

Disclimax-A type of climax community which is maintained by either continuous or intermittent disturbance (i.e.-grazing, burning, logging) to a severity that the natural climax community is altered.

Disseminule-A detached structure capable of reproducing a plant.

Disturbance-Any event which removes a significant amount of the living biomass from a site; a perturbation.

Dominant-A plant or group of plants which by their collective size, mass, or number exert the most influence on other components of the ecosystem.

Duff-The surface layer of the forest floor consisting of freshly fallen and partially decomposed leaves, needles, twigs, stems, bark, and fruits.

Ecosystem-An aggregation of organisms of any size, considered together with their physical environment.

Edaphic controls-A term applied to any soil characteristic that affects plant growth.

Endemic-An organism, or pertaining to an organism, which is restricted to a stated portion of the earth's surface.

Epidemic-Affecting large numbers of a population at the same time.

Exotic-A plant introduced from another country.

Fluvial-Pertaining to or produced by the action of a stream or river.

Forb-An herbaceous plant other than a sedge, grass, or other plant with similar grass-like foliage.

Glacial Lake Missoula-A Pleistocene proglacial lake which formed when glacial melt water was trapped behind an ice dam on the Clark Fork River in northwestern Montana. The lake filled and emptied many times. The deeply eroded landscape of central Washington state (scablands) was formed by catastrophic releases of water from this lake.

Graded beds-A type of arrangement of sediment layers in which each layer displays a gradual change in particle size, usually from coarse at the bottom to fine at the top.

Graminoid (gramineous)-A herbaceous grass or grass-like plant.

Haploxylon-A subgenus of *Pinus* with conspicuous verrucae on the pollen grain distal membrane. Includes white pines such as limber pine and whitebark pine.

Herb-A plant that dies back to the ground surface each year.

Holocene-An epoch of the Quaternary period. It began about 10,000 years ago and continues to the present time.

Hypsithermal-In eastern north America, a part of the Holocene (about 9000 to-2500 B.P.) during which climatic conditions were thought to be warmer than earlier or later times.

Indicator species-A species which is sensitive to important spatial or temporal variation of vegetation characteristic of a site such that-it's constancy or abundance reflect significant changes in abiotic or biotic environmental factors.

Interglacial-Pertaining to the time between episodes of glacier development, maximization, and recession.

Interstadial-Pertaining to a warmer substage (interstade) of a glacial episode marked by a temporary retreat or stillstand of glacial ice.

Invasion (plant)-The entrance of an organism into an area where it was not formerly represented.

Invasive-Having the ability to become established in an area rather aggressively.

Janus-A legendary King reputed to the first ruler of Italy. He developed into the Roman god of all beginnings for whom the month of January is named. He is represented as having two faces looking in opposite directions because he could see both past and future.

Jokulhaups-An Icelandic term for glacier outburst floods which occur as sudden, sometimes catastrophic releases of water from a glacier or glacier-dammed lake.

Krummholz-The belt of discontinuous scrub or groveland at alpine timberlands, composed of species which have the genetic potential of the tree life form, but in this ecotonal belt are both strongly dwarfed and misshapen.

Laminae-A set of distinct, thin layers in a stratigraphic cross section.

Late glacial-A northern European term for the final phase of the Pleistocene, about 13,000 to 10,200 B.P. The period was characterized by a decisive amelioration of the climate and retreat of ice sheets.

Laurentide Ice Sheet-A continental ice sheet which formed in the Hudson Bay area and grew south and westward during the last part of the Pleistocene some 75,000 to 10,000 years ago.

Lava tube-A hollow space beneath the surface of a solidified lava flow formed when slower cooling subsurface lava withdraws from the surface crust.

Layer-The lifeform (tree, shrub, or herb) which defines the characteristic physiognomy of the vegetation (at any geographic or classification scale) being considered.

Layer group-A unit of successional classification in which a diagnostic seral indicator species occurs at 5% or greater coverage.

Layer type-A unit of successional classification in which a particular plant species dominates a portion of. the layer group.

Loess-A blanket deposit of wind blown dust.

Mantle (soil)-The earth's surface where geologic and biologic factors over time have created a soil mass different from the original materials. It serves as a natural medium for plant growth.

Matrix-A term used to define the most connected portion of the landscape, that is, the vegetation type that is most contiguous.

Mesic-A habitat characterized by moderate moisture conditions. Drier than hydric, moister than xeric.

Mesophytic-Moist loving plant - a species or association of species which cannot survive extreme conditions of temperature and aridity.

Microclimate-Any set of climatic conditions differing from the macroclimate, owing to closeness to the ground, to vegetation influences, to aspect, to cold air drainage, etc.

Mineral suite-A set of minerals that occur in close association generally representing related formation.

Mount Mazama-The name given to a former volcanic mountain which erupted about 7000 B.P. (8000 tree-ring corrected years ago). Thick deposits of volcanic ash (tephra) from this eruption blanketed much of the northwestern United States. Crater Lake, Oregon, fills the depression formed by the collapse of the mountain's top.

Neolithic-In archaeology, the period in human prehistory characterized by the domestication of plants and animals.

Noxious (species)-A plant species that is undesirable because it conflicts, restricts, or otherwise causes problems under the management objectives.

Overstory-Collectively, the dominant plant stratum, the plants below are the understory.

Paleoclimatic-Pertaining to climates of the geologic past.

Paradigm-A model; standard; ideal; pattern.

Plant association-A unit of vegetation classification based on the projected climax community type.

Plant community-A general term for an assemblage of plants living together and interacting among themselves in a specific location; no particular ecological status is implied.

Plant community type-An aggregation of all plant communities with similar structure and floristic composition. A unit of vegetation within a classification with no particular successional status implied.

Pleistocene-An epoch of the Quaternary period. It began about two million years ago and ended about 10,000 years ago. Synonymous with Ice Age.

Pliocene (epoch)-The last epoch of the Tertiary period during which man and most species of modern mammals came into existence, 2 to 7 million years ago.

Plunge pool-A deep hollow scoured in a streambed at the foot of a waterfall.

Pluvial lake-A lake formed during a period of heavy rainfall; specifically a lake formed in the Pleistocene epoch during a time of glacial advance. See Pluvial Lake Lahontan and Pluvial Lake Bonneville.

Pluvial Lake Bonneville-A Pleistocene age pluvial lake which covered a vast portion of western Utah and into eastern Nevada. Great Salt Lake, Utah is the modern remnant of Lake Bonneville. See pluvial lake:

Pluvial Lake Lahontan-A Pleistocene age pluvial lake which occupied a large area of western Nevada. Modern lakes which represent remnants of Lake Lahontan include Pyramid, Humboldt, and -Walker Lakes in Nevada and Honey Lake, California. See pluvial lake.

Pollen influx-Accumulation of pollen in sediments per unit of volume or time. Absolute pollen influx is the number of pollen grains per centimeter square per year derived from pollen concentration and rate of sedimentation.

Pollen spectra-The percentages of pollen and spores in a single pollen sample.

Primary tephra-Said of deposits of volcanic ejecta which remain as deposited by airfall from a volcanic cloud. In cores from lakes or bogs these deposits represent volcanic ash which fell on the water surface at the time of the volcanic eruption. See redeposited tephra.

Progeny-Decendents or offspring collectively.

Quaternary-A geologic period (Great Ice Age) beginning about two million years ago and extending to the present. It consists of two epochs - the Pleistocene and the Holocene.

Radiocarbon age-An age determination made on organic substances by measuring decay of ^{14}C, a radioactive isotope of carbon. See B.P. and Tree-ring corrected.

Redeposited tephra-Said of deposits of volcanic ejecta which fell out of a volcanic cloud in one setting and were later moved to another setting by earth processes. In cores from lakes or bogs these deposits represent volcanic ash usually carried into the water by surface runoff sometime after the volcanic eruption. See primary tephra.

Refugia-Isolated areas which, with respect to fauna and flora, have remained relatively unchanged in contrast to surrounding areas which have been markedly affected by environmental changes.

Relief (topographic)-The relative difference in elevation between the hilltops or mountain summits and the lowlands or valleys of a region. .

Rhizomatous-Having rhizomes, rootlike stems which grow underground producing above-ground stems and root systems.

Riparian-Pertaining to the land, next to water, where plants dependent on a perpetual source of water occur.

Riverine-All wetlands and deepwater habitats contained within a natural or artificial channel, which periodically or continuously contains moving water, or which forms a link between two bodies of standing water.

Root collar-A line of junction between a root and its stem.

Rhyolitic-Pertaining to rhyolite a light colored fine grained volcanic rock.

Seral-1. Successional; 2. A species or a community which will be replaced in the successional process.

Seral stage-A step or identifiable stage of a successional sequence (the sere).

Sere-The sequence of stages or communities that develop following a particular disturbance type; e.g., a fire sere.

Series-An aggregation of taxonomically related associations that takes the name of climax species that dominate the principal layer. A taxonomic unit in a classification.

Slump (soil)-The downward slipping of a mass of rock or soil moving as a unit or as several subsidiary units, usually with backward rotation on a more or less horizontal axis parallel to the cliff or slope from which it descends.

Stand-Vegetation occupying a specific area and sufficiently uniform in species composition, age arrangement, structure and condition as to be distinguished from the vegetation on adjoining areas.

Steady state-An equilibrium; a stable level in ecosystem processes over time.

Steppe-Vegetation dominated by grasses and occurring where climate is too dry to support tree growth.

Stratigraphic position-Refers to the dating of a particular layer in a sequence of sedimentary deposits according to the relative order in which all the layers making up the sequence were deposited. Generally this means that any given layer is considered older than layers above it and younger than layers below it.

Structure-The physical elements of ecosystems; the size and arrangement (both vertical and horizontal) of trees within a forested stand.

Succession-The unidirectional change in species proportions of a stand or the complete replacement of one community by another. This may be progressive from early seral stages toward climax or retrogressive from late seral stages toward very early seral stages.

Succession (primary)-The change in plant species occurrence or abundance on areas bared by recent physiographic processes.

Succession (secondary)-The sequence of vegetative change initiated when a previously colonized area is disturbed by natural or human caused events.

Successional pathway-The probable course of community development within a defined framework of seral stages for a particular disturbance regime.

Tephra-A collective term for wind transported volcanic ejecta.

Tephrochronology-The dating of layers of volcanic ash in order to establish a sequence of geologic or archaeological events. This is possible because the tephra produced during any given eruption often have unique physical and chemical properties which allow the correlation between an ash deposit and the eruption which formed it.

Ternary plots-A triangular diagram that graphically depicts the composition of a three part mixture.

Till-Unsorted boulders, gravel, sand, silt, and clay deposited by glaciers without reworking by melt water.

Tiller-A sprout or branch which grows from the base of a plant, especially those of the grass family.

Tolerant (shade)-A physiological characteristic that allows a plant to develop and grow in the canopy shade of other plants.

Tree-ring age-An age determination made on wood based on the counting and correlation of annual growth ring patterns (dendrochronology). The method includes the cross-dating of living and fossil trees of overlapping ages such that the sequence of growth patterns for a region may extend into the distant past.

Tree-ring corrected-The method of radiocarbon dating assumes a constant rate of atmospheric carbon isotope production and decay. This assumption however does not hold. Therefore, radiocarbon ages cannot be directly converted into calendar years. To overcome this, values for radiocarbondated tree-rings of known age are applied to correct radiocarbon dates to actual calendar ages. Differences between a radiocarbon and a tree-ring age can be significant. For instance, the radiocarbon age for the eruption of Mt. Mazama is about 7000 B.P., but the tree-ring corrected age is closer to 8000 years ago.

Understory-Collectively, those plants beneath the dominant plants, beneath the overstory.

Ungulate-Cloven hoofed animals.

Woodland-Vegetation dominated by a rather closed stand of trees of short stature.

Younger dryas-A European term used for an interval of late Glacial time (about 10,000-11,000 B.P.) during which the climate cooled favoring reexpansion or slowing of retreating glaciers. This event may be recognized throughout the northern hemisphere.

Xeric-Characterized or pertaining to conditions of scanty moisture supply; drier than mesic.

Xerothermic-Dry and warm periods of the recent past; plants adapted to dry/warm conditions.

Zone-The geographic area of uniform macroclimate where the climatic climax associations share the same characteristic species of the principal layer.

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Paleovegetation studies have shown that vegetation has changed in composition and extent in the intermountain Pacific Northwest over the past 20,000 years. Today, both natural and human-induced disturbances have long-term influence on the structure and composition of eastside vegetation. Disturbance may enhance landscape diversity; therefore, the scale of modifying events and activities needs to shift from species and stand to the landscape level. Knowledge of plant succession is the foundation of a sound vegetation management program where the primary goal is to retard, arrest, or accelerate the natural forces of vegetation change.

Keywords: Pleistocene vegetation, pollen analysis, disturbance, stand development, succession, steepe ecosystem, forest ecosystem, shrublands, scablands, landscape.

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