

Chapter 5

Dynamics of Ponderosa and Jeffrey Pine Forests

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FOREST DESCRIPTION¹

Ponderosa (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*) forests are ecologically diverse ecosystems. The communities and landscapes in which these trees dominate are variable and often complex. Because of the economic value of resources, people have used these forests extensively.

Humans have greatly altered the structure of ponderosa and Jeffrey pine forests. Heavy livestock grazing, logging, fire exclusion, and climatic events since settlement by Euro-Americans have produced less sustainable forests (Covington and Moore 1994). Comparative photographs from Montana (Gruell *et al.* 1982), South Dakota (Progulske 1974), Colorado (Veblen and Lorenz 1991), Idaho (Boise National Forest 1993), and Arizona (Covington and Moore 1994) provide qualitative evidence that ponderosa pine forests were more open and parklike before the 1920's, with mostly large, mature, and often uneven-aged trees. Dense thickets of seedlings and saplings were rare according to early forest surveys (Ayres 1900, 1901; Beale 1858 as cited in Cooper 1960, Dutton 1887), yet these are a common part of the forest today. Late successional and old ponderosa pine forests now occupy only 2 to 8% of their presettlement abundance in the National Forests of central Oregon (Scientific Society Panel 1993). They have been replaced by dense, multilayered forests that are susceptible to disturbances of historically unprecedented extent and severity (Hessburg *et al.* 1993, Lehmkuhl *et al.* 1993, Covington and Moore 1994). Habitat has changed for the many bird, mammal, reptile, and amphibian species that live in ponderosa pine forests (Thomas *et al.* 1979b, Patton 1988). Scientists concerned about the ecological status of ponderosa pine forests and the large decline in the extent of old forests have called for ecological restoration of these ecosystems (Mutch *et al.* 1993; Covington and Moore 1992, 1994; Everett *et al.* 1994).

The vast literature on ponderosa pine forests reflects their extensive range, varied composition, and variety of uses. The ecology and management of ponderosa pine forests has recently been summarized by Baumgartner and Lotan (1988) and Lotan and Morgan (1993); both include extensive literature citations. Silvicultural recommendations for different regions are provided by Barrett (1979, 1980), Alexander (1986, 1987), various authors in Pearson (1950), Burns (1983), Schubert (1974), Thomas (1979), and others.

Forest Extent

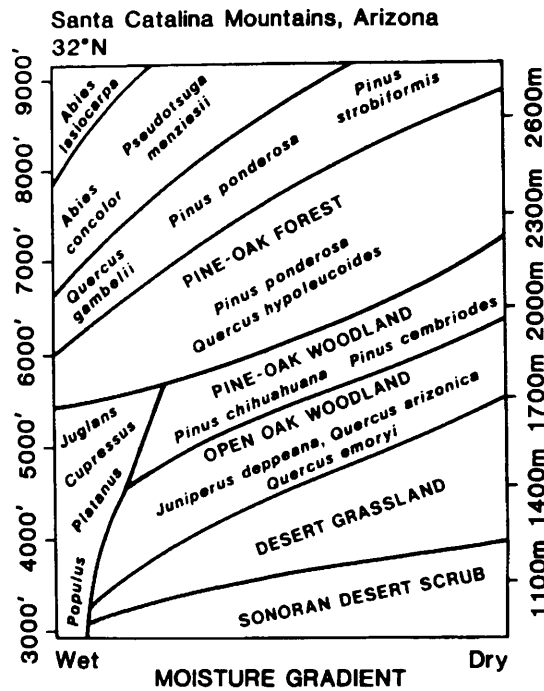
Ponderosa pine forests are found on more than 60 million acres in the western United States (Oliver and Ryker 1990; see Map 1 for combined ponderosa and Jeffrey pine distributions). The species is often an early seral species in mixed conifer forests but is the climax tree species on drier sites. The elevational and moisture conditions where these forests are characteristically found vary geographically (figure 1) (Barbour 1988, Peet 1988). Warm, dry summers and cold, wet winters are typical. Ponderosa pine is one of the most widely distributed and economically important pines in western North America (Oliver and Ryker 1990).

Jeffrey pine is found primarily in the Coast Range and Sierra Nevada mountains of California but also occurs in southwestern Oregon and western Nevada. Jeffrey pine is especially drought tolerant and cold hardy, suiting it to dominate on harsh, infertile sites (figure 2). Jeffrey pine resembles ponderosa pine in appearance (Jenkinson 1990).

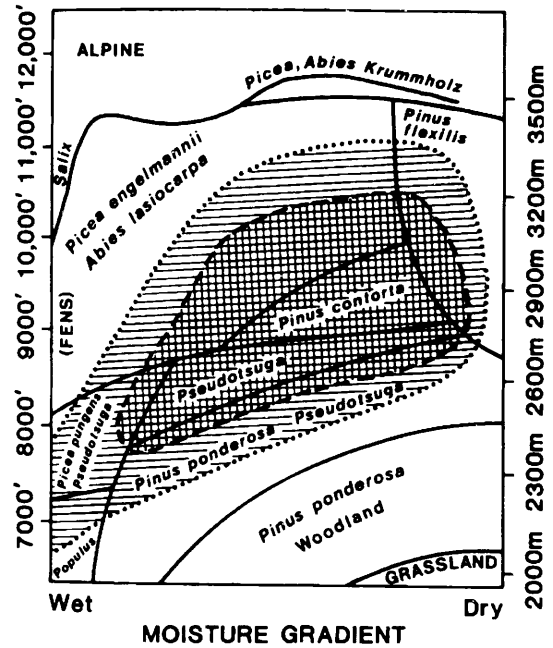
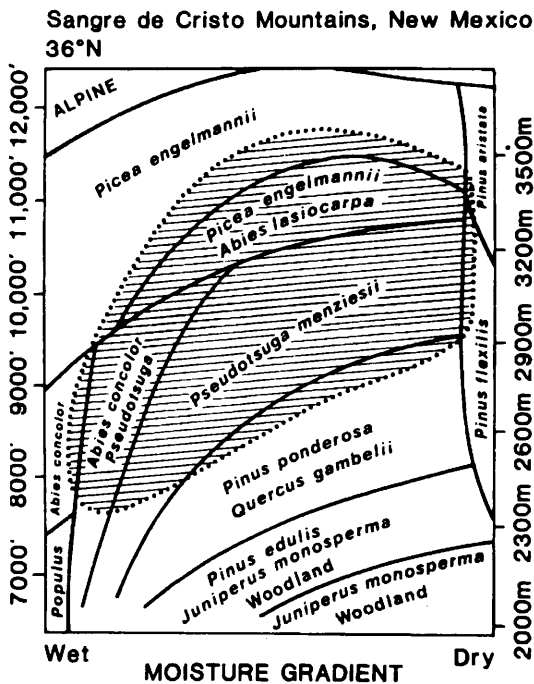
Landscapes, Communities, and Stands

Over an extensive range, ponderosa pine forests are found in a variety of environments and across

¹ Most of the information presented here is drawn from the extensive literature on ponderosa pine because the few studies of Jeffrey pine ecology are mostly limited to northern California (Jenkinson 1990). Because the two species are similar, and ponderosa pine occurs in many of the forests where Jeffrey pine is found (Barbour 1988, Jenkinson 1990), the information included here will likely apply to Jeffrey pine forests as well.

A

Front Range, Colorado
40°N

**C****B**

Bitterroot Mountains, Montana
46°N

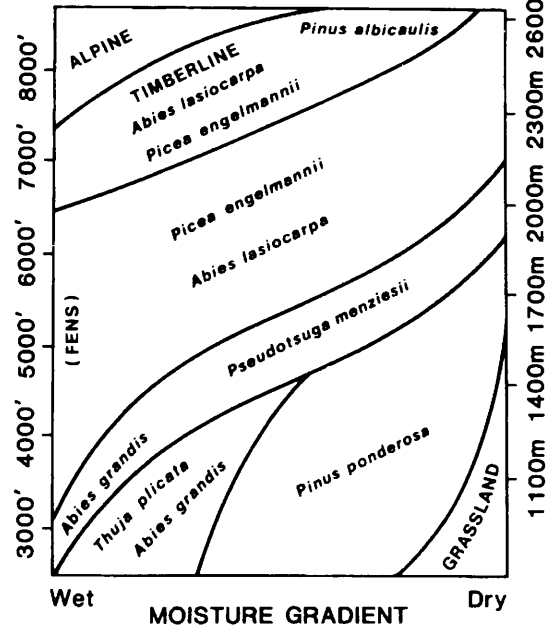
**D**

Figure 1.—Ponderosa pine forests occupy mostly dry, low to mid-elevation sites, but the distribution varies geographically. These gradient mosaic diagrams illustrate variations in vegetation compositions with elevations and topographic positions for 4 sites along a latitudinal sequence. In B and C, the shading down to the left indicates the range of *Populus tremuloides* as an important post-disturbance species, whereas shading down to the right indicates the range of *Pinus contorta* as an important post-disturbance species (from Peet 1988).

land ownerships with strikingly different management objectives. The genetic variability in ponderosa pine is also great. The two recognized varieties, Pacific ponderosa pine (*Pinus ponderosa* var. *ponderosa*) and Rocky Mountain (*P. ponderosa* var. *scopulorum*) differ, and there is significant genetic variation within and between stands (Rehfeldt 1986a, 1986b, Conkle and Critchfield 1988, Linkhart

1988a,b). As a result, fire frequency, tree regeneration success, relative growth rates of trees, tree susceptibility to diseases and insects, and potential forest productivity for timber, wildlife, and other uses vary with geographic location, soil type, and stand conditions throughout the range of this species.

The natural diversity in stand and landscape structure has been augmented by past logging, diseases,

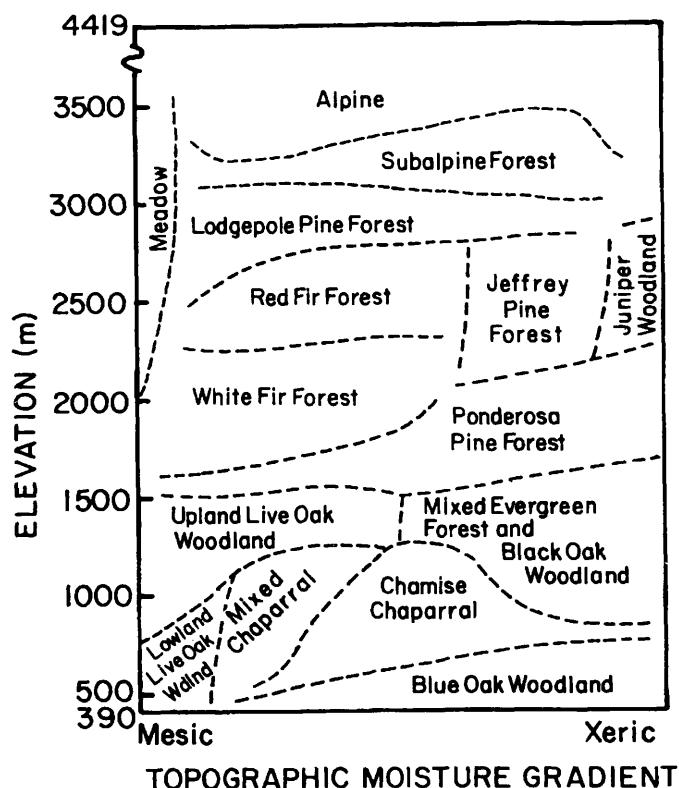


Figure 2.--Jeffrey pine occurs in ponderosa pine forests but is also found in mostly pure stands on drier, more severe sites (from Barbour 1988).

insects, and fires. Ponderosa pine forests vary in stand density, age class distribution, tree vigor, presence of diseases and insects, and patchiness. Both ponderosa and Jeffrey pine trees can occur in dense thickets or in open parklike stands with an understory of bunchgrasses or shrubs. Both species form extensive pure stands or occur as seral dominants in a mixture with other conifer tree species. Both tree species are intolerant of shade and stagnate in dense stands; sapling densities may be as high as 42,000 stems per hectare (Jenkinson 1990). Even in open stands, tree boles are ordinarily clear of branches for much of their lower half. As trees age, the crowns change from short and conical to flat-topped (Harlow *et al.* 1991). In mature trees, branches are large and the foliage is predominately on the outside of the crown where it is exposed to higher light intensities. This structure is well-suited to birds that perch or feed within the crown; the crowns of large trees can shelter birds and insects from weather. The trees have deep tap roots and many lateral roots that extend horizontally at moderate depths through surface soils, often beyond the extent of the tree crown.

Forests are typically patchy, usually structured as groups of 3 to 44 trees of similar diameter (White 1985). Although Cooper (1960) found that groups of trees were of similar age, more detailed analysis on

an unharvested site near Flagstaff, Arizona, showed that ages of trees within the 0.1 to 1.7 ha groups differ by 33 to 268 years (White 1985). On similar sites in Arizona, patches varied in size from 0.03 to 0.26 ha, averaging 0.06 ha (Cooper 1960, White 1985, Moore *et al.* 1993). Where ponderosa pine is a seral species, stands may be even- or uneven-aged. Trees growing where ponderosa pine is the climax dominant are usually uneven-aged. Multiple canopy layers are common, although parklike forests with a single tree canopy layer and a continuous sward of grasses, forbs, and shrubs are also common (Everett *et al.* 1994). Tree regeneration is sporadic, but generally more reliable on the more mesic sites where ponderosa pine is seral. Tree-ring studies indicate that in the past, successful tree establishment was infrequent and depended on a favorable combination of fire or other disturbance to reduce competition from herbaceous vegetation; climate, including spring moisture and little frost heaving (Pearson 1923); reduced competition with grasses and shrubs; and a favorable seed crop. Seed production varies greatly from year to year (Schubert 1974, Barrett 1979).

Understory vegetation in ponderosa pine forests varies greatly in structure and composition. Typically, diverse communities of perennial grasses, forbs, and/or shrubs form in tree canopy openings and where tree density is low. Trees affect productivity of the herbaceous vegetation, which in turn affects the abundance of many insects and wildlife species. When trees are dense, less light and nitrogen are available (Moir 1966), and nitrogen accumulates less rapidly (McConnell and Smith 1970). Most of the herbaceous vegetation is found in the interspersed meadows and openings. Herbaceous production declines sharply as tree basal area and therefore canopy cover increases (figure 3). Few grasses, shrubs, or forbs are found where the tree overstory is dense.

The plant communities associated with climax and seral pine forests are described by authors of the various habitat type, plant association, and community type classifications. Many authors also include extensive information on management, productivity, and successional relationships. Lotan and Morgan (1994) list such classifications for ponderosa pine forests.

Ponderosa pine forests are mosaics of meadows, riparian areas, shrublands, and woodlands intermixed with pine trees. Forest landscapes are a complex of communities with open grassland parks, mixed with dense stands of trees and meadows; all are often mixed with other forest, shrub, and wood-

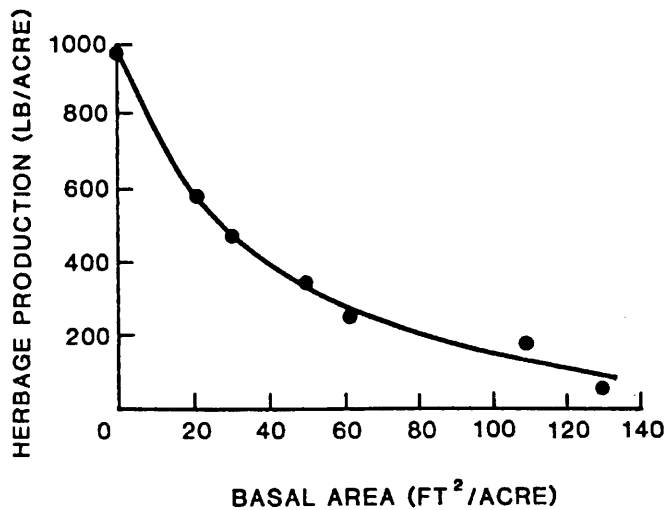


Figure 3.--Productivity of the herbaceous understory vegetation declined sharply as overstory tree density increased in Arizona. Production was greatest in open stands, in thinned stands and in forest openings (from Clary 1975).

land types where topography is complex. The diverse structure of the forested landscapes provides habitat for diverse plant, animal, and insect species.

HUMAN USE OF FOREST RESOURCES

People value ponderosa and Jeffrey pine forests for timber and other wood products, forage for domestic livestock, wildlife habitat, recreational opportunities, watershed protection, and spiritual and aesthetic values. Today and in the past, the ponderosa pine zone is the most heavily used forest zone in Colorado (Myers 1974) and elsewhere. Human use occurs year-round, varying from recreation, residential, and wood production, to wildlife habitat and livestock production (Myers 1974).

Many ponderosa and Jeffrey pine trees were harvested in the early 1900's to support human settlement. Many thousands of hectares were harvested for fuel, mining timbers, railroad ties, and lumber during the late 1800's in the Rocky Mountains (Alexander 1986, Schubert 1974, Steele 1988), in the Pacific Northwest (Barrett 1979), and in California (Oliver and Ryker 1990). To meet market demands, the large-diameter ponderosa pine were often high-graded from the forests with little attention to what was left. Extensive burning accompanied early mining, logging, and railroad construction (Gruell *et al.* 1982). The combination of harvesting and burning was sometimes severe enough to greatly prolong vegetation recovery. Grazing by domestic livestock was extremely heavy in the early 1900's and during World War I (Oliver *et al.* 1993). Disease, insects, and fires have also influenced stand structure and composition.

Today, many state and local economies in the western United States benefit from the harvesting and manufacture of wood products from ponderosa and Jeffrey pine. For instance, half of the economic base in some counties in eastern Oregon is derived from ponderosa pine industries (van Hooser and Keegan 1988). Ponderosa pine contributes significantly to the timber sector of the economies of northern California, Washington, Idaho, Montana, New Mexico, and Arizona; in the latter two states ponderosa pine is the species most often harvested (van Hooser and Keegan 1988). The nontimber uses of ponderosa and Jeffrey pine forests, including grazing, recreation, watershed protection, tourism, and hunting, also contribute significantly to local economies.

Humans have long used ponderosa pine forests. American Indians often purposely and inadvertently ignited fires to facilitate travel; to improve hunting; to enhance production of desirable food, medicine, and forage plants; and for communication (Barrett and Arno 1982). The distribution and structure of ponderosa pine forests were partially determined by fires ignited by lightning and American Indians (Gruell 1983).

Wood Products

Ponderosa pine is widely harvested. The value and volume of its lumber make it one of the most important lumber species in the interior west and one of the most important western coastal tree species (Blatner and Govett 1988). Harvesting and processing the lumber and wood products from ponderosa pine contributes substantially to the state and local economies of the western United States; about 35,000 people are employed each year (van Hooser and Keegan 1988). In the 1920's partial cutting was common throughout the Rocky Mountains (Schubert 1974, Gruell *et al.* 1982, Oliver *et al.* 1993). Clearcutting and partial cutting have predominated since the 1960's, particularly in the Pacific Northwest (Oliver *et al.* 1993).

Timber harvesting to meet the much greater demand for large-diameter logs has contributed to the dramatic change in forest structure. The most valuable wood products come from large-diameter logs (Ayer-Sachet and Fahey 1988). The moldings and frames for doors and windows cut from the outer shell of large logs with few knots command the greatest prices. Plywood is also cut from large-diameter logs. When trees are of small diameter and have lots of branches, the logs are small with lots of knots and yield much less valuable wood. Such logs are processed into dimension lumber, particle board,

house logs, posts and poles, firewood, or wood pulp for paper; these logs also produce the majority of the chips, sawdust, shavings, and bark byproducts. As the large-diameter trees with few branches on the lower stem cut from old forests become fewer and/or less available, they will become even more valuable.

Grazing, Wildlife, Water, and Recreation Resources

Extensive and valuable forage in ponderosa pine forests supports an important livestock industry (Skovlin *et al.* 1976). Many palatable shrubs and grasses grow in ponderosa pine forests. Grazing capacity varies from 0.8 to 6 hectares per animal unit month (Clary 1975, Currie 1975). The dense stands provide shelter from summer sun and winter storms. Openings between stands produce twice as much forage and are used more than forest stands (Skovlin *et al.* 1976).

Cattle and sheep grazing was extensive and heavy early in this century. Increasing rapidly from about 1880, the number of sheep grazed peaked in the 1920's and 1930's (Oliver *et al.* 1993). Heavy grazing by cattle started before 1900 and continues into the present on many sites (Oliver *et al.* 1993). This heavy grazing reduced fine fuels that carried fires and contributed to less frequent fires in the last century in many ponderosa pine forests. Madany and West (1983) implicated livestock grazing as a primary factor influencing alteration of ponderosa pine forest structure since European settlement in Utah.

Many wildlife species use ponderosa pine forests. Patton (1988) estimated that more than 275 bird and mammal species use these forests seasonally or year-round. In the Blue Mountains of Oregon and Washington, ponderosa pine forests provide feeding habitat for 154 species and reproducing habitat for 112 species of reptiles, amphibians, birds, and mammals (Thomas *et al.* 1979b). In comparison, 148 species feed and 129 species reproduce in mixed conifer forests; 106 feed and 84 species reproduce in grand fir forests (Thomas *et al.* 1979b).

Wildlife species are important in the functioning of ponderosa pine ecosystems. Many snag-dependent wildlife are insectivorous and probably limit the size of insect populations, at least at endemic levels (Thomas *et al.* 1979a). Many small mammals and invertebrates within forests influence ecosystem dynamics. For instance, Skinner and Klemmedson (1978) showed that approximately 6 kg/ha/yr more nitrogen is returned to the forest floor via feeding debris from squirrels feeding in pine trees in com-

parison to trees where there are no squirrels feeding. Many small mammals feed upon the mycorrhizal fungi and distribute the spores of the fungi in the Southwest (States 1979 cited in Patton 1992) and the Pacific Northwest (Maser and Trappe 1984). Where grass and shrub understory productivity has declined, this has significantly degraded the habitat for insect, small mammal, and songbird species dependent upon that vegetation for hiding and feeding.

Ponderosa pine forests produce only small to moderate amounts of water as stream runoff. Watersheds can be managed to increase water yield for downstream use, alter the timing of runoff, reduce erosion and sedimentation, or control flooding, but the yields are low (see review by Lotan and Morgan 1993).

Opportunities abound for year-round recreation in ponderosa pine forests; these forests are used extensively for hiking, skiing, camping, bird watching, and other recreational uses. Open park-like stands with scattered large trees and an abundance of grass and shrubs are aesthetically pleasing (Schroeder and Daniel 1981, Brown and Daniel 1986), particularly where they are mixed with meadows, riparian areas, and occasional dense stands.

PRESETTLEMENT FORESTS

Many forests were once ponderosa pine savannas (Dutton 1887; Beale 1858 in Cooper 1960; Biswell 1973), with a discontinuous overstory of scattered, large pine trees and a diverse and extensive understory of perennial grasses and shrubs -- features identified as important to flammulated owl foraging ecology (Chapter 4). Weaver (1974) quoted C.E. Dutton's description of ponderosa pine forests of northern Arizona in the 1880's: "The trees are large and noble in aspect and stand widely apart... Instead of dense forests, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade." Early historical descriptions, including maps and photographs, of forests in the northern Rockies are found in Leiberg (1899, 1900), Ayres (1900, 1901), and similar early forest surveys from throughout the western states. Leiberg's (1899, 1900) photographs of ponderosa pine forests are of open, parklike forests with bunchgrass or shrub and grass understories, with scattered snags, logs, and pines. Ayres (1900) found ponderosa pine forests were "very open and easily navigated on horseback."

Now, such forests have well-developed understories of young ponderosa pine or are codominated by Douglas-fir, grand fir, and other trees that are less

fire-resistant or produce less valuable lumber than ponderosa pine and Jeffrey pine. Extensive changes in forest structure have been documented throughout the Southwest (Cooper 1960; Gruell *et al.* 1982; White 1985; Covington and Moore 1992, 1994), in Montana (Habeck 1990, Arno and Scott 1993), in the Pacific Northwest (Barrett 1979, Everett *et al.* 1994), Idaho (Steele *et al.* 1986, Barrett 1988), Utah (Madany and West 1983), Washington (Weaver 1959), and California (van Wagtendonk 1985, Laudenslayer *et al.* 1989). Barrett (1979) estimated that within the last 25 years other conifers have replaced ponderosa pine as the dominant overstory species on over 2 million hectares in the Pacific Northwest. Tree establishment peaked in the 1920's in southern Utah (Madany and West 1983) and in Arizona and New Mexico (Arnold 1950). The ratio of trees less than 100 years old to those greater than 100 years old was 15 times greater where livestock grazing was extensive (ratio 11.0) than on a similar site inaccessible to livestock (ratio of 0.7) (Madany and West 1983). Pearson (1950) estimated that two-thirds of the ponderosa pine trees currently living in the Southwest were established about 1920 as the result of livestock grazing, increased spring precipitation during an otherwise droughty period, and an abundant seed supply.

As tree density increased, perennial grass cover declined. Arnold (1950) documented grass cover reduction to 25% of what it had been in 1911, 39 years earlier. Livestock grazing was a critical factor in tree establishment (Madany and West 1983), although drought and decreased fire frequency also contributed. Perennial grasses compete with pine seedlings for moisture and have an allelopathic effect on germinating tree seedlings (Jameson 1968). Madany and West (1983) compared grazed and inaccessible sites in southern Utah. They found few thickets of young pine in ungrazed stands and attributed the dramatic contrast in stand structure to heavy livestock grazing in the early 1900's. Although fire exclusion would eventually have a similar effect, the conversion of savanna into forest was enhanced with livestock grazing. Grazing also reduced fine fuels and contributed to the decline in fire frequency in the late 1800's shown in many fire history studies.

Covington and Moore (1992, 1994) simulated changes since settlement for ponderosa pine forests in Arizona. Tree density increased from an average of 23 trees/acre in presettlement forests to 832 trees/acre today. Today, basal area is 4-7 times higher, crown closure has increased by 3-7 times, fuel loading is about 9 times greater, and herbage production is 4-9 times less than on the same sites 100 years earlier. Today, most of the trees are less than 4 inches

in diameter (Covington and Moore 1994). Forest structure changed from an open pine savanna with abundant grasses to dense forest, a condition which likely provides lower-quality flammulated owl foraging habitat (Chapter 4).

Paleoecology

The recent changes in composition and structure of ponderosa pine forests remind us that forest structure is dynamic on several temporal and spatial scales. Mehringer (1985) and others describe the shifts in vegetation composition over millennia documented through studies of pollen and macrofossils from bogs and pack-rat middens. These changes reflect the lack of long-term permanency of vegetation associations (Mehringer 1985, Habeck 1988). Studies of pollen and other evidence of past climate suggest that during the Holocene epoch, 4,000 to 8,000 years ago, species migrated northward by 500 to 600 km (Wells 1983) and upward in elevation (Mehringer 1985) in the Rocky Mountains and Great Basin. Ponderosa pine was relatively scarce in the Southwest during the last glacial period. In the Southwest, vegetation zones have migrated 900 to 1,400 m upward since the last glaciation 12,000 to 14,000 years ago (Hall 1985). There, climates were extremely dry and warm 5,000 to 7,000 years ago (Hall 1985). Changing ratios in the abundance of charcoal and pollen reflect changing fire regimes in the Holocene epoch (Mehringer 1985).

Historical Fire Regimes

Since 1900, fires have been less frequent and more severe in ponderosa pine forests throughout western North America (Arno 1988, Steele *et al.* 1986, Barrett 1988) in both wilderness and areas subject to intensive management. In the Southwest, where fires were typically 1,200 ha in size prior to 1900, some fires now reach 4,000 to 8,000 ha (Swetnam and Dieterich 1985, Swetnam 1990). Crown fires were extremely rare or nonexistent prior to 1950 in the southwestern United States (Cooper 1960). Today, the likelihood of crown fires is increasing. Large, severe wildfires have become common throughout the range of ponderosa pine, suggesting that human activity, including fire exclusion efforts, have changed the fire regime to one of large fires burning in heavy fuels (Arno and Brown 1991). In comparison to surface fires, crown fires are far more difficult to suppress, more threatening to human life and property, and where unprecedented, are more damaging. Stand replacement fires which cover more

than a few acres remove flammulated owl habitat, and, depending on successional patterns, that habitat may be removed for decades to centuries.

In low-elevation forests, historical fires were typically nonlethal surface fires that burned large areas but killed few large trees. On more mesic sites, including those at higher elevations and many sites where ponderosa pine grows but other trees are climax, fire effects were more complex and variable. Fires occurred at longer intervals (40 to 150 years) in a mosaic of nonlethal understory and lethal stand-replacing fires (Arno 1980). Many patches also remained unburned as the fires spread where fuels, topography, microclimate, soils, and changing weather and fuel moisture were conducive. These fire regimes created and maintained a heterogeneous landscape.

Prior to 1900, low-intensity surface fires burned ponderosa pine forests every 1 to 30 years, at least since 1500, and probably since the last glaciation (Arno 1988). Fires were frequent in both seral and climax forests. Flammable fuel accumulated as needles and branches fell and as trees, shrubs, grasses, and forbs grew. The long needles with their high surface-area-to-volume ratio dried out quickly, creating a porous fuel bed. Surface fires spread easily, particularly in open stands with continuous grass or shrub layers.

In the Southwest, fires occurred every 2 to 12 years in the 1700's and 1800's (Cooper 1960, Dieterich 1980, Swetnam and Dieterich 1985) and were more frequent than in eastern Oregon where the mean interval between fires was 25 to 40 years (Hall 1976). In eastern Washington, fire-free intervals varied from 6 to 47 years (Weaver 1959, 1967). In western Montana, Arno (1976) documented average intervals between fires of 6 to 10 years in climax ponderosa pine stands and 7 to 19 years where ponderosa pine is seral to Douglas-fir. In Jeffrey pine forests and mixed conifer forests, mean intervals between fires prior to 1875 were 8 years in pine-dominated sites and 16 years in more mesic sites dominated by true firs (Kilgore and Taylor 1979). Barrett and Arno (1982) compared fire scars on trees from environmentally similar sites that differed in use by American Indians in Montana. Fires occurred twice as often on valley bottom and lower elevation sites that were heavily used by American Indians. Chronologies indicate similar fire intervals back to 1500 (Barrett and Arno 1982).

As Europeans arrived, prospecting, mining, land clearing, railroad building, and other human activity led to a major increase in fire frequency during the late 1800's (Arno 1980). Fire frequency has de-

clined dramatically since then as livestock consumed the grass that fueled many fires, roads created fuel breaks, cultivation and settlement of the valleys limited fire spread there, and periodic burning by American Indians ceased. Fire suppression became increasingly well-organized and efficient between 1900 and 1930 so that by mid-century, most fires of low to moderate intensity could be extinguished (Agee 1990). Due to logging and mining-related activities and fewer fires, fuels accumulated, leading to more intense and more destructive fires.

Steele *et al.* (1986) found that severe fires became more common after 1895 in the ponderosa pine/Douglas-fir forests of central Idaho. Fire frequency decreased, from an average of 10 to 22 years between fires prior to 1895 to only occasional fires since then. Agee (1990) calculated that 210,000 hectares of ponderosa pine forests burned each year prehistorically in Oregon. This is equivalent to about 7% of the range of ponderosa pine forests in Oregon and is far above the area that burns now either in wildfires or prescribed fires, even in years in which fires are very extensive (Agee 1990). In Montana, Habeck (1990) suggested that the size and severity of fires affecting two separate parts of an old remnant forest in 1977 and 1985 were the consequence of no fires occurring since 1918 where fires had once occurred every 7.1 years from 1557 to 1918. No fires occurred until 1977 and 1985, when severe fires killed most trees on two separate slopes.

Old-Growth Forests

Old-growth forests have important biological and social values. They are habitat for a variety of animal, plant, and insect species and can provide long-term biological records of climate. Socially, they are valued for the economic value of some large-diameter trees, for recreation, and as part of our natural heritage. "Old growth" is variously defined by ecological (structure and function), social (lack of harvest or other evidence of human use), wildlife habitat (stand structure), and forest planning (age or size structure) criteria (Hunter 1989, Hayward 1991, Kaufmann *et al.* 1992). Given the controversies associated with describing old growth, the term old-growth here refers to those forests that fit Hunter's (1989) criteria that species composition has stabilized, average net annual growth is close to zero, growth rate is below the lifetime average, the forests are significantly older than the average interval between stand-replacing disturbances, dominant trees are at least as old as the average life expectancy for the species on the site, forests have not been

intensively or extensively cut, and people have never converted the forests to another type of ecosystem. Typically, snags, canopy gaps, and multiple tree canopy layers are present, and shrub, herb, and grass species are relatively abundant; these conditions appear favorable to flammulated owls (USDA 1992).

Old forests are inadequately represented in the landscapes of eastern Oregon and Washington according to Everett *et al.* (1994). They summarized the data of Lehmkuhl *et al.* (1993); who estimated the extent of old, mature, and parklike ponderosa pine and Douglas-fir forests currently (1985 to 1990) and in the past (1932 to 1959) in six river basins. The percentage of the total area occupied by old forest declined by 52-82% in 4 of the 6 watersheds (Lehmkuhl *et al.* 1993, Everett *et al.* 1994). Old forests increased in one watershed by 26% and did not change in another watershed.

Some characteristics of old forests occur where multilayered canopies have developed recently in mature forests. However, where those canopy layers have developed and shade-tolerant species have established in abundance, the associated risk of loss to fire, insects, and disease is higher than in old forests (Lehmkuhl *et al.* 1993). Increasing continuity of species and structures increases the potential extent and severity of damage (Hessburg *et al.* 1993).

It is difficult to find old ponderosa pine forests that have not been influenced by fire exclusion, grazing, timber harvest, or other management. The ecological status of small remnant forests is affected by the management in surrounding forests to such a degree that the ecological value of the old forests may be compromised. Moir and Dieterich (1988) stated that most of the old ponderosa pine forests in the Southwest were deteriorating due to fire exclusion.

If we understood the structure and ecological processes in old forests, we could use that to guide management. An understanding of the historical range of variability in ecosystem structure can be used to guide management (Swanson *et al.* 1993, Morgan *et al.* in press). It is particularly useful for understanding the processes of old forest development, but an understanding of the range in abundance and pattern of old forests would be helpful both in defining the range of desired future conditions and the limits of acceptable change (Morgan *et al.* in press), and to define the conditions that flammulated owls occurred in prior to industrial influence.

Covington and Moore (1992, 1994) warn that defining old-growth forests based upon current conditions within old remnant forests may not be "compatible with the natural conditions prevalent throughout the evolutionary history of the organisms living in western forests." They argue that we

must reconstruct past forest structure based upon detailed analysis of the age of trees within current stands. They were particularly concerned that current conditions are decidedly unnatural. In addition, we must consider the extent to which snags and downed woody debris were abundant prior to settlement.

Based on analysis of the age of trees of presettlement origin, canopy cover varied from 17 to 22% (White 1985, Covington and Sackett 1986) in the Southwest. Pearson (1923) noted that ponderosa pine canopy cover seldom exceeded 25%. Density varied from 7 to 62 trees/ha in Utah (Madany and West 1983) to 52 to 148 ponderosa pine growing with 8 to 129 Douglas-fir trees/ha in 8 stands in Montana (Arno and Scott 1993). Several different sites have been studied in Arizona where estimates of tree density regenerating prior to European settlement vary from 32 trees/ha (White 1985), to 57 to 138 (Covington and Moore 1992) and 86 to 111 trees/ha (Cooper 1960). In all cases, current tree densities are 2 to 37 times this number (Cooper 1960, White 1985, Covington and Moore 1992, Arno and Scott 1993). Habeck (1990) analyzed the size structure of remnant old ponderosa pine, Douglas-fir, and western larch forests near Missoula, Montana. He found an average of 32 and 67 trees/ha greater than 50 cm dbh (diameter at breast height) on warm, dry habitat types on south slopes and cool, moist sites on north slopes, respectively. He estimated that in 1900 these sites supported 93 and 172 trees/ha; today, total tree densities on these sites average 2,296 and 1,906 trees/ha (Habeck 1990).

The structure of old forests reflects the episodic nature of regeneration (Cooper 1960, White 1985, Habeck 1990, Arno and Scott 1993). Within stands, successful establishment was infrequent and episodic, with as many as 40 years between regeneration events. However, regional precipitation patterns favored simultaneous regeneration over large areas (Covington and Moore 1992, Swetnam 1990).

Snags are valuable to many wildlife species as nest and roost sites, as posts for hawking, singing, and perching, and as a feeding substrate (Cunningham *et al.* 1980). Many insect larvae invade recently dead trees (Keen 1955); as a result snags are a preferred foraging substrate for many insectivorous birds (Szaro and Balda 1979). Younger snags contain a larger number of insects (Keen 1955). The degree and type of decay affect the ease with which birds can excavate cavities in snags and how long the snags will stand. As a secondary cavity nester, flammulated owls have a direct relationship with snags; however, the role of snags in flammulated owl foraging ecology has not been explored.

Snag densities in ponderosa pine forests vary; the data of Cunningham *et al.* (1980) suggest that 5.2 snags per ha is an average density for mature ponderosa pine forest. Covington and Moore (1994) estimate that the density of ponderosa pine snags, downed logs, and stumps declined from 5.3 to 1.4 per acre in the last 120 years on an unlogged site in Arizona. Cunningham *et al.* (1980) felt it would be impossible to predict the number of snags standing in pristine old forest. However, promising approaches include simulations (Keane *et al.* 1990), analysis of old photographs (Lehmkuhl *et al.* 1993), and reconstruction of presettlement stand structure based upon tree rings (Covington and Moore 1992, 1994).

Snags are produced when forest fires, insects, diseases, or lightning kill trees. About 30% of standing snags fall within the first 5 to 15 years after the trees die (Keen 1955, Cunningham *et al.* 1980). In California, Keen (1955) found that only 10% of snags were standing after 25 years. In contrast, Cunningham *et al.* (1980) found that 40% of the snags were standing after 25 years and 25% were still standing after 50 years in Arizona. The sites studied in Arizona are drier than in California, which might limit rates of decay (Cunningham *et al.* 1980).

A major question concerns how much downed and dead woody debris was present in presettlement forests, but it was probably less on frequently burned sites than is called for in many old-growth criteria. Downed logs and branches greater than 8 cm in diameter provide crucial ecological functions, including shading microsites for conifer regeneration, serving as sites of mycorrhizal activity and sediment traps, and affecting soil erosion, energy flow, and nutrient cycling (Harvey *et al.* 1987, 1988). The downed woody material is used by more than 175 species of small mammals and birds (Maser *et al.* 1979). Decaying logs provide refuge for fungi during and immediately following disturbance (Harvey *et al.* 1979, 1988). They are often dense with roots, fungal hyphae, nitrogen-fixing bacteria, and other organisms (Harvey *et al.* 1979, 1988). The ecological role of woody debris varies with climate, biomass, size, arrangement, decay, and forest structure (Kaufmann 1990). Woody debris has accumulated since the advent of fire exclusion, even where stands have been harvested (Parsons and DeBenedetti 1979, Barrett 1988).

SUCCESSION AND DISTURBANCE

Fire is the most common natural disturbance and one of the most important ecosystem processes in

ponderosa and Jeffrey pine forests. Disturbance by fire, insects, disease, lightning, and wind are inevitable in ponderosa pine forests. The healthy functioning of ecosystems is dependent on periodic tree mortality that recycles nutrients, enhances decomposition, favors regeneration, and maintains photosynthesis and production. In addition, as decaying wood is incorporated into the soil, it enhances nutrient cycling, water retention, and mycorrhizal populations; many roots are found in the organic layers in the soil (Harvey *et al.* 1979, 1987, 1988).

Excluding disturbance from pine forests is not only impossible, but it has undesirable ecological consequences. Insects and diseases are essential components of ecosystems, for they are regulators of ecosystem productivity and stability (Perry 1988, Schowalter 1988).

Fire as an Ecosystem Process

Fire has played a critical ecological role in ponderosa and Jeffrey pine forest ecosystems. Substantial changes in the temporal and spatial pattern of fires significantly affect the structure, function, and sustainability of these forest ecosystems. Fire plays a direct role in vegetation succession, nutrient cycling, soil structure and stability, and regeneration (Kaufmann 1990). Fire also influences age structure, species composition, and productivity, which in turn influence flammulated owls (Chapter 4). With less frequent fires, entire landscapes have changed, especially where fire exclusion coincided with extensive timber harvest and grazing (table 1).

Although fires are often suppressed, low-intensity surface fires benefit ponderosa pine forests. In the absence of fire, open stands of ponderosa pine have been replaced by dense stands that may have reduced value for flammulated owls. On many sites, less frequent fires have promoted succession to less fire-resistant and often more flammable tree species. Such stands are commonly less productive for quality timber and forage, more susceptible to disease and insect problems, less aesthetically pleasing, and more prone to damaging crown fires. Forest health is declining dramatically in some regions such as the Blue Mountains of Oregon (Mutch *et al.* 1993). Epidemic insect infestations and large catastrophic wildfires have increased tree mortality, causing undesirable ecosystem changes. Weaver (1974) voiced concerns about the effects of fire suppression:

The great increase in fire hazard is the most ominous change since earlier days. The very success of foresters in suppressing fires has radically changed conditions described by Muir and other

Table 1.—Forest ecosystems change when fires are less frequent (Arno 1976, 1988, Barrett 1988, Cooper 1960, Covington and Moore 1992, 1994, Covington and Sackett 1984, 1986, 1990, Keane *et al.* 1990, Laudenslayer *et al.* 1989, Lotan and Morgan 1993, White 1986, Steele *et al.* 1986, Weaver 1974).

When fires are less frequent:

- Tree density increases, especially small-diameter tree
 - Species composition changes
 - More shade-tolerant trees establish
 - Shrub and herbaceous vegetation is less diverse
 - Understory vegetation is less productive
 - Fuels accumulate on the forest floor (duff, litter, woody debris) and in the crowns of trees
 - Organic matter decomposition slows
 - Nitrogen mineralization declines
 - Nutrient cycles stagnate
 - Crown fires are more likely
 - Crown fuel loading increases
 - Fuels are more continuous horizontally
 - Fuels are more continuous vertically
 - Fire size and intensity increases
 - Trees are less vigorous
 - Tree mortality due to insects and disease increases
 - Patterns and processes are simplified at many spatial scales
 - Stands are less aesthetically pleasing
 - Landscapes are more homogeneous
 - Canopy closure is greater
-

early observers. Great advances have been made in fire prevention and suppression, and fewer fires escape control. When they do, however, and they still do and will continue to, they usually are devastating. Uninterrupted fuel accumulations in the past 40-50 years together with the development of reproduction and brush thickets have made it extremely difficult to control such fires, and the costs of control may properly be described as fantastic [p. 300].

Fuels accumulate in the absence of fire. Much of the fuel loading in ponderosa pine stands consists of forest floor material (litter, duff, and small-diameter woody debris). The amount of forest floor material can affect production and composition of understory vegetation (Pase 1958), soil temperature and moisture regimes, tree germination and survival (Pearson 1950), soil nutrient availability (Moir 1966), and erosion (Johnson 1940). Fuel loading in ponderosa pine forests is extremely variable (Sackett 1979).

As litter accumulates in the absence of fire, rates of organic matter decomposition and nitrogen mineralization decrease (White 1986). Although some nitrogen is volatilized and lost during fire, such loss is limited, and nitrogen availability often increases through nitrogen fixation if fires are not severe. Covington and Sackett (1984) and Ryan and Covington (1986) found increased availability of nitrogen, phosphorous, potassium, calcium, and mag-

nesium in the first year following a prescribed burn. Four years after burning, nutrient content of soils and foliage were the same in burned and unburned stands (Covington and Sackett 1984, Landsberg *et al.* 1984). In Arizona, repeated burning at intervals approximating the presettlement fire-free interval increased extractable nitrogen, suggesting that low-intensity fires enhance nutrient cycling (Covington and Sackett 1986). Fire exclusion and the selective logging of larger trees increased the intensity and duration of epidemics of root diseases, dwarf mistletoes, and insects (Hessburg *et al.* 1993). If current trends continue, not only might high tree mortality during epidemics prevent development of late successional forests, but they may also increasingly threaten remnant old forests (Covington *et al.* in press).

Fire Effects

Fire exclusion has contributed to dramatic changes in ponderosa pine forest structure. Fire is an important ecological process in the Southwest (Covington and Moore 1994), Utah (Madany and West 1983) Montana (Gruell *et al.* 1982, Keane *et al.* 1990), Idaho (Steele *et al.* 1986, Barrett 1988), Oregon and Washington (Weaver 1959, Lehmkuhl *et al.* 1993, Everett *et al.* 1994), and California (van Wagtenonk 1985, Laudenslayer *et al.* 1989).

Ponderosa and Jeffrey pine are more resistant to

damage from surface fires than any associated tree species except western larch (Flint 1925). Both are very resistant to scorch, for their high, open crowns, large buds, and high foliar moisture content limit desiccation from the heated air above the flames. Both also have thick bark that insulates the cambium on large trees. Seedlings are often killed by fires, and even large trees are easily killed by fires that burn through the crowns of the trees. Trees are more likely to die when fuels have accumulated through timber harvest or fire exclusion, where stands are dense (more than 100 trees per hectare), or where ladder fuels form as shrubs and small trees that can carry flames into the crowns of the large trees (Kilgore and Curtis 1987).

If trees are weakened and stressed by excessive scorch or cambial damage, bark beetles or diseases often kill them (Harrington 1987). The percentage of the crown that is scorched is a good predictor of mortality in ponderosa pine (Saveland and Neuenschwander 1989), and mortality is low until more than 90% of the crown is scorched (Wyant *et al.* 1986, Harrington 1987, Saveland and Neuenschwander 1989). Cambial damage seldom kills trees unless there is damage in all four quadrants of a stem section.

Cooper (1960), White (1985), Habeck (1990) and Arno and Scott (1993) described stands that developed through episodic regeneration. Regeneration follows death of overstory trees killed by lightning, insects, disease, windthrow, or fire. Establishment is episodic, relying on a combination of conditions that allows for seedbed preparation (usually by fire), reduction of competition, sufficient seed, climatic conditions suitable for germination and survival of seedlings, and fuel and fire conditions conducive to seedling survival. Such events are seldom synchronous. Irregular fire intervals play an important role in regeneration where fires are very frequent. Longer intervals between individual fires would allow ponderosa pine to achieve sufficient size to survive subsequent fires while also permitting encroachment of more shade-tolerant and less fire-tolerant tree species (Keane *et al.* 1990).

Fires often alter the composition and productivity of the vegetation. The ecological role of fire in ponderosa pine forests, particularly as fire affects species composition, has been summarized in general by Wright (1978) and by habitat type groups by Davis *et al.* (1980), Fischer and Clayton (1983), Crane and Fischer (1986), and Fischer and Bradley (1987).

Most of the shrub species common in ponderosa pine forests recover very rapidly following fire; many are favored by frequent fires. Very frequent (1

to 5 years between burns) fires favor herbaceous vegetation over shrubs. Most understory species are dependent on recurrent fire or other disturbance to maintain productivity. Many species resprout or establish quickly from buried seed. Overstory density, which often increases in the absence of fire, has a major impact on understory productivity. Wright (1978) provided an excellent overview of the ecological effects of fire in ponderosa pine forests. Another good source of such information is the Fire Effects Information System, a computerized synthesis of literature (McMurray 1988).

Prescribed fire is useful for managing structure and composition of vegetation, enhancing nutrient cycling, and reducing the probability of destructive fires. Using frequent prescribed fires can be an integral part of enhancing and maintaining the health of ponderosa and Jeffrey pine ecosystems (Mutch *et al.* 1993). Moir and Dieterich (1988) highlight the importance of fire to direct succession toward an old forest condition. They feel that recurrent fires are needed both to maintain quality old forest and to lessen the probability of stand-replacing fire events. They are very concerned that management over the last 100 years has jeopardized the ecological conditions and values of old forest. Dwarf mistletoe is now a major cause of mortality in large ponderosa pine, which may predispose these trees to bark beetle attack.

Martin *et al.* (1989) recently reviewed the use of prescribed fire to reduce wildfire hazard. Weaver (1955) found an 82% reduction in number, a 65% reduction in average size, and a 94% reduction of the total area burned in the 3 fire seasons following prescribed burning of 26,000 hectares on the Fort Apache Indian Reservation in Arizona. In Washington, Weaver (1957) similarly found that 90% fewer hectares burned, and damage and costs were reduced by 94% and 79%, respectively, following prescribed burns. Fuels do accumulate following fire, particularly if foliage or trees die, so frequent fires may be required to maintain low fire hazards. Guidelines for prescribed burning in ponderosa pine forests have been written for the Southwest (Harrington 1981) and Intermountain West (Kilgore and Curtis 1987).

Timber Harvest

Ponderosa pine forests can be successfully managed for timber production under a variety of even- and uneven-aged systems. Where ponderosa and Jeffrey pine are managed intensively, even-aged harvest and regeneration systems are used most often.

See Smith (1986) for a general discussion of the practice of silviculture. Barrett (1980), Burns (1983), and Lotan and Morgan (1993) provide descriptions of silvicultural systems applied in ponderosa and Jeffrey pine forests and how these vary geographically.

Even-aged systems such as clearcut, seed tree, and shelterwood are designed to regenerate all trees at about the same time. In clearcuts, all trees are harvested at once in blocks, strips, or patches that are usually 4–40 ha in size (sometimes much larger) depending on species ecology, administrative constraints, and economic considerations. With the seed tree and shelterwood systems, large residual trees are left to provide seed. In shelterwood cuts, the residual trees also provide shade and wind protection for the young tree seedlings. The overstory trees are usually removed as soon as regenerating trees are established. In any of these systems, large trees can be retained for all or part of the rotation. Such retention adds vertical structure to the managed stands, provides seed to regenerate small gaps, and through time contributes to soil development once the trees die and fall to the ground.

Uneven-aged silvicultural systems are used to create and manage forests with 3 or more age classes. Single trees or small groups are removed in periodic harvests. Sometimes resembling small clearcuts, such systems rely primarily upon natural regeneration. In theory, trees of all ages and diameters are harvested at each entry, including the younger and smaller trees in the stand. However, in practice this is not always done. Selection cuts are designed to mimic gap-replacement forest succession and thus create small-scale diversity.

Regeneration can be obtained naturally or artificially. On a Douglas-fir habitat type in central Idaho, natural regeneration was most successful within group selection, seed tree, or 0.4 to 0.6 ha clearcuts, and most seedlings were found within 30 m of the seed source (Steele *et al.* 1989). In addition, up to 20% of the ponderosa pine seedlings established from seed cached by animals or birds. In contrast, ponderosa pine did not always readily establish following logging or burning on a grand fir habitat type (Steele *et al.* 1987).

Often, harvests in ponderosa and Jeffrey pine forests is opportunistic and does not follow a particular silvicultural system. While this was more true in the past, many trees are cut to meet short-term objectives without long-term site productivity in mind.

Harvesting usually simplifies forest structure at spatial scales from individual trees to stands and forest watersheds. However, harvesting can be designed to enhance structural diversity at any of these

scales through retention of residual trees, variation in patch size, use of some very long rotations, and sensitivity to existing structural diversity. Prescriptions should consider landscape-level issues such as the connectivity between patches of different types and the risks (e.g., fire spread) and benefits (e.g., species dispersal and habitat quality) of juxtaposition in spatial patterns at multiple scales.

Although snags can pose fire and safety hazards and be the target of firewood cutters, silvicultural treatments can readily be designed to create and provide the snag density and quality needed for particular wildlife species. Thus, green trees can be retained and/or girdled, and dead or dying trees can be left standing to create snags with the diameter, height, and degree of decay needed by particular cavity-nesting birds (Thomas *et al.* 1979a) or to provide woody debris to soil to maintain long-term site productivity.

Insects

Insects are most abundant in early successional stages and in old forest, both conditions where forest structures are diverse and there are abundant grasses and shrubs. Furniss and Carolin (1977) state that there are up to four times as many lepidopterans associated with ponderosa pine and Douglas-fir forests as other forest types. Most of the information on insects in ponderosa pine forests applies to those insects that feed on trees. As many as 198 different insect species feed on ponderosa and Jeffrey pine foliage, seed, phloem, and other tissues (Furniss and Carolin 1977, Schmid 1988, Jenkinson 1990, Oliver and Ryker 1990).

Bark beetles, including mountain pine beetle (*Dendroctonus ponderosae*), western pine beetle (*D. brevicornis*), *D. jeffreyi*, and other *Dendroctonus* and *Ips* species, are the most likely insects to kill ponderosa and Jeffrey pine trees. Trees die through a combination of blue stain fungus transmitted by the beetle and from phloem consumption by bark beetle larvae. At endemic levels, old and less vigorous trees die, usually in patches. However, when bark beetle outbreaks occur, even young, small-diameter trees die. Tree vigor affects the ability of the tree to survive; it is the larger trees with thick phloem and declining growth rates that are most susceptible. Trees in dense stands supporting basal areas over 34 m² per hectare are more likely to be attacked; thinning to maintain vigor of individual trees is effective (Sartwell and Stevens 1975). Bark beetles typically attack trees that are weakened by disease, competition, defoliation, injury, or drought.

Mountain pine beetle epidemics develop over several years (Sartwell 1971). At endemic levels, fewer than 12 trees/ha are killed each year either as widely scattered single trees or in groups of 2 to 3. During the first year of an epidemic, 12 to 30 trees/ha are killed, sometimes in groups of 3 to 5. Two to four years later, 75 to 370 trees/ha may die each year. Bark beetle populations usually decline naturally within 6 to 8 years. Outbreaks are shorter on good sites than on poor ones (Sartwell 1971). There is some evidence that predation by insectivorous birds affects bark beetle populations, particularly at endemic levels (Thomas 1979). For this reason and because susceptible trees are more scattered in spatially diverse stands (Perry 1988), patchy forests with mixed age and species composition are less prone to bark beetle outbreaks. Once predicted to decline in abundance after virgin timber was cut, bark beetles currently kill many trees in dense, even-aged stands over large areas (Sartwell 1971).

Dwarf Mistletoe and Other Pathogens

Dwarf mistletoes cause the most common disease in ponderosa and Jeffrey pine. *Arceuthobium campylopodum* infects both ponderosa pine and Jeffrey pine in California and the Northwest. In the southwestern United States, *A. vaginatum* infects trees on one-third of the commercial forest (Oliver and Ryker 1990), slowing tree growth and killing ponderosa pine. Mortality rates due to dwarf mistletoe are higher in the Southwest than in other parts of the range; dwarf mistletoe is absent from the Black Hills of South Dakota (Hawksworth and Shaw 1988). Alexander (1986) considered dwarf mistletoe one of the most serious diseases of ponderosa pine.

Dwarf mistletoes are parasitic flowering plants. Plants establish from seed and grow on branches and stems of trees. Infected branches often swell and witches' brooms may develop. Although dwarf mistletoes are more common on poorer sites, the greatest development is on fast-growing, vigorous trees. The parasite spreads by seed, so lower branches and adjacent trees are more affected. The infection often spreads from taller to shorter trees. Dwarf mistletoes alter the structure of a forest by reducing growth and increasing tree mortality. Mortality during drought is more severe. Severely infected stands of ponderosa pine can become stagnated, or, if mortality is high, may revert to a grass, forb, and/or shrub stage. Severe infestations result when the parasite continually intensifies over long periods of time. Infected trees are less vigorous and often susceptible to bark beetles or other diseases.

Fire was the primary natural control for dwarf mistletoe. Prescribed fire can be used to reduce the severity of dwarf mistletoe infection (Harrington and Hawksworth 1992). Infected trees tend to have lower crowns, more of the highly flammable witches' brooms and a fire-induced mortality rate twice that of uninfected trees (Harrington and Hawksworth 1992).

Root diseases include annosus (*Heterobasidium annosum*), armillaria (*Armillaria* spp.), and black stain (*Leptographium* [syn. *Verticicladiella*] *wagneri*). Root rot kills trees in patches; root-rot infection centers spread outward at up to 1 m per year (Oliver and Ryker 1990). Active infection centers can result in windthrow as roots are weakened. Ponderosa pine is resistant to root diseases compared to other conifers with which it is found (Oliver and Ryker 1990).

Heart rot is caused by fungi. Trees infected with heart rots have softer wood, which facilitates excavation by woodpeckers (Gilbertson 1980). Ponderosa pines infected with heart rot produce snags preferred for nesting by woodpeckers in Montana (McClelland 1977).

Other Disturbance

Lightning ignites fires and strikes trees, often damaging but seldom killing trees. Mortality is rare unless trees are more than 175 years old (Pearson 1950); mature and decadent trees are more often killed. Mature and decadent trees are more likely to fall in the wind, but the well-developed root system limits windthrow.

Ponderosa pine is sensitive to air pollution (see review in Lotan and Morgan 1993). Ozone (Miller *et al.* 1963) and acid rain (McColl and Johnson 1983) and other airborne pollutants cause physiological damage, decline in vigor, and eventual mortality. Stressed trees are also more susceptible to insect and disease mortality. Air pollution presumably caused the common chlorosis and related forest decline in Jeffrey pine in the Sierra Nevada and San Bernadino mountains in California (Barbour 1988).

SUCCESSIONAL PATTERNS

Successional patterns have been described for ponderosa pine forests in Montana (Fischer and Clayton 1983, Fischer and Bradley 1987), in Utah (Bradley *et al.* 1992), in Idaho (Steele *et al.* 1987, 1989), and in Arizona and New Mexico (Moir and Dieterich 1988). The successional patterns described here are drawn from these sources. This description emphasizes the successional patterns where fire is the primary dis-

turbance. Later discussion includes the effects of logging and grazing. This discussion of successional patterns applies to individual patches within stands.

Recurrent low-intensity fires created and maintained old forest on dry, warm sites where perennial grasses dominated the understory vegetation (figure 4) (letters in subsequent paragraphs refer to figure). Any fire burning in open, park-like ponderosa pine stands (A) will create the mineral soil seedbed for trees to regenerate. Open stands will be maintained if subsequent fires occur soon enough to kill all or most of the seedlings. In the absence of fire for long intervals, tree seedlings grow to sufficient size to survive subsequent fires. If the grasses and shrubs are not very vigorous, pine seeds are abundant, and weather is favorable, many seedlings will establish at once (B2); if not, the younger trees will be uneven-aged (B1). When the surviving seedlings are of similar age, with time, the stands become dense and crowded and of low productivity (D1 and D2). If low intensity fires occur, they thin these stands, but severe stand-replacing fires become increasingly likely. Severe fires replace the stand, as all the trees within a patch or within the entire stand are killed, resulting in a grass or shrub-dominated community (F). This is the most likely scenario where fires have been excluded (Moir and Dieterich 1988). Open, park-like stands can develop if fires of low to moderate intensity thin seedlings (C3). Open stands of pole-sized (D3) and larger (E3) trees are the most likely candidates for developing into old forest stands (Moir and Dieterich 1988). Stand development depends on the establishment, growth, and death of individual trees (White 1985).

Succession from a grass community (F) depends on whether many seedlings establish at once and whether fires occur before many of the seedlings are large enough to survive burning. Dense, closed-canopy stands can result (H1, I1, H2, I2). Such stands develop where fires have been excluded for 30 years or more (Moir and Dieterich 1988). Again, if fires are infrequent, stand-replacing fires become more and more likely, which results in a return to the grass stage (F). If low to moderate intensity fires occur in the pole stands (within 10 to 15 years in Arizona, Moir and Dieterich 1988), open, parklike stands of progressively larger-diameter yellow pine trees (I3, J3, A) may result through recurrent fires and advancing succession. The old forests (A) consist of large trees (often greater than 50 cm dbh and 150 years or more old) with snags and occasional downed logs (Moir and Dieterich 1988). If fires do not occur often, the old forest may degenerate when thickets of young trees establish under an open stand of large

diameter trees and snags (Moir and Dieterich 1988). Clearly, it is difficult to develop the diverse structure of old ponderosa pine forests without recurrent fire, particularly on sites where ponderosa pine is seral. Moir and Dieterich (1988) suggest that open, 150- to 200-year old stands (I3) are the best candidates for developing the diverse structure and unique functional attributes of old forests.

On more mesic sites the patterns of succession are similar (figure 5), but the forests tend to be more dense, regeneration is more often even-aged, and shrubs are a more common part of the understory (Fischer and Clayton 1983). "Doghair" thickets of small-diameter trees are also more common. The doghair thickets don't readily burn, but when they do, stand-replacing fires often result. In the absence of thinning by fire or cutting, these stands stagnate for many years. On still more mesic sites where grand fir is the climax tree species, open, park-like stands of ponderosa pine, western larch, and other tree species occur, but only if fires are frequent enough to limit encroachment by the more shade-tolerant and less fire-resistant fir.

Successional patterns differ depending on the associated tree, shrub, and grass species. For instance, gambel oak (*Quercus gambellii*) and aspen (*Populus tremuloides*) resprout vigorously following fire; both dominate following stand-replacing fires. These and other shrubs may present significant competition that limits the number and growth of young ponderosa pine seedlings (Steele *et al.* 1987, 1989; Bradley *et al.* 1992). Unfortunately, successional patterns are not described for most ponderosa pine forests. Steele *et al.* (1987, 1989) include a wealth of information about the succession within the tree, shrub, and forb layers on two habitat types in central Idaho.

Grasses and shrubs are most productive when tree canopy density is low. As a result, the open stands are very important to insect production, which explains the observation of many bird species feeding in these stages (Thomas *et al.* 1979b). The goals of intensive management for timber production are to shorten early succession and eliminate the latest stages.

Recurrent, low-intensity fires result in the presettlement pattern of succession leading to open, parklike, uneven-aged pine stands in which stand-replacing fires are very unlikely. Succession in the absence of fire will most likely result in a snag forest with a grass or shrub understory when a high-intensity stand-replacing fire inevitably results (Moir and Dieterich 1988, Covington and Moore 1994). As fire frequency has declined, not only remnant old forests, but stands in many other stages of succession are also at risk from stand-replacing fires

I. SUCCESSION FROM THE OPEN, PARKLIKE, OLD GROWTH PONDEROSA PINE STATE

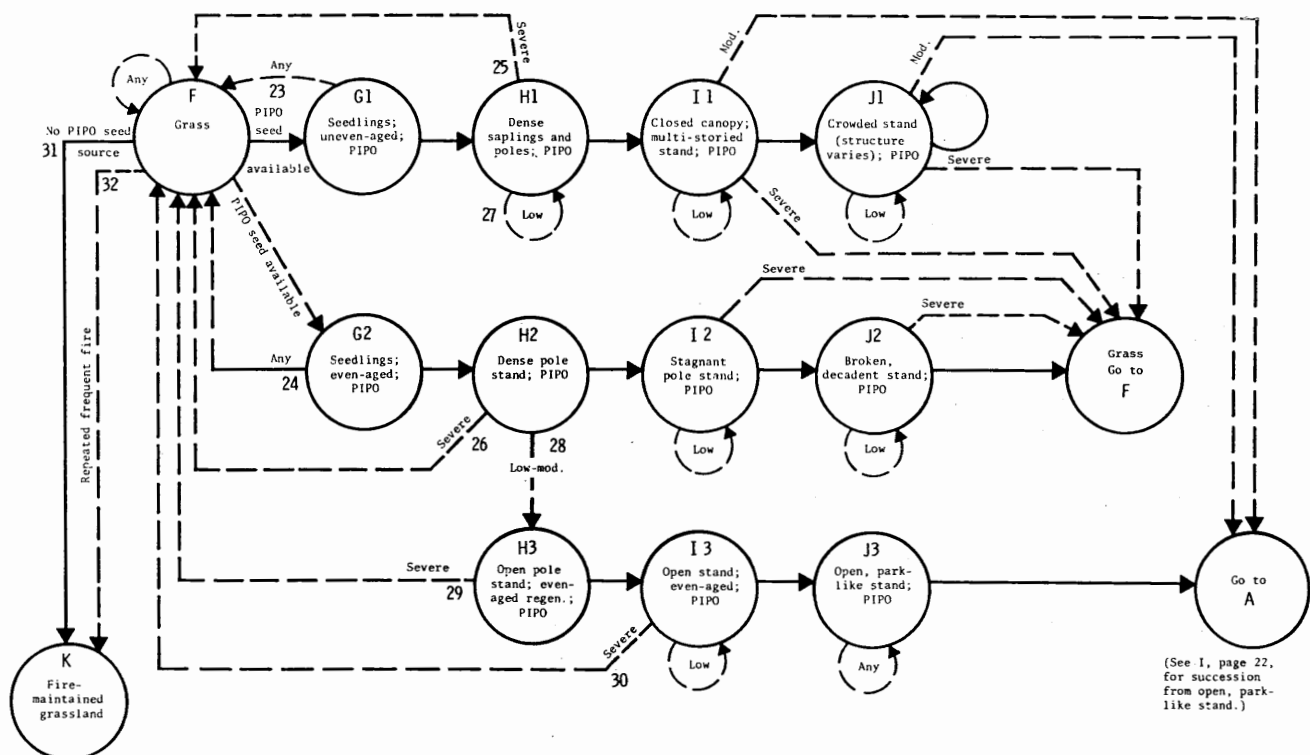
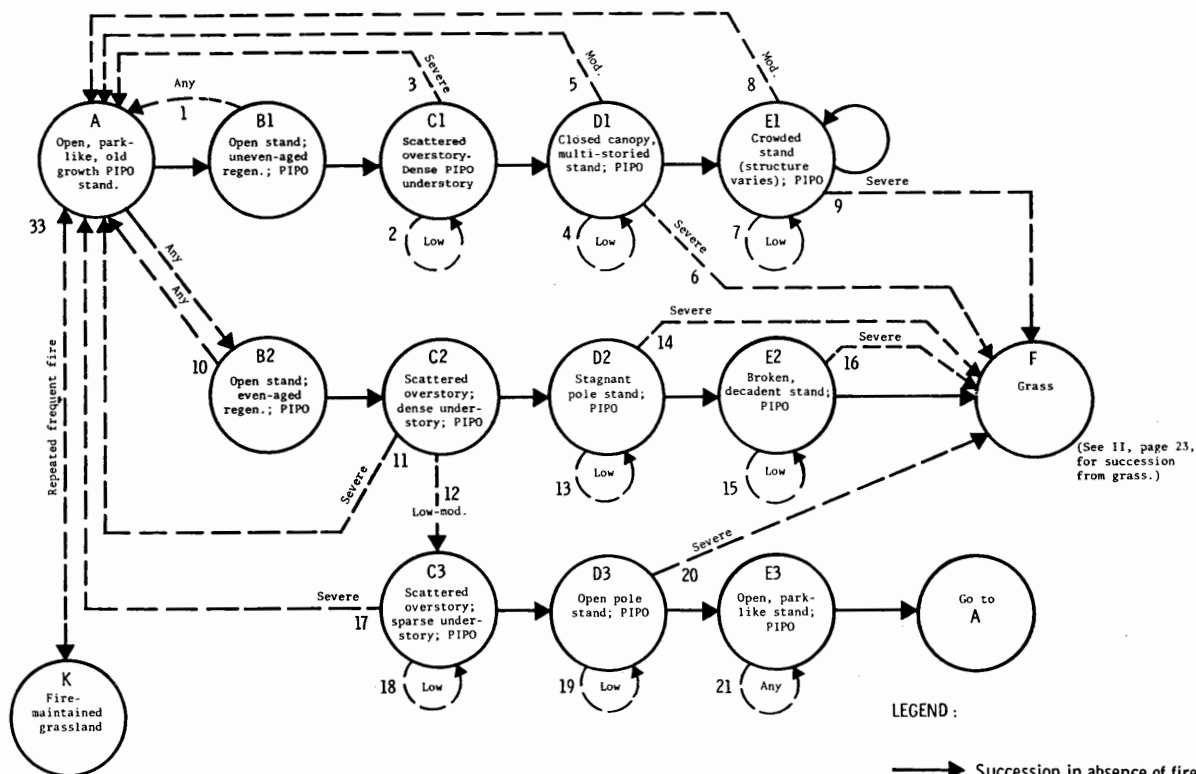


Figure 4.--Hypothesized successional pathways in dry, warm ponderosa pine forests in Montana, Arizona, and New Mexico. Such sites include habitat types where ponderosa pine is the sole climax dominant tree growing with perennial bunchgrasses such as wheatgrasses (*Agropyron* spp.), fescue (*Festuca* spp.), or low shrubs such as bitterbrush (*Purshia tridentata*) or snowberry (*Symphoricarpos albus* or *S. occidentalis*). Adapted from Fischer and Clayton (1983).

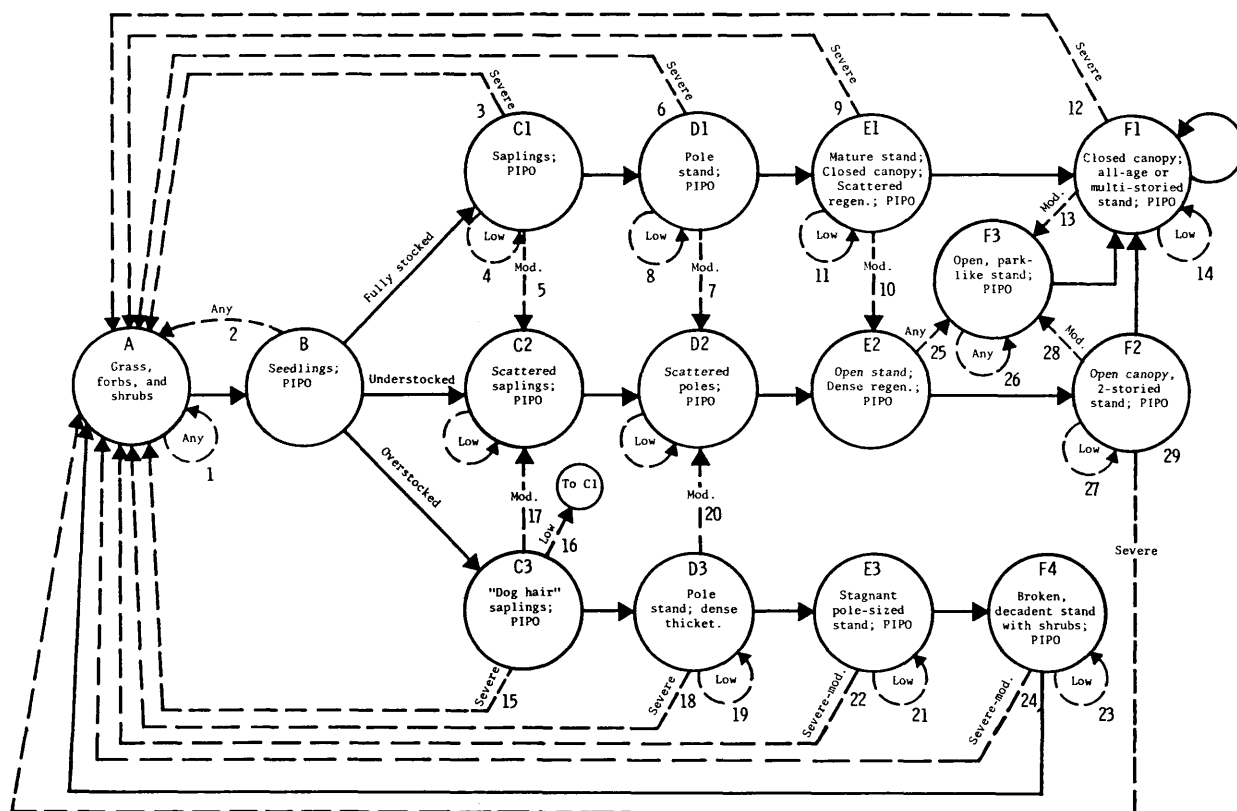


Figure 5.--Hypothesized successional pathways in warm, moist ponderosa pine forests in Montana. Such sites include habitat types where ponderosa pine grows with snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), and buffaloberry (*Shepherdia canadensis*). Adapted from Fischer and Clayton (1983).

(Lehmkuhl *et al.* 1993). Arno (1988) and Moir and Dieterich (1988) feel that prescribed fire could be used very effectively to alter successional pathways to encourage development of the unique structure of old forests.

Contrasting Patterns of Succession Following Logging and Fire

The frequency of forest disturbance from timber harvesting varies with the management objectives, the silvicultural system applied, and the site productivity. It is difficult to generalize about differences in succession following logging and fire because both are variable in severity. Also, fire is frequently used following harvest operations. As with fire, the more severe logging disturbances are less frequent. In the absence of harvest, trees are killed by diseases, insects, fire, and windthrow, in order of decreasing importance (Schubert 1974).

Harvesting operations and fires that are most severe remove most of the tree canopy volume, expose and displace much mineral soil, and remove or displace most organic material on the soil surface. Less severe harvest and fire result in minimal disturbance of understory vegetation.

Logging and fire have variable but significantly

different effects on soils and organic matter. Unfortunately, soil ecosystem structure and function are not well understood, despite the fact that soil processes determine many aboveground structures and functions. Soil organic matter is very important to the long-term productivity of forest soils (Harvey *et al.* 1979, 1987). Because soils are fundamental to biogeochemical cycling, alteration of the physical and chemical properties of soils may affect whole forest ecosystems. Where organic matter has been removed completely or displaced during disturbance, growth may be slowed and the overall productivity of the site reduced. Short, ectomycorrhizal roots of seedlings and old trees are concentrated in or just below soil organic layers (Harvey *et al.* 1988). Surface organic layers also protect the soil and root systems from compaction that occurs when heavy machinery is driven over soil (Gracean and Sands 1980). Erosion can increase dramatically under poor management, particularly on steep slopes with unstable soils and where there is little duff or vegetative cover to protect soils (Gary 1975). Water quality declines if disturbance of the surface soils is excessive or if the trees shading streams and filtering sediments are removed. If soils are disturbed and the cover of forest litter is reduced through road construction, harvesting, and/or severe fires, infiltration will decline

and increased erosion may result.

Timber harvest and prescribed fire increases understory forage production (Ryker and Losensky 1983). Herbaceous production increased following fires that killed some trees and consumed duff and litter, thus creating a more open forest with increased rates of decomposition of the forest floor (Oswald and Covington 1984); nutrient values also increased (Harris and Covington 1983, Andariese and Covington 1986).

One of the major differences between logging and fires is the abundance of residual snags and woody debris. Stand-replacing fires differ from clearcuts because, although trees are killed by fires, the trees become snags and eventually woody debris incorporated into the forest soil. In addition, timber harvest tends to simplify the horizontal and vertical structure of forest ecosystems. Fires leave more diverse patterns and composition, particularly if the fires are not stand-replacing over large areas.

Arno (1988) recommends managing both climax and seral ponderosa pine stands with a combination of cutting techniques, such as thinning and improvement cuts, in combination with regular prescribed burning. He believes this would promote development of productive stands, favor regeneration, and reduce the risk of damage in severe wildfires.

FUTURE VEGETATION PATTERNS

Where fire frequency has declined, we now often find thickets of small suppressed grand fir and Douglas-fir trees being severely defoliated by western spruce budworm; killed by bark beetles, root diseases, and dwarf mistletoe; and threatened by wildfires (Hessburg *et al.* 1993, Mutch *et al.* 1993). Such forests are not sustainable (Hessburg *et al.* 1993, Everett *et al.* 1994). They provide reduced habitat for many wildlife species (Covington and Moore 1994), and provide few of the values people draw from ponderosa pine forests (Covington and Moore 1994). Even remnants of old forests that are veterans of repeated disturbance are at greater risk when they are surrounded by dense continuous forests.

Ecological Restoration

Covington and Moore (1994) feel that if we are to restore forest structure to conserve biological diversity, we must do so within the next 15-30 years. After that, crown fire, insects, and diseases will kill many of the trees of presettlement origin (Covington and Moore 1994). Restoration of this type may have

important implications for flammulated owls.

Fire will be useful in ecological restoration. Fire can be used to maintain open, parklike stands of ponderosa pine and dominance by ponderosa pine in mixed stands. This has been shown in simulations of the effects of different fire regimes (van Wagendonk 1985, Keane *et al.* 1990) and results of prescribed fires conducted at regular and varying intervals (Harrington and Sackett 1992). Prescribed burns will be required in addition to natural lightning fires if the goal is to mimic the effect of presettlement disturbance regimes on ecosystems, particularly where stands have now become isolated enough to prevent fire spread from adjacent areas. Reintroduction of prescribed fire into stands where fires have been suppressed for a long time will, however, require great care. Unless the accumulated down and dead woody debris, duff, and litter and dense patches are reduced gradually in successive fires or are physically removed prior to burning, even large trees with thick bark may suffer high mortality in low-intensity fires (Sackett 1980, Harrington and Sackett 1992). Restoring the ecosystems using fire will often require initial mechanical treatments. Experiments to combine prescribed fire with removal of small-diameter trees and fuels on the forest floor are underway in Arizona (Covington and Moore 1994) and elsewhere.

In old-forest stands in Arizona, where fires had been suppressed for more than 100 years, large-diameter pines with thick bark and high open crowns died following prescribed burning (Harrington and Sackett 1992). Mortality was caused by root damage induced through soil heating due to slow burning of very heavy duff and litter accumulations. Raking heavy duff and litter accumulations from around the base of these large trees will improve survival in the first burns that follow long periods of fire exclusion. Successive burns can also be used to reduce fuels to acceptable levels without site damage (Weaver 1957, Biswell 1963).

Restoring the health of many ponderosa pine forests will require large-scale use of prescribed fire with judicious partial cutting to maintain much lower tree densities and a more open coniferous forest understory than now exists in ponderosa pine and western larch stands (Mutch *et al.* 1993). Mutch *et al.* (1993) recommend a 10-fold increase in the use of prescribed burning to restore the health of ponderosa pine and mixed-conifer forests in the Blue Mountains of Oregon. To do so will require new and sometimes dramatically different financing, planning, and conducting prescribed fires (Mutch *et al.* 1993). Fires, whether prescribed or wildfires, pro-

duce smoke that can impair visibility, air quality, and human health. Thus, increased use of prescribed fire will have to be based on careful analysis and public understanding of the tradeoffs among "increased prescribed fire, inevitable wildfire, ecosystem health, and public exposure to smoke" (Mutch *et al.* 1993).

Changing Environments

Climates could change significantly over the next 100 years if the equilibrium temperature of the earth increases by 3 to 5 degrees C as has been projected in global circulation models (Joyce *et al.* 1990). The models all differ in projections for temperature and precipitation changes in specific areas, but rapid change is inevitable and will affect community composition, species fitness, and ecosystem functions. Increasing CO₂ concentration (to double by the middle of the next century) (Shands and Hoffman 1987), increased temperatures, and changed amount and seasonal pattern of precipitation will affect growth and survival of individual organisms, thus altering the species composition and structure of plant communities (Ryan 1991).

Changing climate will directly affect regeneration, photosynthesis, nutrient cycling, decomposition, and other ecosystem processes (see review by Ryan 1991). High temperatures, drought, and nutrient deficiencies lead to stress-induced mortality (Waring 1987). Tree mortality due to insects, diseases, and fires will be the earliest visible effect of global climate change (Joyce *et al.* 1990). More importantly, climate affects fire regimes (Swetnam and Betancourt 1990) that will magnify the effects of climate on ecosystem processes and influence species migration (Ryan 1991). Swetnam and Betancourt (1990) demonstrated the synchrony of large fires throughout the Southwest and low spring precipitation, reduced tree growth, and climate in the tropical Pacific (El-Niño). Below-ground processes may ameliorate or exacerbate vegetation responses to climate change (Klopatek *et al.* 1992).

We cannot currently predict the consequences of changes with certainty. Leverenz and Lev (1987) projected changes in the range of ponderosa pine under several scenarios of climate change. Climate changes will have the most dramatic effects on the extreme sites within the range of a species, i.e., the sites where ponderosa and Jeffrey pine are climax. The overall temperature changes are similar to those experienced during the last 12,000 years (see Paleoecology section), but they will be more rapid. With their heavy seeds, infrequent seed crops, and low dispersal rates, ponderosa and Jeffrey pine could

find it very difficult to keep up with changing distributions of suitable habitat. Old forests, which include trees that regenerated in an earlier climate, could be vulnerable, particularly if fuel and structure are such that they are already at risk for stand-replacing fires. Unfortunately, we don't understand how ecosystems will respond to climate change (Ryan 1991), so it is difficult to project how individual species and the communities in which they exist will change in response to the combined and synergistic changes in temperature, moisture, and CO₂ concentration.

INFORMATION NEEDS

We must seek to fill gaps in our ecological knowledge if we wish to predict the consequences of disturbance, whether human-induced or natural. Little attention has been focused upon below-ground processes, yet soils support forest ecosystems. We also do not understand landscape-scale interactions between spatial pattern and ecosystem processes. More research has been done on the ecology of trees than other vegetation, and on the ecology of big game than other fauna, including insects. Information on the amount, spatial pattern, and structure of old forest is rare (Everett *et al.* 1994). Even so, we understand far more about structure than we do about the function of ecosystems. We also do not fully understand the interactions among fire, insects, diseases, and their combined influence on ecosystem function. Understanding the natural disturbance regimes with which ecosystems evolved is central to successfully predicting the consequences of management (White 1979, Morgan *et al.* in press). If we could describe them, we could use the natural range of variability in disturbance frequency and the resulting landscape structure as a guide to management decisions (Swanson *et al.* 1993, Morgan *et al.* in press).

Filling these critical gaps in our understanding is challenging. Given the scale and the complexity of the questions involved, simulation models and careful monitoring of ecosystem responses to landscape management are two promising approaches. Models such as FIRESUM (Keane *et al.* 1990) that are based on the ecological processes involved in forest succession will be helpful in furthering understanding of the ecosystem dynamics. Lack of information should not delay adaptive management (Walters 1986). Given the diverse and rapidly changing physical, biological, social, and political environments in which we find ponderosa pine forests, we are compelled to change our management.

Our ecological understanding of the structure and

function of old forests is limited and will depend upon more extensive study of remnant forests and simulation modeling. Although some mature forests could be managed to develop characteristics of old forests, we don't know how much is necessary to increase or maintain the current abundance of old forests (Everett *et al.* 1994). That should not, however, prevent management, including prescribed burning and ecological restoration of old ponderosa and Jeffrey pine forests.

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