

Chapter 10

Dynamics of Subalpine Forests

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INTRODUCTION

The boreal owl's fairly specific habitat requirements restrict its range in the conterminous U.S. to subalpine forests (see Chapter 9). These forests provide tree cavities, uncrusted snow that facilitates preying on small mammals, and cool microclimates essential for summer roosting. Such forests also provide habitat for the owl's prey, which consists primarily of red-backed voles, mice, and other small mammals. Significantly, these prey animals often eat lichens and the sporocarps of fungi. Both are common at high elevations or along drainages in the middle and northern Rocky Mountains, the Blue Mountains, and the northern Cascade Range. This chapter focuses on the distribution, structure, and dynamics of subalpine forests in these areas, with emphasis on the Rocky Mountains.

DISTRIBUTION AND STAND CHARACTERISTICS

North America's subalpine forest ecosystems vary in altitude according to latitude and other geographic considerations. Elevation ranges from about 2,600 m to 3,200 m in the middle Rockies; but is lower (1,300-1,900 m) in the northern Rockies, Blue Mountains, and northern Cascades (Romme and Knight 1981, MacMahon and Anderson 1982, Peet 1988). In all areas, the forests extend downward along drainages. The subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) that commonly dominate Rocky Mountain subalpine forests are genetically and ecologically similar to balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), their boreal counterparts (Elliott-Fisk 1988, Peet 1988). Commonly associated species in the Rocky Mountains include lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*). In the northern Rockies, whitebark pine (*P. albicaulis*) grows near the upper limits of the spruce-fir forests and Douglas-fir (*Pseudotsuga menziesii*) is common at the lower limits.

Mountain hemlock (*Tsuga mertensiana*) and silver fir (*Abies amabilis*) dominate subalpine forest in the northern Cascades and in the northern Rockies west of the continental divide (Daubenmire and Daubenmire 1968, Arno 1979, Franklin 1988). Subalpine fir occurs with these more common trees, but Engelmann spruce is less frequent in the Cascades than in the Blue Mountains and Rocky Mountains. Alpine larch (*Larix lyallii*) and whitebark pine occur at alpine treeline. At lower elevations, probably beyond the normal range of the owl, the forests are dominated by Douglas-fir, western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*), western white pine (*P. monticola*), lodgepole pine, and other species (Franklin and Dyrness 1973, Franklin 1988). The Blue Mountains do not have western hemlock or western red cedar, but grand fir commonly occurs with subalpine fir, Engelmann spruce, lodgepole pine, and Douglas-fir — at least at lower elevations.

The late-persisting snow cover, cool growing season, and dense canopy of subalpine forests collectively prevent any uniform understory development. Often the shrubs, forbs, grasses and sedges are quite sparse, a feature that probably facilitates predation by the owl during the summer and fall. The understory species are characteristic of moist forests and include *Vaccinium scoparium*, *V. globulare*, *V. membranaceum*, *Pachistima myrsinites*, *Pedicularis racemosa*, *Arnica cordifolia*, *A. latifolia*, *Juniperus communis*, *Calamagrostis rubescens*, *Pyrola secunda*, *Carex geyerii*, *C. rossii*, and numerous others (10-45 spp/0.1 ha; Peet 1988). At lower elevations the understory species are different and become quite tall and dense. For example, *Menziesia ferruginea*, *Rhododendron albiflorum*, and *Ledum glandulosum* form an understory that can be 2 m tall in the Cascades and parts of the northern Rockies (Franklin and Dyrness 1973, Franklin 1988). Such forests probably provide lower quality foraging habitat for the boreal owls because of more dense cover for their prey.

Complementing the vascular plants, lichens also

can be quite common, especially in the Pacific Northwest and the mountains of Idaho and Montana. *Bryoria* spp. comprise most of the arboreal lichen biomass, which can be substantial. Lichen biomass ranges from 19 to 35 mt/ha in stands dominated by either subalpine fir or silver fir (Rhoades 1981). The lichens grow as epiphytes on trees; but they are available to small, terrestrial mammals when twigs, branches, or entire trees fall to the ground. The growth of lichen taxa that are important for small mammals apparently depends on forest microclimate (Hale 1983, Lesica *et al.* 1991, Hayward and Rosentreter 1994). Besides shade, subalpine forests provide abundant surface area for lichen establishment; and as the lichens grow, still more surface area is created for the interception of rain. Also, the lichens add surface area on which water condenses when clouds move through the canopy, as often happens at high elevations. Drier forests typically have less lichen biomass, which means fewer small lichen-eating mammals, and therefore potentially less abundant prey for boreal owls.

Stand-replacing fires only infrequently burn subalpine forests, and most of the dominants tolerate the shaded understory environment. These two factors eventually lead to an all-aged or uneven-aged, multi-layered forest. Trees grow to large sizes for the species and site conditions, often persisting as snags for many years after their senescence (Mielke 1950). Such features, along with frequent canopy gaps and abundant wood on the forest floor, are characteristic of old subalpine forests (Kaufmann *et al.* 1992). Many animals in such forests depend, directly or indirectly, on energy flow through food webs based on forest floor detritus.

Comparing Subalpine and Boreal Forests

The boreal forests of Canada and Eurasia often have a species composition and uneven-aged forest structure that is similar to subalpine forests. Balsam fir and either white spruce or black spruce (*Picea mariana*) are the dominant species (Elliott-Fisk 1988). Also, even-aged, seral forests dominated by jack pine (*Pinus banksiana*) are widespread. Jack pine can have serotinous cones and apparently fills the same ecological niche as lodgepole pine in the Rocky Mountains. Aspen and paper birch (*Betula papyrifera*) are found locally in moist upland habitats, and black spruce and tamarack (*Larix laricina*) are abundant in bogs or muskegs (along with sphagnum moss and a variety of ericaceous shrubs). While similar in many ways, subalpine and boreal forests differ in terms of climate and continuity.

The climate is more humid in boreal forests than in some subalpine forests, especially those on the leeward side of major divides. Lower atmospheric pressure at higher elevations causes more rapid evaporation and drying than near sea level where the boreal forests usually occur (Smith and Geller 1979), though frequent rainfall in the subalpine zone could negate this influence of atmospheric pressure. However, the generally more humid nature of boreal forests is suggested by forest classifications based on mosses as well as on trees and other species (Elliott-Fisk 1988). This classification scheme is not commonly practiced in subalpine forests. The more humid nature of boreal forests also leads to abundant lichens that contribute significantly to the food web of the boreal owl.

Subalpine and boreal forests also differ by their degree of continuity or in patch size. Elliott-Fisk (1988) noted that closed boreal forests have a uniform structure over large areas. That might be expected in areas with relatively little variation in topography and elevation and larger average fire size. In contrast, subalpine forests commonly exist as small patches in ravines or only on certain mountain slopes.

The physical characteristics of the dominant trees in both subalpine and boreal forests vary greatly among regions and across different site conditions. Shallow soils at higher elevations (subalpine forests), or higher latitudes (boreal forests), will not produce trees that are as tall as on warmer or more mesic, nutrient-rich sites. Total tree basal area may be high in some stands, approaching 70 m²/ha (Peet 1988), but this too varies greatly with environmental conditions and time since last disturbance. Old forests used by boreal owls probably have tree densities that range from 1,000-2,000 trees/ha and basal areas that range from 50-70 m²/ha. The diameter of dominant trees will be greater where stand-replacing disturbances are less frequent, with spruce in subalpine forests sometimes reaching diameters of 1.5 m and ages over 600 years (Oosting and Reed 1952). Usually, fir does not live much more than 250-300 years and does not grow to be much larger than 50-75 cm dbh. Tree heights might be greatest (sometimes up to 30 m or more) in subalpine forests growing in ravines at lower elevations, where wind and other environmental conditions are moderate and the fire-return interval is long (Romme and Knight 1981).

Boreal forests typically have smaller trees than subalpine forests because of more frequent fires. The greater fire frequency results from fewer topographic barriers, which increases the probability of burning over a much larger area. Most fires are quite destruc-

tive to both subalpine and boreal forests because of the abundant fuel that accumulates by the time spruce, fir and other climax species are dominant.

SUBALPINE FORESTS SINCE THE PLEISTOCENE

During the Pleistocene Epoch, glaciers covered much of the subalpine region where boreal owls now thrive in the Rocky Mountains and northern Cascades. Next to the glaciers, tundra vegetation dominated large areas (Baker 1983, Franklin 1988, Whitlock 1993). Subalpine forests, and presumably the boreal owl, might have extended their range to lower elevations or much further south than they do today; or possibly, they were restricted to small isolated groves that were not covered by ice. Whitlock (1993) concluded that most of the shifts in species composition were altitudinal rather than latitudinal. She also concluded that, about 11,500 years before present (ybp), the climate was 5-6° C colder and alpine treeline was about 600 m lower than it is today (Whitlock 1993). As the ice retreated, an open spruce parkland developed and persisted for about 1,000 years. Subalpine forests began to develop over large areas about 10,500 ybp (perhaps 12,500 ybp in the Cascades). The warmer, drier altithermal (hypsihermal) caused reduced densities of spruce and fir for a 4,000-5,000 year period (9500-5000 ybp); but these trees expanded again following the initiation of the Little Ice Age about 4,000 years ago (Whitlock 1993). Still, subalpine forests cover smaller areas than the forests at lower elevations and they often occur in isolated groves. Moreover, it seems clear that subalpine forests have changed substantially during the last 10,000 years. Owl populations surely changed as well.

Looking to the future, global warming (regardless of the cause) undoubtedly would push subalpine forests to higher elevations or latitudes, thereby restricting the land area that they now cover (Romme and Turner 1990). Of the many owl species, the boreal owl would be affected most adversely by this development in the U.S. because of its association with already patchy high-elevation forests.

SPATIAL DISTRIBUTION OF SUBALPINE FORESTS

A distinctive feature of subalpine forests relevant to boreal owl management is their discontinuous or patchy distribution. Abrupt topographic changes, isolation on the slopes of widely separated mountain peaks or drainages, and periodic stand-replac-

ing disturbances that create seral forests collectively cause this discontinuity (Fischer and Clayton 1983, Bradley *et al.* 1992a,b). Peet (1988) described the nature of disturbance and succession in writing, "... the vegetation is perhaps best thought of not as a uniform stable cover but rather as a mosaic, with the character of each tesera (patch) frequently changing and the borders being periodically defined." Similarly, Borgias and Fonda (unpublished manuscript on the North Cascades) referred to the subalpine forests as a "fire etched mosaic." Daubenmire and Daubenmire (1968) wrote, "The vegetation (of the northern Rocky Mountains) consists mainly of a wide variety of intergrading, disturbance-induced communities . . ." Because the distribution of subalpine forests is patchy, the distribution of boreal owls in mountain ranges probably is patchy as well (Hayward *et al.* 1993) — possibly a significant contrast to the more continuous boreal forests of Canada. Understanding the processes related to the patchy nature of these forests is critical to management of the forest system and boreal owls.

The discontinuous distribution of the subalpine forests required by boreal owls can be attributed to several factors related to the probability of fire ignition and spread. In many areas, old subalpine forests develop only where fires are less frequent, e.g., on higher mountain slopes and along drainages (Franklin and Dyrness 1973, Romme and Knight 1981). Fuels remain moist for longer periods in both habitats, thereby reducing the probability of ignition. Also, valley bottoms are less likely to burn because fires usually move up drainage slopes rather than along valley bottoms. Similarly, higher mountain slopes with subalpine forests sometimes are appropriately viewed as isolated, topographic "islands." In such areas, a fairly small land area is subject to lightning strikes, and when a fire is started, it typically burns upward to treeline. Fire spread to other mountain peaks can occur through spotting, which adds further heterogeneity to the forest mosaic.

Notably, some mountains have comparatively flat plateaus that are high enough to provide the cool, subalpine environment apparently required by the boreal owl (e.g., the Middle Rocky Mountains; MacMahon and Anderson 1982). Owl habitat may be more uniformly distributed in such areas, but they also burn more uniformly and more frequently, thereby preventing the development of the old forests that the owls frequently use.

Another factor leading to discontinuity in owl habitat — possibly more discontinuity than for owls living at lower elevations — are the frequent meadows that interrupt subalpine forests. In general, these

meadows are caused by fine-textured geologic strata such as shales that are not favorable for tree establishment. Other meadows are found in low, comparatively flat depressions where herbaceous plants have become established and the soil often is too wet for upland conifers.

Forest fragmentation by clearcutting is another cause of habitat discontinuity. As described below, forest characteristics which result from clearcutting are not analogous to forests resulting from natural disturbance agents. Fragmentation of landscapes through clearcutting, then, may have different consequences for boreal owl populations than the pattern of fragmentation observed in unmanaged landscapes.

SUBALPINE FOREST DYNAMICS

Causes of Disturbance

Fire

Large-scale, stand-replacing fires are infrequent in the cool, moist subalpine forest environment, occurring only during exceptionally dry and windy summers. Such conditions occurred in the Greater Yellowstone Area in 1988. Extensive areas of old forest may burn under these conditions, presumably reducing the amount of boreal owl habitat; but such fires probably occur at fire-return intervals of 150 to >350 years (Arno 1980). When fires do occur, they do not burn uniformly so patches of old forest persist. Old forest conditions cannot develop in less than 150 years, so fires at more frequent intervals prevent old forest formation in subalpine forests. Characteristically, however, natural fires occur at longer intervals. Wind and insects are more frequent causes of disturbance than fire in many subalpine forests (Franklin 1988, Veblen *et al.* 1991a,b); disturbance by these agents typically increase the probability of fire.

Insects

The spruce beetle (*Dendroctonus rufipennis*) affects subalpine forests more than does any other insect (Schmid and Frye 1977, Baker and Veblen 1990, Veblen *et al.* 1991a,b). This insect is capable of killing a substantial proportion of the spruce overstory across thousands of hectares, and outbreaks occur throughout the range of Engelmann spruce (Schmid and Frye 1977). Outbreaks generally occur following disturbances such as blowdown, which increases beetle habitat and thereby stimulates beetle population growth.

The western spruce budworm (*Choristoneura occidentalis*) may be important locally in subalpine

forests, but it typically attacks Douglas-fir at lower elevations (Schweitzer *et al.* 1975, Brookes *et al.* 1987, Swetnam and Lynch 1989, Baker and Veblen 1990). Other insects such as pine sawflies (*Neodiprion spp.*), Engelmann spruce weevils (*Pissodes strobi*), and needle miners (*Taniva sp.*, *Coleoepchnipes spp.*), kill individual trees or even small patches (McGregor and Quarles 1971). At lower elevations, the Douglas-fir tussock moth (*Orgyia pseudotsugata*), Douglas-fir beetle (*Dendroctonus pseudotsugae*), mountain pine beetle, and larch casebearers (*Coleophora laricella*) may also cause disturbance. Lodgepole pine can be killed by mountain pine beetles (*Dendroctonus ponderosae*) over large areas, but usually not in the subalpine zone because winter temperatures are too low for the beetle (Amman 1989).

The effects of insects on forest composition depend on various factors of which the following four are particularly salient: 1) the composition of the forest prior to the insect outbreak; 2) the relative susceptibility of the tree species to the insect involved; 3) the duration of the outbreak, which can be affected by climatic conditions; and 4) the landscape mosaic in which the outbreak occurs. Thus, a mountain pine beetle outbreak will have a minor effect on owls if comparatively few lodgepole pines grow in the stand, because spruce and fir are not susceptible to this insect. Only small canopy gaps would be created in this scenario. In other scenarios most of the trees could be killed, changing the forest structure dramatically.

The causes of insect outbreaks are still poorly understood. Generally, conifers produce sclerophyllous plant tissues that are resistant to attack and resins that are capable of blocking insect invasion. When stressed, however, whether by climatic conditions or competition from neighboring trees for water, nutrients, or light, their resistance is weakened. Outbreaks of both insects and diseases are then more likely to occur.

Disease

Pathogens appear to be a minor cause of disturbances in both subalpine and boreal forests (Elliott-Fisk 1988, Franklin 1988, Kaufmann *et al.* 1992). However, root rots (*Armillaria spp.* and *Phellinus wierii*) are commonly associated with subalpine forests and they can cause changes in forest structure (James *et al.* 1984, Matson and Boone 1984). Heart rots, canker diseases, and foliage diseases affect groups of trees locally, creating canopy gaps. Mistletoe (*Arceuthobium spp.*) affects forest structure over large areas, but more commonly in seral forests at elevations lower than where boreal owls occur.

Timber Harvesting

During the last century, timber harvesting has become an important disturbance in subalpine forests. Prior to this time, very few trees were harvested by humans (usually small ones to be used for fuel and poles). Large trees were first harvested in significant quantities in the mid- to late-1800's when immigrants from the east needed mine timbers and railroad ties. The market for sawtimber expanded rapidly during the following century and created a significant timber industry throughout the Rocky Mountains, Blue Mountains, and Northern Cascades. For various reasons, clearcutting was the preferred silvicultural system. Though different in several significant ways, both fire and clearcutting are stand-replacing disturbances. Selective harvesting, in contrast, leaves many live trees and is more analogous to some insect epidemics or wind storms.

The rotation age for harvesting subalpine forests typically ranges from 75-120 years. Forests cut at this frequency do not develop old forest characteristics such as abundant lichens and fungal sporocarps (important in the boreal owl food chain as food for red-backed voles). These characteristics likely require 150-200 years to develop. Furthermore, the application of a stand-replacement harvest at this frequency is quite different from natural disturbance regimes, which included frequent small-scale gap disturbances and a longer average stand replacement frequency. Currently, we do not know how long is required for the development of second-generation old forest following stand replacement harvests. Nowhere in western North America has this been accomplished. We also lack knowledge of differences in seral development following harvest versus natural disturbances. In particular, knowledge is lacking on the differences in detrital food webs, understory plants, and lichen populations. Typically, fires, insect epidemics, and wind storms leave large volumes of wood that, for millennia, have been incorporated into the soil. Timber harvesting removes a large proportion of that wood.

Contrasting Effects of Different Disturbances on Succession

Fire and clearcutting affect subalpine forests quite differently than do insects, pathogens, wind storms, and selective harvesting. Whereas stand-replacing disturbances kill both small and large trees, usually exposing the mineral soil for seedling establishment and initiating sec-

ondary succession, the other kinds of disturbances typically kill only the larger trees. They also add detritus to the forest floor and hasten the development of a multi-storied, uneven-aged climax forest; the understory vegetation is affected very little.

Various successional pathways for the development of spruce-fir forest following disturbances are possible, depending on the nature and intensity of disturbance, species composition prior to disturbance, soil and microclimatic characteristics, and climatic conditions after the disturbance (figure 1 from Stahelin 1943, see also Fischer and Clayton 1983 and Bradley *et al.* 1992b). Engelmann spruce, lodgepole pine, and sometimes aspen are the first dominants after stand-replacing fires in the Rocky Mountains (Brown 1975, Fischer and Clayton 1983, Crane and Fischer 1986, Fischer and Bradley 1987, Johnson and Fryer 1989, Veblen *et al.* 1991b, Bradley *et al.* 1992a). They may develop together or separately depending on moisture availability, seed availability, and, in the case of aspen, root systems that were not killed by the fire. In the northern Cascades, mountain hemlock and silver fir can be the pioneer species; but they persist in the climax forest along with subalpine fir that invades later (Franklin and Dyrness 1973). In the Rocky Mountains, subalpine fir becomes an important species after a century or more. Engelmann spruce persists during the entire successional sequence, but lodgepole pine becomes less common. The probability of developing an old-growth, uneven-aged forest increases with fire suppression and the relative moistness of the site (Day

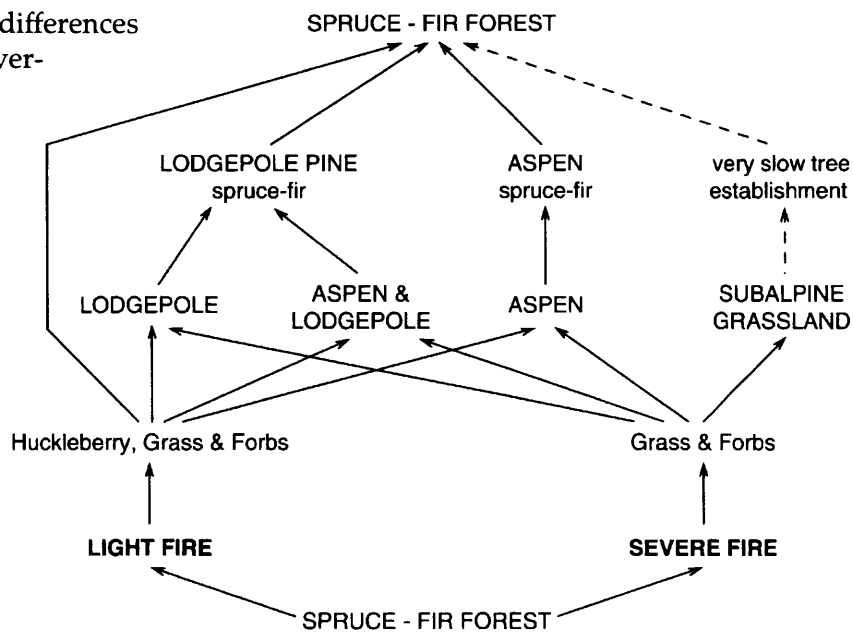


Figure 1. – Alternative successional patterns in central Rocky Mountain subalpine forests after light and severe fires (adapted from Stahelin 1943; see also Fischer and Clayton 1983, Fischer and Bradley 1987, Bradley *et al.* 1992a,b).

1972, Romme and Knight 1981). However, succession occurs slowly in the cold subalpine zone, often requiring 200 years or more. Rebertus *et al.* (1992) suggest that some important attributes of old forest may take substantially longer to develop, even on high quality sites. For example, density of large trees may take 500-700 years to peak, but a high density of large snags and logs takes even longer. Succession is equally slow in the Blue Mountains and northern Cascades.

After a forest is clearcut for the first time, succession of dominant trees proceeds similarly to that following a stand-replacing fire. Unlike the effects of fire, few dead trees remain after a clearcut. New tree establishment also might be slower without the bare mineral soil created by burning. Significantly, however, seedling establishment is often very slow at higher elevations after both burning and clearcutting (Alexander 1987). Conceivably, climatic conditions now are less favorable for seedling establishment than they were two or three centuries ago when the harvested forest became established. At high elevations it may not be possible for clearcut or burned forests to develop into the kind of old forests that boreal owls currently use. Now that may be possible only at lower elevations, and then only if rotation ages are long enough.

Tree establishment is less problematic lower in the subalpine zone, where both lodgepole pine and Engelmann spruce are well adapted as pioneer species. In particular, lodgepole pine often is the predominant seral species following a fire, especially when many of the trees have serotinous cones. These cones are produced during most years, but they remain closed for decades until opened by intense heat, such as during a fire. More than a million lodgepole seeds per hectare can be dispersed in a single year (Lotan 1975), often leading to the development of "doghair" stands. The growth of individual trees is slow in such dense stands, but the trees still produce new seed and they may survive for well over a century, though attaining less than 10 cm in diameter. Doghair stands have little understory growth to support the rodent populations preyed upon by owls. Conceivably, these dense stands could provide a barrier to owl movement.

While clearly an adaptation for fire, many of the serotinous cones with their enclosed seed could be burned during intense fires. The result would be fewer pine seedlings during the first few years. Lodgepole pine seedling density was found to be spatially variable three years after the Yellowstone fires of 1988, with the lowest densities in the middle of very hot burns and the highest densities near the edges of burns, where the fires were less intense and

where live trees persisted with unburned cones (Anderson and Romme 1991). Lodgepole pine density apparently is a function of fire intensity and seed mortality during fire as well as the percentage of trees that are serotinous. The development of old, second-generation forests probably takes longer after very hot fires.

Significantly, some lodgepole pines do not produce serotinous cones. The trait seems to be genetically determined, but it has at least three recognized phenotypes: closed cones that require temperatures of 45-60°C for opening, intermediate cones that require cooler temperatures (35-50°C), and non-serotinous cones that open at warm ambient temperatures of 25-50°C (Perry and Lotan 1977). All three phenotypes can be present in each stand, which helps explain why new seedlings emerge following disturbances other than fire. Muir and Lotan (1985a,b) observed that the proportions of the trees that are serotinous and non-serotinous depend on the nature of the last disturbance. Fires lead to a high proportion of the serotinous genotype because the heat opens the cones and an abundance of seed is dispersed when conditions for seedling establishment are ideal. However, non-serotinous trees are favored if the last disturbance was an insect epidemic or wind storm because most of the seed in serotinous cones is not dispersed; the primary seed source is from non-serotinous cones. Muir and Lotan (1985a) suggested that having both cone types present in a stand increases the chance of a species surviving any given kind of disturbance, and that management, both in wilderness and in timber production areas, should allow for both fire and non-fire disturbances so that a range of genotypes can be maintained. A significant element of biological diversity thereby endures.

Though lodgepole is clearly a seral species, some stands begin to develop multi-storied, old forest characteristics later in succession as the first generation of trees die, and as spruce, fir, and more lodgepole pine grow from the understory in gaps. The forest becomes uneven-aged, even with lodgepole pine in the overstory, and fallen logs become a prominent feature of the forest floor. Fungal sporocarps and other rodent food may become more abundant in the gaps than they were in the seral even-aged forest. Lichens could become more common also, though this probably depends on climatic conditions as well as successional stage (R. Rosentreter, pers. comm.).

The relative abundance of climax species varies greatly from place to place. In general, the largest and oldest trees in the Rocky Mountains are Engelmann spruce; the species may live 500 years or longer

(Oosting and Reed 1952, Shea 1985, Alexander 1987, Veblen *et al.* 1991b). Subalpine fir usually is more common, but the trees are smaller and younger, rarely more than 250 years old (Veblen 1986a,b, Peet 1988). Fir also produces 10-20 times more seedlings. Apparently, the new roots of fir seedlings are better able to penetrate the leaf, twig, and wood detritus that accumulates over the forest floor, while spruce seedlings usually emerge where mineral soil has become exposed, such as around the tipped root system of fallen trees. Some investigators also have observed spruce seedlings on rotting logs where the decomposing wood remains moist well into the summer (Lowdermilk 1925, McCullough 1948, Oosting and Reed 1952, Loope and Gruell 1973, Cui 1990). Spruce trees produce large amounts of seed every 2-5 years, subalpine fir about every 3 years (Alexander 1987).

Unlike the pines and Douglas fir, spruce and fir are capable of vegetative reproduction (layering) when lower branches are pressed to the ground by snow. The branch often develops adventitious roots, after which the end of the branch begins to grow upright into a new tree. Eventually, the branch connection to the parent tree decomposes. Clusters of subalpine fir often can be attributed to this cloning process.

The fact that subalpine fir reproduces more effectively (than Engelmann spruce) in the forest environment has led to speculation on how spruce persists as a co-dominant in the forest. Veblen (1986a) concluded that coexistence is possible because fir is shorter-lived but produces many seedlings, while Engelmann spruce compensates for poor reproductive success with increased longevity. Thus, the greater proportion of subalpine fir seedlings and saplings does not mean that it will eventually become the sole dominant.

It is tempting to view uneven-aged subalpine forests as being in a state of equilibrium. However, Aplet *et al.* (1988) studied several stands of spruce-fir-pine forest that spanned a 500-yr period (a chronosequence) and found that periodic disturbances cause continual changes in tree population structure. They hypothesized that, following a large scale disturbance such as a crown fire, all three species colonized the site together at the beginning of secondary succession. After 100-200 years, spruce could no longer reproduce in the forest understory, a period they labeled the "spruce exclusion phase." After another 100 years many dominant fir, spruce, and pine began to die, facilitating the "spruce reinitiation phase," during which canopy gaps appear and spruce (and perhaps lodgepole pine) are

again able to reproduce. The final phase they recognized was a "second generation spruce-fir forest" with considerable fuel accumulation. This phase would be very flammable during the next dry summer, but it would also support many fungi and a large lichen biomass. This may be a plausible successional sequence, but another crown fire could prevent the old spruce-fir forest from developing. As others have observed (Romme and Knight 1981, Johnson and Fryer 1989), the fire return interval may be short enough to ensure burning within the life span of the trees that invaded following the previous fire. Under such conditions, "old-growth" subalpine forests may never develop, although some characteristics of old forest may appear. As others have pointed out, however, many old spruce-fir stands classified as old growth may be transitional stands that are still primarily influenced by the original stand-replacing disturbance (Hayward 1991, Rebertus *et al.* 1992).

The stand development pattern described by Aplet *et al.* (1988) is undoubtedly influenced by insect outbreaks. As described previously, a common insect in spruce-fir forests is the spruce beetle, a bark beetle with a life cycle similar to the mountain pine beetle (Schmid and Hinds 1974, Alexander 1987, Baker and Veblen 1990, Veblen *et al.* 1991a). The spruce beetle attacks older stands with a high proportion of Engelmann spruce in the overstory. Usually, the susceptible stands have slow tree growth, suggesting that the trees are of low vigor. Abundant downed trees, whether due to logging or windthrow, may provide the energy base for initial development of the outbreak. The infestation opens the canopy, greatly accelerating the growth of the abundant, non-host subalpine fir plus spruce that are too small to be susceptible to attack. The growth of other plants is stimulated as well. The beetle thereby increases the proportion of the forest biomass in subalpine fir and other plants. Lodgepole pine and aspen may also become more common. Fuel biomass and continuity increase, which increases the probability of fire.

Unfortunately, most research on succession in western coniferous forests has focused on the trees. Much less is known about temporal changes in the abundance of lichens, fungal sporocarps, and non-arboreal understory plants such as grasses, forbs, and shrubs. Understory plant growth increases when competition for water, nutrients, and light diminishes following disturbances. Conversely, the understory biomass gradually declines as canopy gaps close. Gap formation can have dramatic local impacts on the understory. For example, a fallen tree

suddenly places an abundance of epiphytic lichens within reach of the small terrestrial mammals on which the boreal owl preys. Moreover, the death of individual trees can lead to an increase in fungal sporocarps (S. L. Miller, pers. comm.) and the growth of shrubs such as *Vaccinium scoparium* — other important food sources for small mammals. Thousands of years of wood production and slow decay in the cool subalpine environment have led to the detritus-based food web characteristic of old forests. The time required to reestablish such food webs after different kinds of stand-replacing disturbances is not known.

Small-scale disturbances in old forest apparently could improve boreal owl habitat by creating more snags in which woodpeckers can excavate cavities that boreal owls eventually occupy. Also, periodic tree mortality may reduce forest transpiration, at least for a time, which leaves more moisture in the soil to support the fungi and lichens that are important to the owl's prey. Forest gaps also may increase visibility, thereby improving prey capture. Many dead standing trees existed in pre-settlement subalpine forests, giving the forest a "salt-and-pepper" appearance (Baker and Veblen 1990). The forest today is more uniform due to timber harvesting that leaves fewer snags and to fire suppression that essentially has the potential of "homogenizing" the forest over large areas (Habeck and Mutch 1973). Simultaneously, the forests are being fragmented by clearcutting. As the participants of one recent workshop concluded (Kaufmann *et al.* 1992), forests and landscapes are being created that never existed previously. Can such "novel" forests serve as habitat for the boreal owl? What management practices should be implemented to maintain or create the kind of habitat required by the boreal owl and other species dependent on mature subalpine forests? Existing old forests surely will be affected by stand-replacing disturbances in the future. What kind of management is required to ensure that adequate owl habitat will be available where subalpine forests are isolated and often cover a small area? These questions are appropriate for forest planning in regions with subalpine forests.

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