Structure and Dynamics of Old-Growth Engelmann Spruce-Subalpine Fir in Colorado[1]

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The development of old-growth spruce-fir forests in Colorado is highly variable and depends on disturbance history and site conditions. On relatively favorable post-fire sites, spruce sometimes develops a bimodal or discontinuous age structure that persists for >500 years. Some sites that were identified as high-quality old growth, physiognomically, were actually post-fire stands in a transition old-growth stage. On less favorable sites it appears that post-fire recruitment of spruce and fir is more gradual, and all-aged populations develop. Fire, spruce beetle outbreaks, and windthrow all play an important role in shaping the development of old-growth spruce-fir forests, and ultimately in their demise. We need more long-term mortality studies to better understand the role of disturbance in old growth and implications for designating old-growth reserves.

INTRODUCTION

Old-growth Engelmann spruce (*Picea engelmannii* [Parry] Engelm.)-subalpine fir (*Abies lasiocarpa* [Hook] Nutt.) forests in Colorado have recently been the subject of considerable interest and controversy. The issue came to the forefront in 1989 when Louisiana Pacific Corporation was granted logging rights in a 1000-ha stand of prime old-growth spruce-fir in Bowen Gulch, west of Rocky Mountain National Park (Fig. 1). Protest led to reevaluation, and eventually a cooperative effort by environmentalists, the Forest Service, Louisiana Pacific, and Congress culminated in pending federal designation of 2590 ha of Bowen Gulch as an addition to the Never Summer Wilderness Area. What characteristics make Bowen Gulch and similar stands high-quality old growth? How do old-growth spruce-fir forests develop and what are the stand dynamics associated with this development? These are basic questions that need to be considered for designating and managing old-growth forests.

Definitions of "old growth" are rather elusive and depend on the particular forest type and the classifier's purpose or goals. Most management and recreational objectives emphasize a physiognomic definition of old growth. For example, in old-growth Douglas fir (*Pseudotsuga menziesii*)-western hemlock (*Tsuga heterophylla*), the characteristics most often associated with old growth are: an abundance of large, old trees, snags, logs, and a multi-layered canopy (Franklin et al. 1981, Old-Growth Definition Task Group 1986). These same characteristics, among other things, have been identified as key old-growth elements in many other forest types, including old-growth spruce-fir in the Rockies. In Colorado, the Forest Service and Colorado Environmental Coalition have been using various adaptations of an old-growth scorecard that was developed in the mid 1980s for use in subalpine forests of the Medicine Bow Mountains, Wyoming (U.S. Forest Service [1984?]; Smith 1990; Lowry, this volume) Basically, these survey procedures rate the quality of old growth based on structural characteristics similar to those identified above.

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[1] Paper presented at the Old-Growth Forests in the Southwest and Rocky Mountain Region Workshop, Portal, AZ, March 9-13, 1992.

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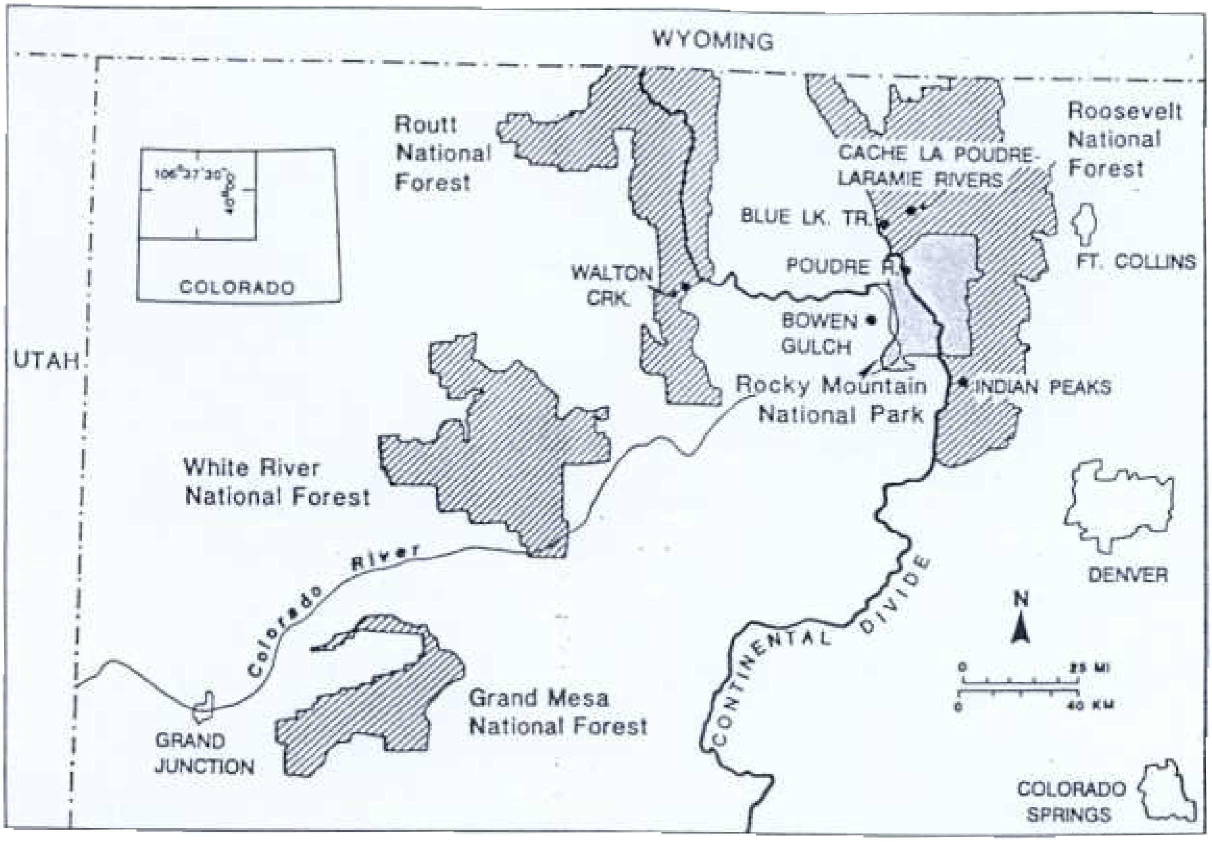

Fig. 1 Location of old-growth spruce-fir study areas in Colorado.

Another way to define "old growth" is based on the process of stand development. For example, Oliver and Larson (1990) defined "true old growth" as "stands composed entirely of trees which have developed in the absence of allogenic processes [stand-initiating disturbances]." Stands approaching this stage but still composed of old, post-fire relic trees, are considered "transition old-growth stands." A similar process-oriented definition was proposed by Hayward (1991), and is based on population dynamics and rates of regeneration and mortality rather than static processes. Hayward defined old growth as a "forest in which the rate of tree regeneration and the age structure are influenced by processes in the stand rather than being correlated to the timing of a major disturbance that influenced the majority of the stand." Ironically, the process-oriented definitions of old growth do not necessarily complement the physiognomic definitions. For example, classic old-growth Douglas fir-western hemlock forests (sensu Old-Growth Definition Task Group 1986) are not in a true old-growth stage (sensu Oliver and Larson 1990), because in most areas Douglas fir is seral to western hemlock (Sprugel 1990). In the following review of old-growth spruce-fir forests in Colorado, we will demonstrate the need to understand and integrate the physiognomic definitions of old growth and the processes that generate them. We emphasize that old-growth definitions should be multifaceted: physiognomic quality should be assessed based on particular goals, whereas an understanding of stand dynamics can reveal how the forest developed into old growth and possibly how it will change in the future. If large areas of spruce-fir are designated as old-growth preserves, such knowledge is important for planning and understanding the natural role of disturbance in the subalpine zone.

SUBALPINE FORESTS IN COLORADO

Over one million hectares of the subalpine zone in Colorado are characterized by Engelmann spruce and subalpine fir, with lesser amounts of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), limber pine (*P. flexilis*), and/or bristlecone pine (*Pinus aristata*) (Alexander et al. 1984, Alexander 1987, Whipple and Dix 1979, Peet 1988). Spruce-fir dominated stands occur on all but the most xeric sites above 3100 m, and in cool, sheltered valleys at elevations as low as 2500 m. The relative dominance of the two canopy tree species and the understory composition vary substantially over a gradient from excessively moist to xeric sites (Peet 1981). Open bog forests occur on the limited areas of level, poorly drained terrain above 2800 m. The mesic spruce-fir type occurs on cool, sheltered, but well-drained sites above 2700 m and is one of the most widespread forest types in the subalpine zone. Open slopes above 3100 m are typically characterized by Peet's (1981) xeric spruce-fir type, with varying amounts of lodgepole and limber pine. Towards lower elevations, the spruce-fir types give way, often along abrupt fire-induced boundaries, to lodgepole pine-dominated forests. A more complete review of the tremendous geographic and site variation in spruce-fir communities can be found in Peet (1981, 1988), Alexander (1985), and Allen and Peet (1990).

DEVELOPMENT OF OLD-GROWTH STANDS

Fires in the subalpine forests are typically stand-devastating, resulting in the extensive exposure of mineral soil and initiating the development of new stands. Depending on site conditions, spruce and fir may share the post-fire site with shade-intolerant species such as lodgepole pine, limber pine, and quaking aspen. Lodgepole pine and limber pine seedlings are physiologically well adapted to grow under the dry conditions of the post-fire environment. Lodgepole pine rapidly colonizes from serotinous cones, limber pine from seed dispersal by nutcrackers, and aspen from suckers. Bare mineral soil exposed by fire is also more favorable to seedling establishment of the pines and spruce than to fir (Alexander 1987, Whipple and Dix 1979, Peet 1981, Knapp and Smith 1982). Depending on the availability of seed, spruce usually colonizes synchronously with, or soon after any shade-intolerant species present, but fir often does not establish abundantly until 50-150 years after stand initiation (Veblen 1986a, Rebertus et al. 1991). The timing and spatial distribution of spruce and fir colonization is strongly affected by the size of the burn and the location of seed sources with respect to prevailing winds (Peet 1981, Tomback et al. 1990). Usually the pines and aspen are seral to spruce and fir, although the patterns vary markedly according to habitat variation and species availability (Whipple and Dix 1979; Peet 1981, 1988; Romme and Knight 1981; Veblen 1986a; Rebertus et al. 1991). On exceptionally harsh sites in the subalpine zone, the usually seral pines or aspen may form self-replacing stands (Moir 1960, Peet 1988, Rebertus et al. 1991). In contrast, on more mesic sites the replacement process may be accelerated (Romme and Knight 1981, Rebertus et al. 1991).

The development of spruce-fir stands has been examined by inference from static age and size structures of stands believed to represent different stages of stand development (Whipple and Dix 1979, Peet 1981, Veblen 1986a, Aplet et al. 1988). The use of static age and size structure for inferring patterns of stand development in spruce-fir forests is problematic for several reasons. First, age data is often imprecise (see Norton and Ogden 1990). With spruce and fir, in particular, there are problems with (1) lack of data on trees with rotten centers, (2) large variation in the difference between total age and age at coring height due to the extreme suppression of spruce and fir seedlings, and (3) difficulty in estimating rings-to-center, especially for trees that were initially suppressed. Second, size structure is not a suitable substitute for age structure because of the poor relationship between size and age in these forests (Veblen 1986a). The chronosequence approach, of course, is based on the assumption that any site differences among the stands selected are unimportant in explaining the differences in size and age structure. Given this untested assumption, and the lack of long-term studies of stand development based on remeasurement of permanent plots, models of stand development cannot be expected to be precise descriptions of the changes that have occurred at any specific site. Nevertheless, there are sufficient data available to generally describe the pattern of stand development expected following a stand-devastating fire. The following description of general trends in the development of a spruce-fir post-fire stand is conceptually based on Oliver's (1981) general model of post-disturbance stand development and synthesizes the interpretations of numerous studies in the Colorado subalpine zone, mostly from the Front Range. There is a great need for complementary studies elsewhere in the state.

Aplet et al. (1988) applied Oliver's general model of post-disturbance stand development to five stands of spruce-fir forest in the Medicine Bow Range. Their presumed chronosequence spans c. 400 years, from stem initiation to old-growth stages. All stands were assumed to have been initiated by wildfire, but they did not present any evidence of subsequent disturbance by fire or beetle outbreak. Their stands represented a substantial range of aspects, which in other studies (Whipple and Dix 1979, Peet 1981, Veblen 1986a) has been shown to have a major influence on the pattern of stand development. Hence, their stands may not represent an actual post-fire sequence. Nevertheless, their model is a useful approximation of some general trends in post-fire stand development of spruce-fir stands for sites lacking pines.

The early colonization of spruce on post-fire sites results in a peak in the age frequency distribution that is recognizable in some spruce-fir forests for >500 years (Figs. 2 and 3). According to Aplet et al. (1988), after 100-250 years of initial recruitment, spruce enters a stem exclusion phase that may last >100 years. Fir seedlings, which establish more effectively on litter than do spruce seedlings (Knapp and Smith 1982), become increasingly more abundant during the first 100-200 years after fire. A wave of fir mortality typifies the third century of stand development as the oldest fir approach their maximum longevity (Aplet et al. 1988). Fir occasionally live >400 years, but most trees suffer from heart rot and die when they are much younger (Alexander 1987). As the older fir die, however, they are replaced by the abundant understory fir so that in stands >250 years old, fir typically has an all-aged and all-sized structure (Whipple and Dix 1979, Peet 1981, Veblen 1986a, Aplet et al. 1988, Veblen et al. 1991a). According to Aplet et al. (1988), a second wave of spruce regeneration establishes 200-350 years after fire as the canopy opens up from treefalls of the original spruce and fir colonists (Fig. 3). This results in a bimodal age structure for spruce which persists for several centuries and is consistent with the age structures of some old-growth stands (Fig. 2A-B, H; Day 1972, Whipple and Dix 1976, Peet 1981, Stromberg and Patten 1991, Roovers 1992). Bimodal diameter and height structures are also evident in some old-growth stands within particular sites (controlling for aspect, moisture conditions, etc...); however, size parameters vary with site and degree of suppression, so distributions tend to be more continuous when data are pooled from several different sites (Fig. 4, Roovers 1992).

In other old-growth stands, however, spruce age distributions are not clearly bimodal. They sometimes fit the negative exponential patterns associated with all-aged, self-replacing populations (Whipple and Dix 1979, Veblen 1986a, Veblen et al. 1991a). In many old-growth stands, spruce has a discontinuous or sporadic age frequency distribution in age classes greater than c. 250 years (Fig. 2C, 2F, 2G). In such cases it is not clear if two separate cohorts can be identified as Aplet et al. (1988) postulate as the general pattern.

There have been too few age structure studies of spruce-fir relative to the large amount of variation in developmental pattern expected from site variation to fully evaluate the applicability of the two cohort model of Aplet et al. (1988). It may be that on better quality sites with more rapid rates of stocking, the two cohort pattern holds true, but on less favorable sites the distinction between the post-fire cohort and the stand reinitiation cohort may be blurred. On less favorable sites (either too dry or too wet to allow rapid stand development), an all-aged population of spruce appears to develop without passing through a stage of two distinct cohorts (Whipple and Dix 1979, Peet 1981, Veblen 1986a). For example, in Poudre River Trail (Fig. 2C), the oldest trees in the stand have rapid initial growth and appear to be the initial colonists following a fire c. 450 years ago. Although the rate of establishment for spruce appears to have increased over the most recent 150 years, recruitment has been continuous throughout stand development. Likewise, in Bowen Gulch the age structure of spruce was bimodal on north and south aspects, but was relatively continuous on a boggy site (Roovers 1992).

If we consider the scorecard criteria used to evaluate old-growth spruce-fir stands in Colorado and Wyoming, the highest quality old growth is characterized by large-diameter trees (mainly spruce), abundant large snags and logs, and multi-storied vegetation. On xeric or very wet sites, where presumably a more all-aged population develops, the quality of old growth probably develops asymptotically. On more favorable sites in the Front Range, however, we would expect the quality of some old-growth attributes, like density of large trees, to peak c. 500-700 post-fire (Fig. 5). As the original post-fire cohort of spruce reaches maximum longevity, in all likelihood there will

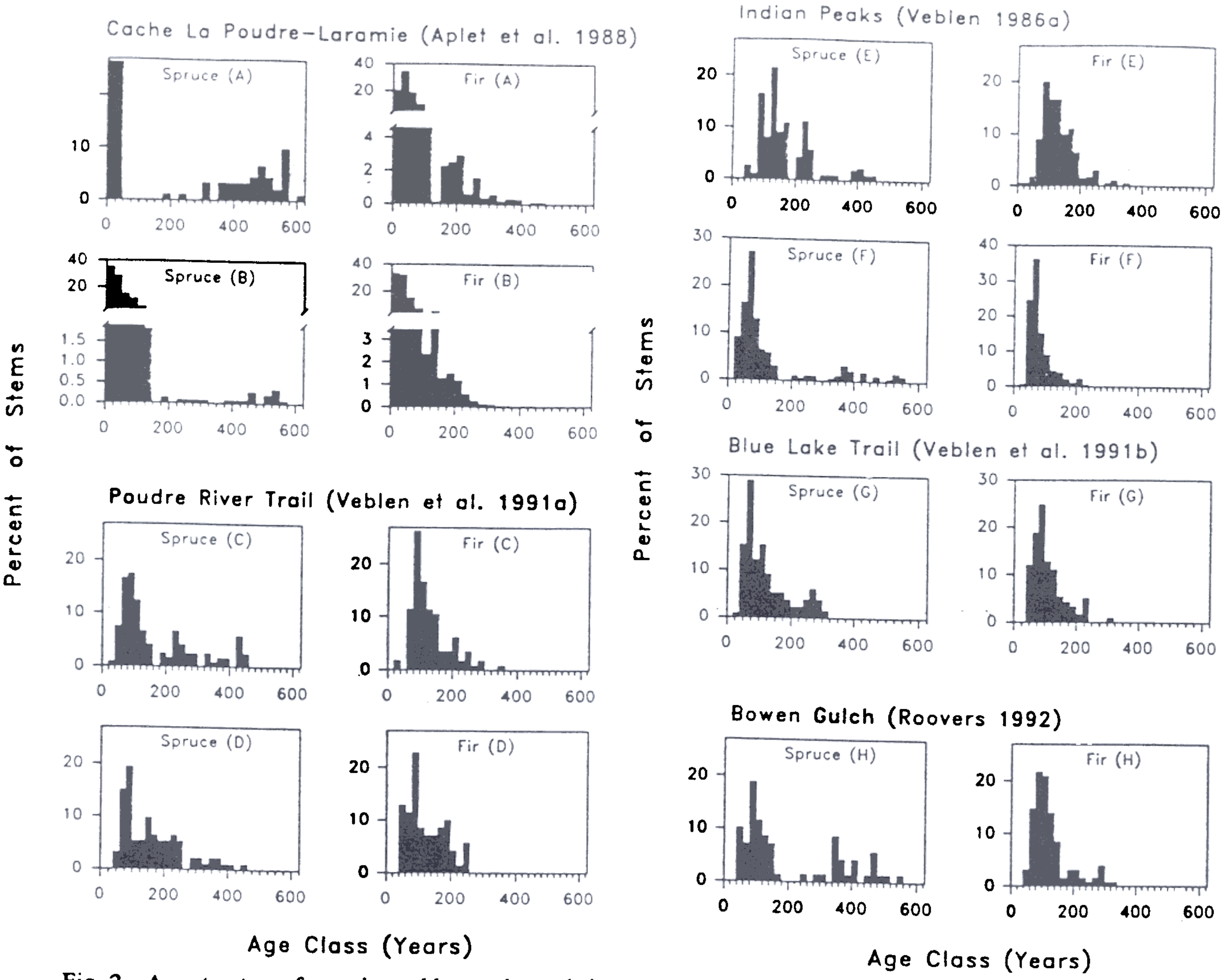

Fig. 2. Age structures for various old-growth stands in Colorado (A-H) reported in the literature (© Ecological Society of America, The Journal of Biogeography, The Torrey Botanical Club). For comparison, all have been expressed as percent of total stems. For (A) and (B), Aplet et al. (1988) used stratified random samples of trees, c. 150-210 trees per site; as well as random samples of stems <5 cm dbh, including seedlings. All other sites include only trees >4 cm dbh, and sample sizes range from 69-257. Ages are at coring height: <10 cm above ground for A and B, and at 40 cm for C-H.

never be as many big trees at one time in any subsequent stage. At Bowen Gulch, for example, most spruce in the oldest cohort display rapid initial growth, indicating they are of post-fire origin (Roovers 1992). Bowen Gulch has an exceptionally high density of large trees, but this appears to be a temporary condition characteristic of a transition old-growth stage, rather than true old-growth (sensu Oliver and Larson). As the post-fire cohort begins to die out, there may be few large spruce to replace them until the second cohort reaches maturity (Fig. 5). Likewise, if we consider large snags and logs, this parameter probably lags behind the density of large trees. As the original cohort dies out, large snags and then large logs will become increasingly abundant c. 500-800 years post-fire. The final old-growth attribute, maximum canopy stratification, is best described by a continuous and wide range of canopy heights, with moderate class diversity. In old-growth spruce-fir forests, maximum stratification is represented by a negative exponential distribution of heights from ground to 40 m (Fig. 4). Maximum stratification is probably attained gradually after c. 300 years of development as fir, and then the second cohort of spruce, become established in openings created by treefalls of the dominant canopy spruce (Fig. 5). As the original spruce colonists disappear, however, so will the upper stratum. The second cohort of spruce will probably rapidly fill these positions.

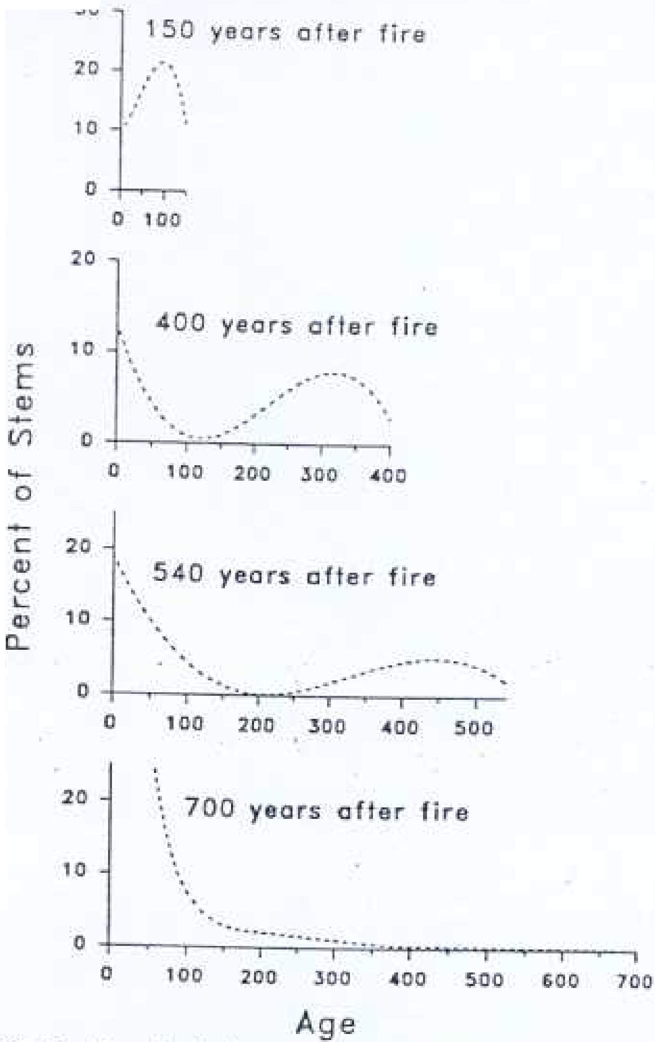

Fig. 3. Hypothetical post-fire development of age structure for Engelmann spruce (adapted from Day 1972 and Aplet et al. 1988).

THE FATE OF OLD GROWTH

Development of Mid and Late Old-Growth Stages

When the original post-fire cohort of spruce gradually disappears (c. 700 years post-fire), it is thought that the bimodal structure will gradually assume something approaching a reverse-j pattern (Fig. 3) (Day 1972, Peet 1981, Aplet et al. 1988). Although no one has demonstrated this development in a chronosequence, reverse-j or irregularly all-aged populations are evident in many old-growth stands (Whipple and Dix 1979, Peet 1981, Shea 1985, Alexander 1987) (Fig. 2). Small peaks in the diameter or age distributions are thought to result from recruitment following disturbances and past variations in mortality (Miller 1970, Shea 1985, Alexander 1987). In old-growth spruce-fir forests periodically affected by spruce beetle outbreaks, wave-like oscillations in basal area are expected (Schmid and Hinds 1974).

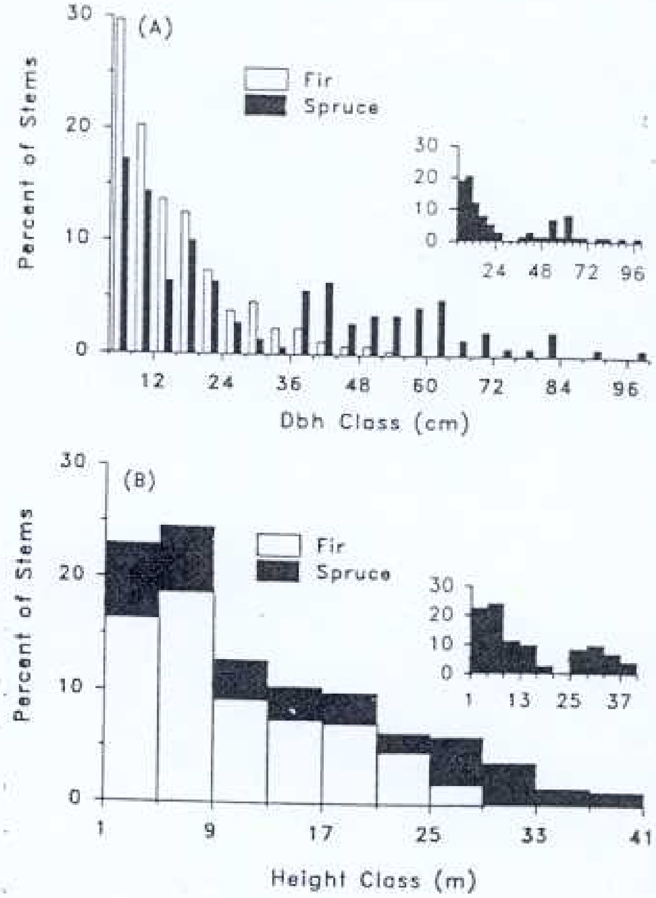

Fig. 4. Dbh (A) and height (B) structure for Engelmann spruce and subalpine fir in old-growth forest, Bowen Gulch, Colorado (after Roovers 1992). In (A) the percent of total stems for each species is given for comparison (n=139 for spruce and n=256 for fir). In (B) the percent of total stems for both species (n=391) is given to show the overall stratification of the canopy. The inset graphs are diameter and height for spruce alone in stands with southerly aspects (n=73 and 71, respectively).

Disturbance and the Landscape Mosaic

A popular notion with the public is that a primeval old-growth spruce-fir forest, stable and unchanged for centuries, covered most of Colorado's subalpine zone prior to European settlement. However, historical records and dendroecological evidence indicate that recurrent coarse-scale disturbances (fire, spruce beetle epidemics, and blowdowns) were an integral part of subalpine forest dynamics: "The coniferous forests of the Rocky Mountains can best be described as disturbance phenomena. Owing to the agencies of fire, wind and insect attack, these forests are periodically destroyed in a patchwork manner, resulting in a mosaic of stands of differing ages and

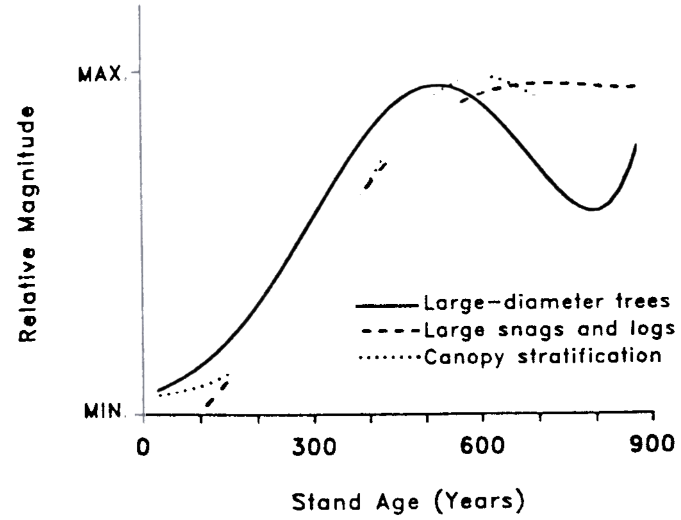

Fig. 5. Hypothetical changes in the magnitude of key physiognomic attributes in old growth during the first 900 years of post-fire stand development, Colorado Front Range. Patterns will vary depending on site and disturbance history. See text for further discussion.

histories" (Peet 1981). Lowry (this volume) estimated that only 12.4% of the spruce-fir in the Arapaho and Roosevelt National Forests was old growth in 1992.

The fire regime of subalpine spruce-fir forests is not known with certainty, but the existing pattern of stand ages suggests that spruce-fir forests were subject to lightning-caused crown fires at intervals ranging from 200-400 years (Peet 1981). Many stands in the subalpine zone of the Colorado Front Range are of post-fire origin from c. mid 1700s (Veblen 1986a, Rebertus et al. 1991). In subalpine forests of Rocky Mountain National Park, Colorado, there was an estimated 1 fire >4 ha per 8100 km^2 per year, prior to 1870 (Clagg 1975, in Romme and Knight 1981). Stand-devastating crown fires were most common, but many fires were probably patchy, skipping across valleys, or burning as surface fires and crowning out wherever fuel and topography were favorable (Romme and Knight 1981, Baker and Veblen 1990). Light surface fires may have been common in open spruce-fir forests near timberline, where fuel loads were less (Baker and Veblen 1990). Stand-devastating fires probably ranged from a few hectares to conflagrations covering tens of thousands of hectares, similar to the 1988 Yellowstone fires. Some areas undoubtedly remain unburned for many centuries or millennia, either by chance or because local physiography inhibits fire (Romme and Knight 1981). There is some evidence of differences in fire frequency over moisture gradients in the Sangre de Cristo Range in southern Colorado compared to the Medicine Bow Range in southern Wyoming (Romme and Knight 1981, Allen and Peet 1990). The illumination of such patterns in the disturbance regime will help us understand where old-growth stands are likely to occur and how long they will persist.

Spruce beetle (*Dendroctonus rufipennis*) outbreaks may be as significant as fire in the development of spruce-fir forests (Baker and Veblen 1990). There have been five or six major outbreaks that have caused widespread mortality in the southern Rockies since the mid 1800s (reviewed by Baker and Veblen 1990). Spruce beetles may kill up to 99% of the spruce trees greater than c. 20 cm dbh, but do not attack subalpine fir or small spruce (Schmid and Frye 1977). Hence, the structure of old-growth forests may be severely altered (Schmid and Hinds 1974, Veblen et al. 1991b). The most serious outbreak of this century occurred in the 1940s and was probably triggered by debris from a severe windstorm in 1939 (Hinds et al. 1965). In White River National Forest 290,000 ha were devastated and variable amounts of damage occurred from Grand Mesa National Forest in the southwest to Arapaho National Forest in north-central Colorado (Hinds et al. 1965, Cahill 1977, Veblen et al. 1991b). Historical records, photographs, and dendroecological evidence also indicate that another major epidemic affected extensive areas of Colorado c. 1850-1880 (Baker and Veblen 1990, Veblen et al. 1991b). During this outbreak, 10-25% of the mature spruce died in the White River National Forest, and 25-40% of the mature spruce on the Grand Mesa were killed (Sudworth 1900a,b; in Schmid and Frye 1977). We know very little about long-term stand development following such outbreaks.

Wind disturbance in spruce-fir forests has been well documented (Alexander and Buell 1955). Blowdowns involving multiple treefalls may add to the mosaicism of spruce-fir stands, but this has not been well documented (Peet 1981). In 1973 a windstorm in Hidden Valley, Rocky Mountain National Park, severely damaged c. 15 ha of subalpine forest (Veblen et al. 1989). Old-growth stands studied by Veblen et al. (1991a) along the Poudre River were classified as 65-92% blowdown (i.e., gaps involving 3 or more canopy trees);

however, these were more fine-scaled windthrow events than the large block affected at Hidden Valley. The 1939 blowdown in White River National Forest and several of the windthrow events documented by Veblen et al. (1991a) appear to have been caused by regionally extensive windstorms.

Under a natural disturbance regime, subalpine forests were probably characterized by a mosaic of stands in various stages of recovery from disturbance, and old growth was just one part of the larger forest mosaic (Peet 1981, Romme and Knight 1981). This mosaic was constantly changing and highly variable from place to place, so the extent of presettlement old-growth forest is uncertain. Green and Van Hooser (1983) classified 75% of spruce-fir forests in Colorado as "sawtimber" in 1977, the majority of which was considered overmature (Alexander 1987). The current subalpine landscape is perhaps more homogeneous (in terms of stand age) than in the presettlement era, mainly due to the synchronizing effect of very extensive, regional disturbances (e.g., fires in the mid 1700s, beetle outbreaks in the mid to late 1800s).

Coexistence of Spruce and Fir

In the central and southern Rockies, spruce and fir coexist as dominants in old-growth stands. In these forests, subalpine fir seedlings and trees less than c. 8 cm dbh are generally severalfold more abundant than those of spruce. In contrast, Engelmann spruce dominates the older age classes (>250 years), but is often poorly represented in the younger age classes (Whipple and Dix 1979, Peet 1981, Veblen 1986b, Alexander 1987, Roovers 1992). The greater abundance of young subalpine fir in old-growth stands would imply a shift in dominance from Engelmann spruce to subalpine fir if the two species have similar mortality rates. Peet (1981) suggested that coexistence of spruce and fir is maintained by disturbance because, in the hypothesized absence of disturbance, the greater regeneration of fir in the understory would lead to the gradual elimination of spruce within c. 1000 years. The hypothetical result of this shift, extensive subalpine fir-dominated stands, however, is not found in the subalpine zone of Colorado (Peet 1981, Veblen 1986b).

The mechanisms permitting the coexistence of spruce and fir are still not clear, although they have been the subject of much interest and debate (Fox 1977, Shea 1985, Veblen 1986b, Aplet et al. 1988). Three non-mutually exclusive explanations for the coexistence of spruce and fir were outlined by Veblen (1986b): (1) regeneration niche differences, (2) nonequilibrium coexistence, and (3) different life histories.

Differences in the regeneration niches of spruce and fir are evident in the establishment requirements for seedlings. Spruce seedlings establish best on bare mineral soil exposed by disturbances, whereas fir regeneration is better in heavy litter (Alexander et al. 1984, Alexander and Shepperd 1984, Knapp and Smith 1982). Where soils are very waterlogged, spruce also establishes well on logs. Although fir tends to be more abundant in the understory, both species are equally shade tolerant (Knapp and Smith 1982). Fir tends to have higher rates of photosynthesis under low light levels, however. In the Medicine Bow Range of Wyoming, Fox (1977) found that saplings of spruce and fir were more abundant in treefall gaps created by the alternate species, suggesting that niche differentiation in the regeneration phase would lead to reciprocal replacement, or alternation of species. Under this model, compositional equilibrium would be maintained by fine-scale treefalls. Shea (1985) found that spruce seedlings were more common under canopy fir. Fir seedlings were also more common under canopy fir in wet sites, but equally common under canopy fir and spruce in more xeric sites. Likewise, Veblen (unpublished data) found weak and inconsistent support for reciprocal replacement between spruce and fir in old-growth stands in the Front Range.

According to the nonequilibrium hypothesis, relatively frequent, coarse-scale disturbances (fire, blowdown, or spruce beetle epidemics) prevent the competitive exclusion of Engelmann spruce by subalpine fir (Day 1972, Peet 1981, Veblen 1986b, Aplet et al. 1988). Spruce tends to establish more abundantly on bare mineral soil exposed by fire compared to fir. Evidence that spruce regeneration is favored by blowdowns and spruce beetle epidemics is less convincing: some new seedlings may become established, but the primary response is the accelerated growth of already established spruce and fir in the understory (Veblen et al. 1989, Veblen et al. 1991b). After a severe canopy disturbance, dominance initially shifts toward fir. If enough spruce survive or re-establish, however, spruce may eventually recapture its lost dominance (Peet 1981, Veblen et al. 1991b).

Finally, according to the hypothesis of different life histories, the greater abundance of young subalpine fir in the understory of old growth is balanced by a substantially lower death rate among adults of Engelmann spruce (Oosting and Reed 1952, Day 1972, Shea 1985, Veblen 1986b). In an old-growth stand studied by Veblen (1986b), fir accounted for only 37% of canopy trees but 76% of fallen trees. The consistently lower frequency of Engelmann spruce as treefalls and its greater longevity imply a lower mortality rate for canopy trees. In Colorado, spruce can live >600 years; whereas fir rarely surpass 350 years.

Aplet et al. (1988) suggested that the second cohort of spruce that establishes late in stand development ensures the continued presence of both species in the canopy for at least another 500 years. Although the fate of the second cohort is less certain, they believed that continued fir mortality would allow relatively continuous spruce recruitment, but also conceded that the second cohort could remain relatively even-aged until the next period of spruce mortality. The continued autogenic development of extensive stands of old growth for several generations is largely a moot point, however, given the susceptibility of old-growth stands to extensive windthrow, beetle attack, and fire (Peet 1981, Baker and Veblen 1990, Veblen et al. 1991a,b).

It is likely that all three factors--differences in regeneration niches, coarse-scale disturbance, and different life histories--all contribute to the continued coexistence of spruce and fir (Veblen 1986b). The relative importance of these mechanisms undoubtedly varies both spatially and temporally.

Mortality Patterns Over Time

Frequently the timber industry and many silviculturalists contend that old-growth spruce-fir forests will only become more decadent with time, i.e., they are a perishable resource (LeBarron and Jemison 1953). The degree to which old-growth forests persist is a critical issue in the preservation of extensive stands, such as Bowen Gulch, and can only be understood by long-term mortality records. Mortality patterns in old-growth spruce-fir in Colorado have been explored using four methods: (1) inference from stands of different ages (chronosequence), (2) re-measurement of permanent plots, (3) estimating dates of tree death by cross-dating snags and logs, and (4) release frequencies.

The chronosequence approach is probably the least reliable method for documenting mortality patterns. Age and size structures from stands of different ages often provide clues of mortality patterns with development, but slight differences in site (e.g., topographic position) may result in very different trends (e.g., Whipple and Dix 1979, Veblen 1986a). Aplet et al. (1988) used the basal area of live and dead-standing trees and logs from stands of various ages to infer mortality patterns through 600 years of stand development. The dead basal area for fir was maximum in a stand c. 275 years of age, and for spruce at 375 years of age. These hypothetical waves of mortality were often supported by their age structure data, but changes in live basal area along the chronosequence may merely reflect site differences. Changes in dead basal area may reflect slightly different disturbance histories, rather than a trend through stand development.

The repeated censusing of permanent plots is the most accurate and reliable method for documenting mortality and recruitment patterns in old growth, but few long-term studies exist. In 1981, permanent plots were established by T. Veblen in old-growth spruce-fir stands near the Rocky Mountain Biological Station and Brainard Lake. Monitoring of tree death in 6 permanent plots of old growth containing >2000 trees (>4 cm dbh) over 9 years indicated annual average death rates of 0.1 to 0.4% for spruce and fir; however, the number of tree deaths was too small for interspecific comparisons. Cross-dating of snags in the plots suggested that mortality for spruce has been highly episodic in the past. In the Fraser Experimental Forest, a 3.2-ha permanent plot in old-growth spruce-fir has been monitored since 1944, but the small size of the plot in relation to surrounding silvicultural treatments complicates the interpretation of mortality data (Alexander and Watkins 1977).

Mortality patterns can also be documented directly by cross-dating intact snags and logs with a chronology developed from live trees. Trees with bark and >60 intact outer rings, usually can be cross-dated, and an estimate of the date of death can be determined. Even if the tree lacks bark,

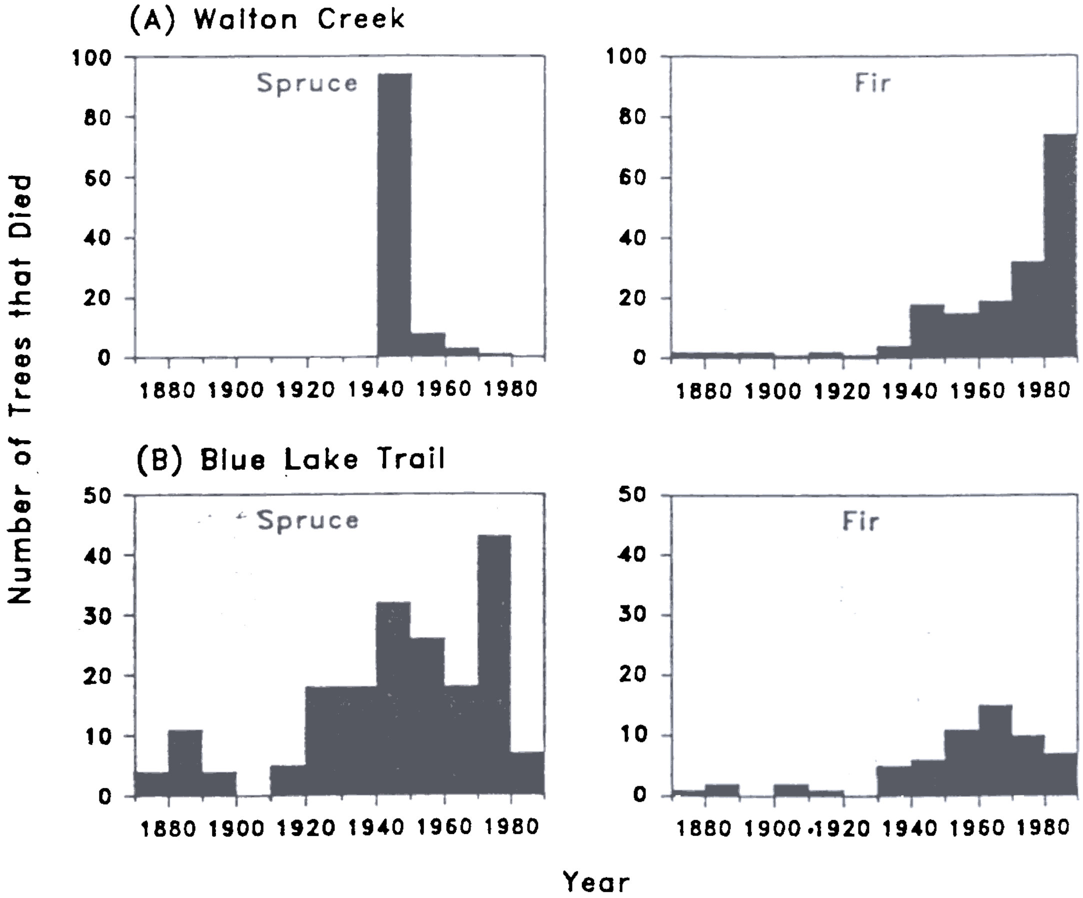

Fig. 6. Mortality patterns for dead-standing spruce and fir from old-growth forests: (A) Walton Creek and (B) Blue Lake Trail (after Mast 1991). The number of trees that died from 1870-1990 by decade is shown. The percentage of dead-standing trees successfully cross-dated ranged from 54-79. Total dead-standing trees/ha were as follows: Walton Creek spruce, 71; fir, 171; Blue Lake Trail spruce, 85; fir, 129.

weathering of the bleached wood is very slow and usually few, if any, outer rings are lost (Mast 1991). Occasionally, spruce remain dead-standing with bark attached for >100 years. A relatively continuous pattern of mortality is illustrated by fir at Walton Creek (Fig. 6A), with the number of trees that died in any particular decade increasing exponentially from 1870-1990 (Mast 1991). Spruce at Blue Lake Trail also displayed continuous mortality since 1870, but the rates were far more episodic, with below average mortality in the 1980s and above average mortality in the 1890s, 1940s, and 1970s (Fig. 6B). This pattern of mortality is also consistent with the release frequencies recorded from live trees throughout the stand (Fig. 7B). In contrast, the mortality patterns for spruce at Walton Creek indicate that this stand was affected by the 1940s beetle outbreak (Fig. 6A, Veblen 1991b, Mast 1991). Further studies on decay rates of spruce and fir will improve our understanding of rates of mortality based on dead-standing trees.

When a canopy spruce or fir dies, the increase in light and other resources results in abrupt and often sustained increases in growth (diameter and height) of subcanopy spruce and fir. Such releases can be dated from tree cores, and if enough cores are sampled throughout the stand, they can indicate the general pattern of past mortality (Lorimer 1985). A 200-year record of releases from three old-growth forests in the Colorado Front Range illustrates some striking patterns (Fig. 7). All three sites (Blue Lake Trail, Poudre River Trail, and

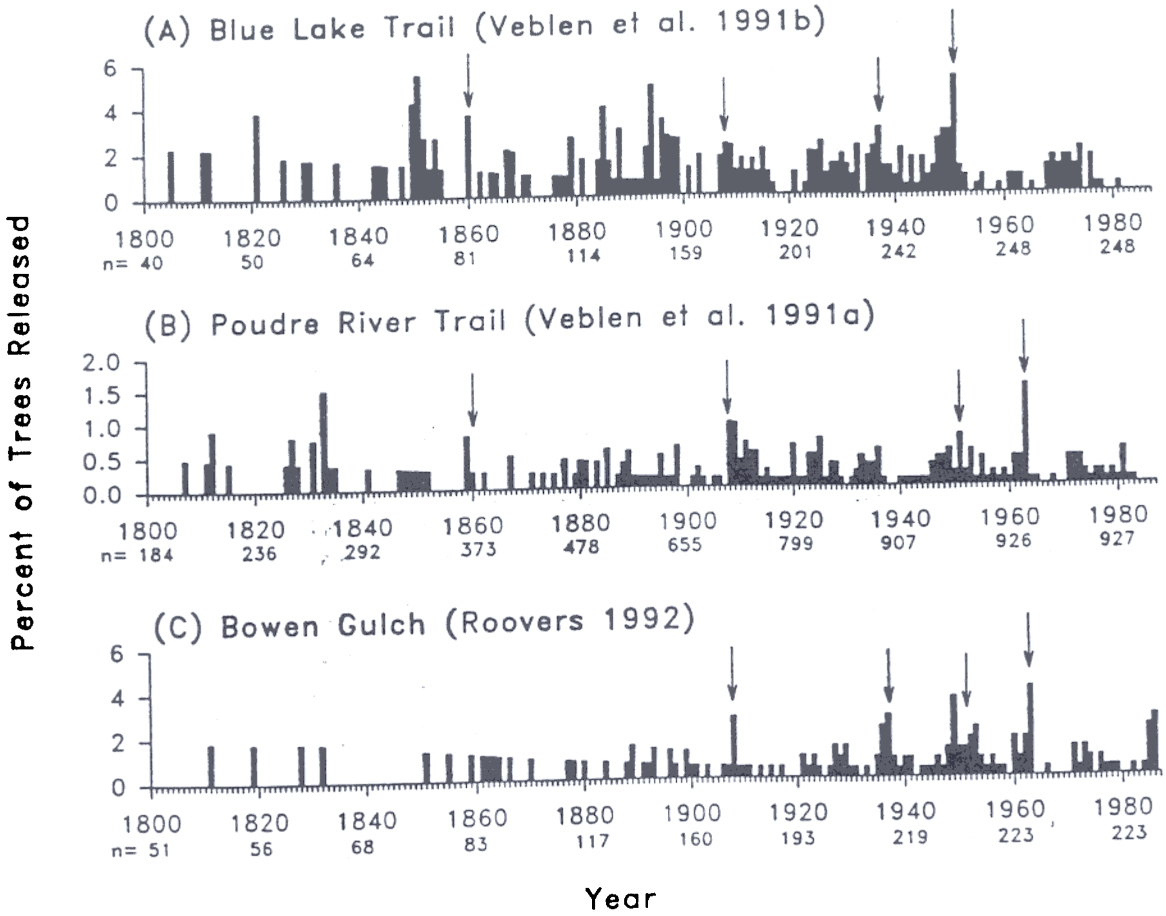

Fig. 7. Percentage of live trees (current cohort) that were released from 1800-1986 for all species in old-growth forests: (A) Blue Lake Trail (after Veblen et al. 1991b; © Ecological Society of America), (B) Poudre River Trail (after Veblen et al. 1991a;© Journal of Biogeography), and (C) Bowen Gulch (after Roovers 1992). A release is defined as a 150% increase in ring width when consecutive groups of five years are compared. Sample sizes (n) are given only every 20 years and appear beneath the year-axis labels. Coincident release dates are indicated by arrows.

Bowen Gulch) exhibit coincident release dates suggesting years of regionally extensive windthrow (e.g., 1860, 1908-09, 1924-25, 1947-51, and 1961-63). At the Poudre River Trail site, many gaps originated during these years (Veblen et al. 1991a). Periods of above average release frequencies, c. 1850-1860 and again in the mid to late 1940s, coincide with major spruce beetle outbreaks in Colorado, but the percentage of trees released was very low compared to severely affected stands in the White River and Grand Mesa National Forests (Veblen et al. 1991b). For example, in old-growth stands at Big Creek Reservoir, Grand Mesa National Forest, 18% of the sampled spruce showed release in a single year, 1946. Hinds et al. (1965) estimated that beetle-killed spruce fall at the rate of c. 1.5% per year, so releases of surviving trees may be associated with tree mortality and/or subsequent windthrow.

The prevalence of wind-snapped treefalls along the Poudre River Trail suggested that trees were often dead or diseased before they fell (Veblen et al. 1991a). We lack etiological studies, however, that demonstrate causes of windthrow. Undoubtedly, many interacting factors are involved, such as wood-rotting fungi (reviewed by Alexander 1987) and low-level attack by endemic spruce beetle populations (Schmid and Frye 1977).

There is some indication that the frequency of windthrow has increased at Bowen Gulch since

1900 (Fig. 7C); however, it is unclear whether this is a long-term trend. This forest is nearing the end of its fifth century of development, and the original spruce colonists are reaching their maximum longevity (Fig. 2H). Thus, increased mortality and windthrow should be expected for the next c. 100 years. Thereafter, windthrow may decline until the second spruce cohort reaches 500-600 years of age. Unfortunately, we lack information on old-growth stands that have developed in the absence of coarse-scale disturbance for >600 years. Veblen et al. (1991a) also provide some evidence that the scale and frequency of disturbance by windthrow steadily increase after c. 300 years of stand development. This increase in windthrow increases the likelihood of another stand-initiating fire or extensive beetle outbreak (Schmid and Frye 1977, Veblen et al. 1991a).

CONCLUSIONS

Despite numerous publications, we really have very few detailed age structure analyses in old-growth spruce-fir forests. In the harsh subalpine environment, slight differences in site may result in major differences in stand development patterns, and ultimately in the characteristics of old growth. It is clear that some very high-quality old-growth stands, like Bowen Gulch, are in a transition old-growth stage, and some of the structural attributes of the forest may change significantly in the next few hundred years. Additional studies also are needed to monitor (or extract dendrochronologically) the patterns of mortality in old growth over longer periods. We have a general idea of how stands develop into old growth, but only a vague notion of what happens thereafter. The susceptibility of old-growth stands to fire, beetle outbreak, and blowdowns still brings into question whether any spruce-fir stands can persist for a thousand years. Ironically, lack of disturbance threatens the persistence of oak (*Quercus* spp.)-dominated old growth in the Midwest, and poses serious management questions of preservability (Boerner and Kooser 1991). In Colorado, the issue is not whether or how long we can preserve an old-growth spruce-fir forest; rather, we need to understand the dynamics of old-growth spruce-fir to plan for continued existence and renewal of places like Bowen Gulch, which add immeasurably to the richness of the landscape.

ACKNOWLEDGEMENTS

Parts of several figures were adapted from published materials with permission from The Ecological Society of America, The Torrey Botanical Club, and The Journal of Biogeography. Research funding was provided by the National Science Foundation (Grant No. SES 8618621), the Council on Research and Creative Work of the University of Colorado, and the School of Natural Resources, University of Missouri.

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