POSTFIRE SUCCESSION AND DISTURBANCE INTERACTIONS ON AN INTERMOUNTAIN SUBALPINE SPRUCE-FIR FOREST

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ABSTRACT

Four general postfire successional pathways leading to a climax Engelmann spruce (*Picea engelmannii* Parry)-subalpine fir (*Abies lasiocarpa* [Hook] Nutt.) forest operate on the T.W. Daniel Experimental Forest in northern Utah. Depending on the successional pathway followed, reestablishment of the prefire climax forest will take 200 to 400 years or more due to a rarity of extreme burning conditions. During the long period between catastrophic stand-replacing fires, a variety of other natural disturbances contribute to the varying structure and composition of vegetation and the fuel mosaic in intermountain subalpine spruce-fir forests. Disturbances may range from chronic and small scale to acute and catastrophic, resulting in a broad range of vegetative responses. In addition to crown fires, other major abiotic disturbances (i.e., landslides, mudflows, severe soil erosion, snow avalanches) and biotic disturbances (i.e., disease and insect outbreaks) control the availability of sites for the initiation of new stands or accelerated growth of understory plants and subcanopy trees.

Understanding the role of natural disturbances in forest ecosystems is key to managing long-return interval fire regimes. This paper explains how the disturbance regime operating in a given landscape influences vegetative dynamics and fuel mosaics and how the state of the vegetation in turn influences these natural disturbance agents. Managers must recognize biotic and abiotic agents of disturbance and their interactions to fully understand fire regimes and the effects of fire suppression and prescribed fire.

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INTRODUCTION

In the spruce-fir zone of the intermountain West, Engelmann spruce (*Picea engelmannii* Parry ex Engel.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) typically coexist as dominants in climax communities forming extensive stands on cool, moist sites above 2285 meters to timberline near 3355 meters (Whipple and Dix 1979, Schimpf et al. 1980, Alexander 1987, Peet 1988, Long 1994). At the upper-elevational limits of Engelmann spruce and subalpine fir, forests become discontinuous, and the two species often grow in clumps of small patches within subalpine meadows (Alexander 1987, Long 1994). On exposed sites at timberline, they may form krummholz (Harlow et al. 1979, Long 1994). Spruce-fir stands may also occur at lower elevations on north-facing slopes, in cold pockets along streams, and in valley bottoms. At lower elevations common seral associates include lodgepole pine (*Pinus contorta* Dougl. Ex Loud), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and aspen (*Populus tremuloides* Michx)(Alexander 1974, Mauk and Henderson 1984).

According to Alexander (1987), spruce-fir forests are suited for multiple use in the central and southern Rocky Mountains. They have high commercial value and provide water, wildlife habitat, forage for livestock, summer and winter recreational opportunities, and scenic beauty (Alexander 1977).

Fire is regarded as the most important mechanism that drives vegetation dynamics in western forest ecosystems (Billings 1969, Loope 1971, Heinselman 1973, Romme and Knight 1981, Peet 1988). Long-return interval, high-intensity, stand-replacing crown fires generally occur in the spruce-fir zone due to the rarity of extreme burning conditions and slow decomposition rates that allow fuels to accumulate at high elevations. The primary response of vegetation to this kind of fire disturbance is the establishment of new stands (Oliver 1981, Veblen et al. 1991). Fire-initiated stands may then follow one of several postfire successional pathways that eventually lead to forests dominated by Engelmann spruce and subalpine fir (Dicus 1995).

During the 300 to 400 or more years between major fire events, however, low-intensity surface fires and other disturbances may occur, including the spruce beetle (*Dendroctonus rufipennis* Kirby (Coleoptera: Scolytidae) outbreaks, wind, and snow avalanches. These may influence vegetative structure, species composition, and successional dynamics in spruce-fir communities (Habeck and Mutch 1973, Werner et al. 1977, Romme and Knight 1981, Aplet et al. 1988, Baker and Veblen 1990, Veblen et al. 1991, Veblen et al. 1994). Although relationships between these disturbances are not completely understood, their interactions likely generate landscape patterns different than those of fire-dependent ecosystems. Resulting landscape patterns

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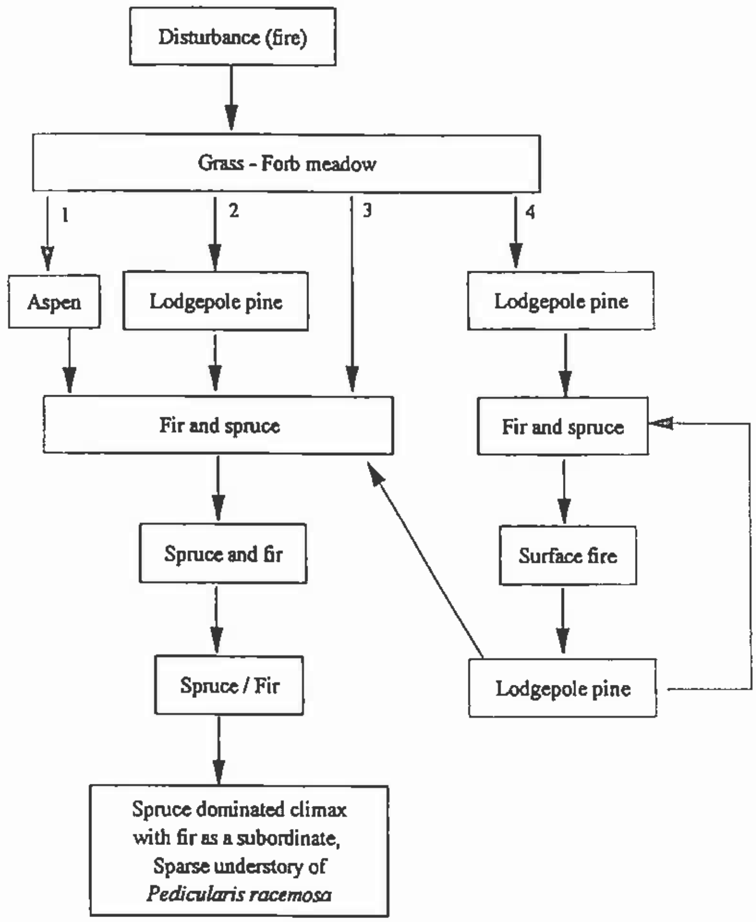

Fig. 1. Suggested successional pathways on the T.W. Daniel Experimental Forest. Modified from Schimpf et al. (1980).

can either enhance or retard the propagation of subsequent disturbances, including fire (Turner et al. 1989). Another important consequence of these disturbances is the maintenance of valuable spruce and fir in subalpine forest communities.

The objective of this research was to examine succession following stand-replacing fires on the T. W. Daniel Experimental Forest, Utah. Of interest was the timing of establishment and subsequent growth of late successional Engelmann spruce and subalpine fir and the influence of disturbances on postfire successional pathways in the intermountain spruce-fir zone. Forest managers can use this information to predict fire potential, assess the appropriateness of prescribed fire for perpetuating valuable subalpine forest communities, and for reducing hazardous fuels in these communities. Strategies involving spruce beetle management are also proposed as alternatives to fire for accomplishing management goals while maintaining ecosystem integrity.

METHODS

Study Area

The T.W. Daniel Forest is located approximately 40 kilometers east of Logan, Utah. Elevations on the forest range from 2377 meters to 2651 meters. The area receives over 100 centimeters of precipitation annually that falls primarily in the form of snow and average monthly temperatures that range from −11°C in January to 17°C in August (Hart and Lomas 1979).

The Daniel Forest contains stands of late successional Engelmann spruce and subalpine fir with scattered subalpine meadows and seral stands of quaking aspen and lodgepole pine. The *Abies lasiocarpa/Pedicularis racemosa* (ABLA/PERA) habitat type covers most of the forest (Mauk and Henderson 1984) and all data were collected in this type.

Procedures

Four successional pathways leading to Engelmann spruce-subalpine fir communities were defined (Figure 1). Pathways 1 and 2 represent postfire colonization by seral quaking aspen and lodgepole pine, respectively, followed by shade-tolerant, late successional Engelmann spruce and subalpine fir. Pathway 3 represents immediate postfire colonization by the late successional species. Pathway 4 represents initial postfire colonization by lodgepole pine followed by a low-intensity surface fire which consumes understory Engelmann spruce and subalpine fir while causing little damage to the lodgepole pine overstory.

A fire history and stand map of the Daniel Forest produced by Wadleigh and Jenkins (1996) was used to locate sites comprised of appropriate stands of aspen, lodgepole pine, and Engelmann spruce-subalpine fir to examine successional pathways 1–3. These stands were initiated by fire between 1890 and 1903 and displayed the characteristic of a single postfire successional pathway. Two lodgepole pine stands that regenerated after stand-replacing fires in 1847 and 1860 (and experienced light surface fire between 1890 and 1903) were selected to examine successional pathway 4. One aspen stand sampled was not within the mapped area. Therefore, a fire history was conducted for that stand using the methods described by Arno and Sneck (1977). Selection of sampled stands also required that greater than 80% of the basal area was represented by the appropriate tree species.

Data were collected from three 1/25 hectare plots randomly established in three stands representing fire-initiated aspen, lodgepole pine, and Engelmann spruce-subalpine fir. Similar plots were established in the fire-disturbed lodgepole pine stands. At each plot center, a 3.5 basal area factor prism was used to insure that the surrounding overstory was consistent with the intended successional pathway. Aspect, slope, and basal area by species were determined at each plot to assist in accounting for variability between plots. The determination of successful establishment for individual trees was based on a minimum height requirement of 20 centimeters. As a result, data include only the first 80 years after fire. All trees of each species in the plot meeting the minimum height requirement were counted and individual tree heights measured. The diameter at breast height (dbh) of trees taller than 1.37 meters was also measured.

All Engelmann spruce and subalpine fir trees large enough to be sampled by an increment borer were cored at stump height and extracted cores were glued to boards for aging. Ages of all small diameter Engelmann spruce and subalpine fir were obtained from cross sections clipped or sawed at stump height. Tree ages were used to determine the year of their establishment.

Seral aspen and lodgepole pine stands were assumed to be even-aged; however, a subsample of ten overstory trees in each plot was aged to insure the plot was located within the desired fire boundary. The age of lodgepole pine was determined by cores taken at stump height. Due to heart rot that was often present in the lower bole aspen, ages were determined by cores taken at breast height with 5 years added to the total ring count (Jones 1967).

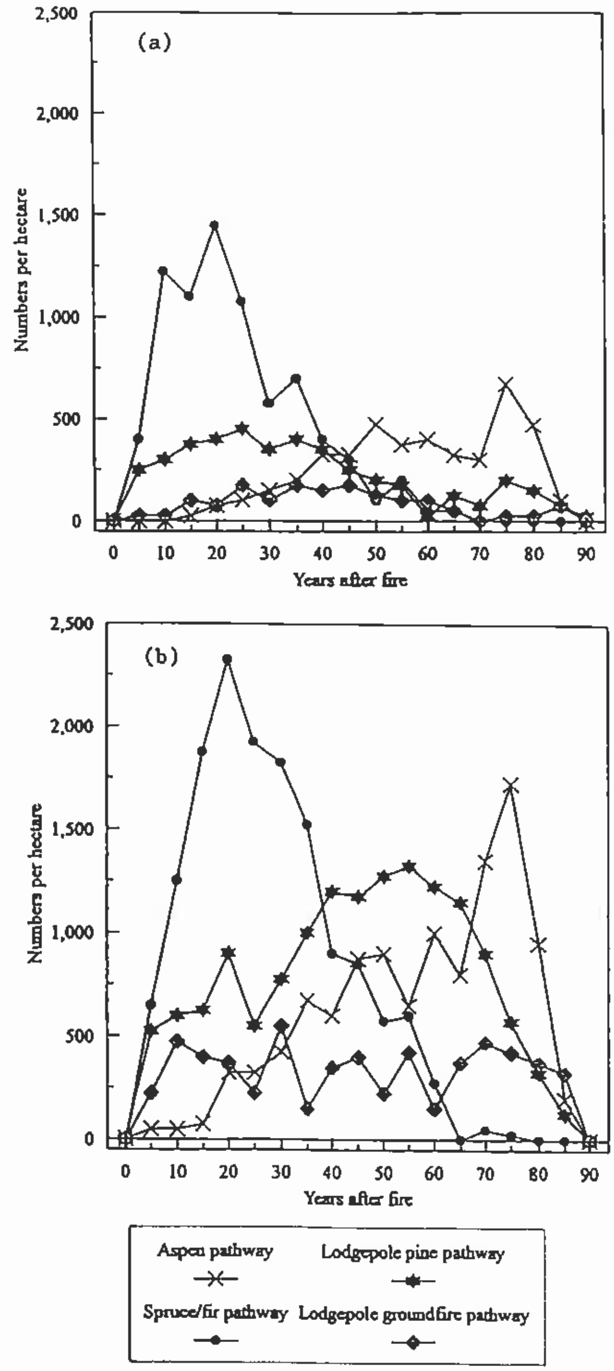

Fig. 2. Engelmann spruce (a) and subalpine fir (b) establishment in each 5-year period following fire.

RESULTS

Data for each postfire successional pathway were pooled after preliminary analyses showed little difference between sample stands of the same pathway. For each successional pathway, the number of Engelmann spruce and subalpine fir established per hectare in 5 year periods are given in Figure 2. These data show that the timing of Engelmann spruce and subalpine fir establishment differed between the four postfire successional pathways. In the Engelmann spruce-subalpine fir pathway, establishment of both species occurred in large numbers within 30 years after a fire, then establishment declined dramatically as trees grew, limiting available space. Engelmann spruce and subalpine fir in the lodgepole pine and the lodgepole pine-surface fire pathways established in fairly consistent numbers through time, but there were more of the late successional species in the lodgepole pine pathway. Few Engelmann spruce and subalpine fir were established in the aspen pathway until 15 years following a fire, but large numbers of both species were present after 70 years.

A cumulative frequency distribution was used to express the difference required for postfire establishment of Engelmann spruce and subalpine fir based on germination in successive 5 year periods following fire (Figure 3). For example, in the Engelmann spruce-subalpine fir pathway, 50% of the late successional species that were present after 70 years had germinated within 20 years after a stand-replacing fire. In the quaking aspen pathway, 55–60 years were required for germination of 50% of Engelmann spruce and subalpine fir that were present.

Regression analyses of Engelmann spruce and subalpine fir height as a function of age for each postfire pathway are shown in Figure 4. Both species achieved the fastest height growth after germination in the Engelmann spruce-subalpine fir pathway, followed by the aspen pathway, the lodgepole pine pathway, and the lodgepole pine-surface fire pathways.

The Engelmann spruce-subalpine fir pathway contained the highest number of late successional trees, followed by the lodgepole pine, the aspen, and the lodgepole pine-surface fire pathways (Figure 5). In all pathways there were two to five times more subalpine fir per hectarethan Engelmann spruce. Engelmann spruce and subalpine fir had heights that ranged from 1–20 meters and diameters that ranged from 2–26 centimeters in the Engelmann spruce-subalpine fir pathway. In the three other pathways, most Engelmann spruce and subalpine fir were less than 2 meters high and 2 centimeters in diameter.

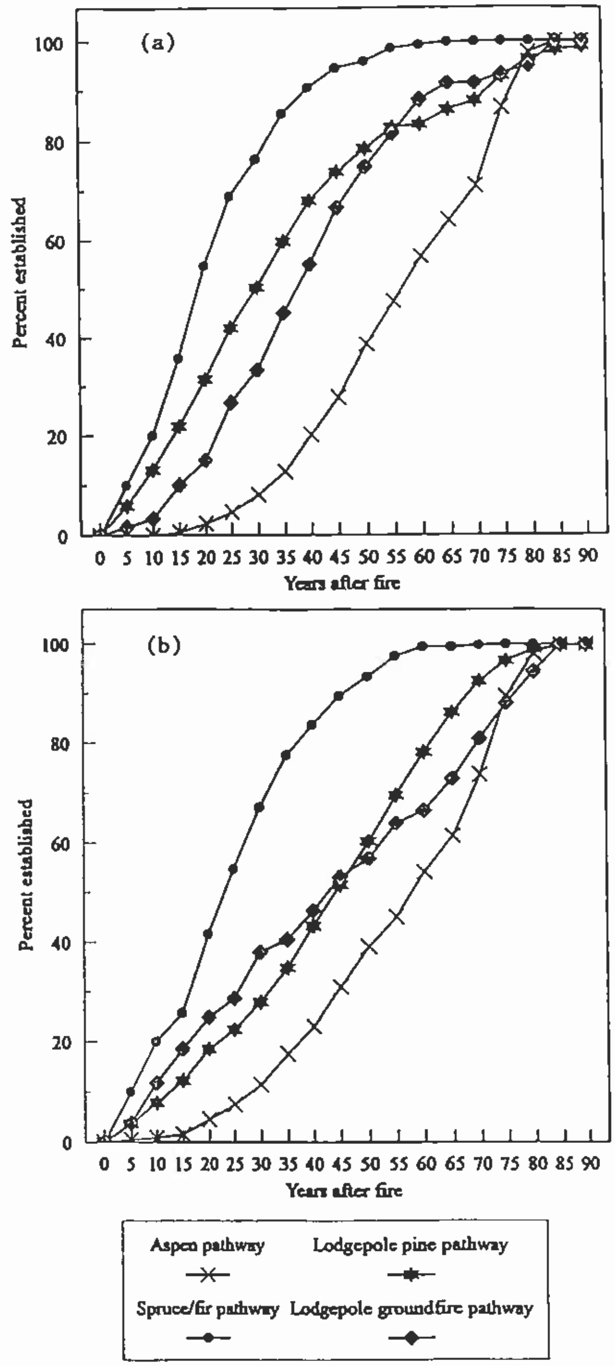

Fig. 3. Cumulative frequency distribution of percentage of Engelmann spruce (a) and subalpine fir (b) establishment in 5-year periods following fire.

DISCUSSION

The Establishment, Development, and Influence of Disturbance on Engelmann Spruce and Subalpine Fir Communities

Under extreme burning conditions, fire potential exists during all stages of forest community development in the spruce-fir zone (Bessie and Johnson 1995). Other important disturbances in the spruce-fir zone also influence establishment and succession by causing abrupt changes in forest communities. These disturbances vary in kind, frequency, intensity and magnitude, thus any kind of disturbance may range from chronic and normal, to acute and catastrophic (White 1979). This results in a broad range of vegetative responses. For example, major disturbances including crown fires, landslides, mudflows, severe soil erosion, and snow avalanches control the availability of sites for the initiation of new stands (White 1979, Oliver 1981). The primary response of vegetation to this scale and intensity of disturbance is the establishment of new stands (Oliver 1981, Veblen et al. 1991). Large-scale canopy disturbances including lethal insect outbreaks and blowdown are selective mortality agents and do not expose mineral soil or remove biomass (Veblen et al. 1991). This type of disturbance serves to reduce competition and increase nutrient availability resulting in the accelerated growth of understory plants and subcanopy trees (Levin and Paine 1974, Veblen et al. 1991). Although seed sources may be available, seedling establishment is generally not successful (Aplet et al. 1988, Veblen et al. 1991, Lertzman 1992). Minor disturbances commonly occur in subalpine for-

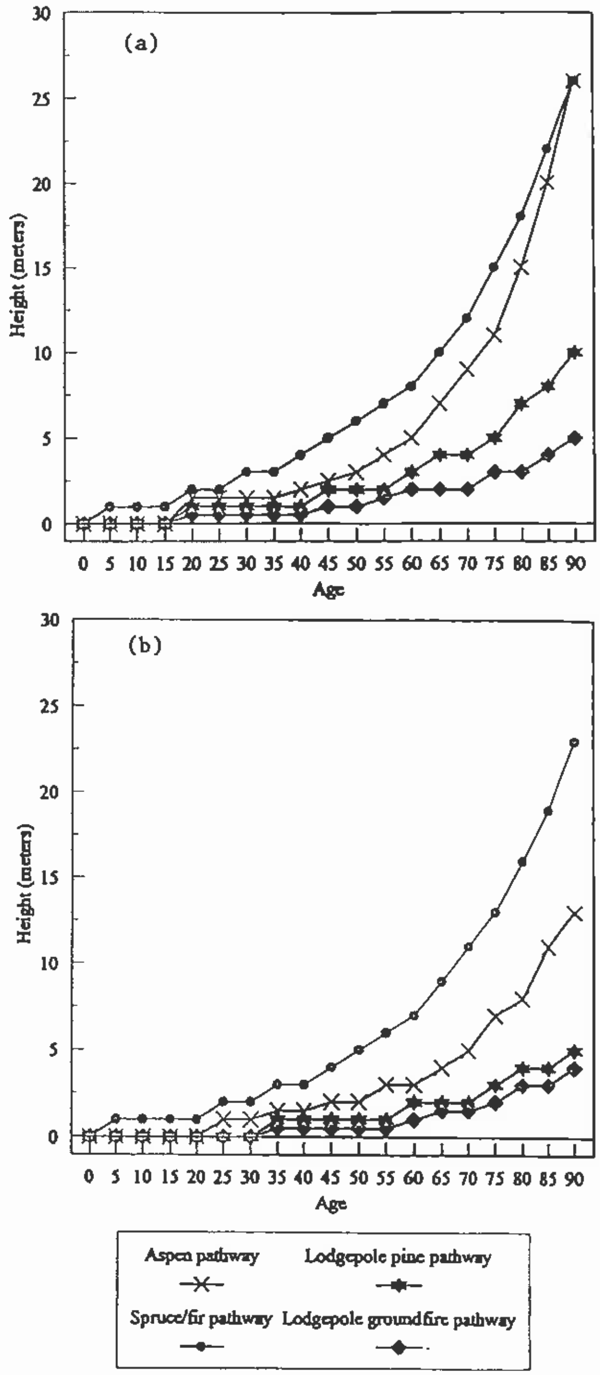

Fig. 4. Engelmann spruce (a) and subalpine fir (b) height growth after germination.

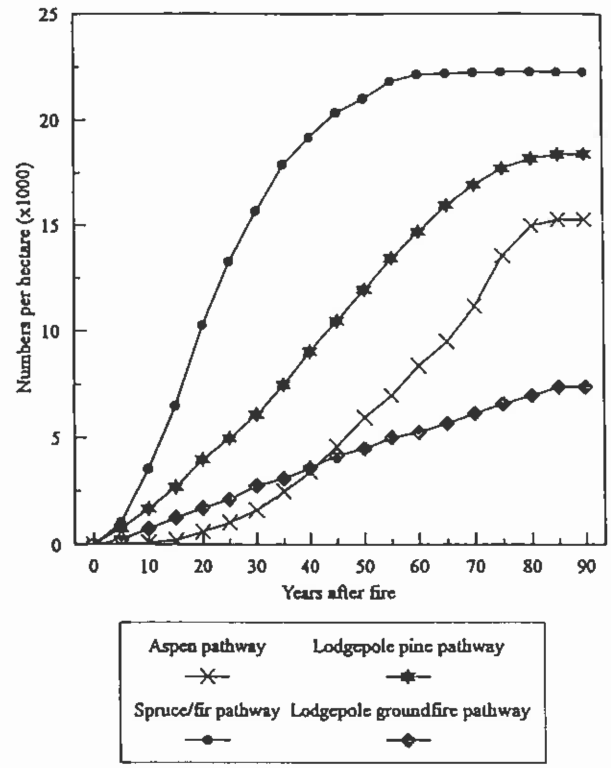

Fig. 5. Total accumulation of Engelmann spruce and subalpine fir following fire.

ests and result in partial removal of the overstory, or the death of individual trees (Oliver 1981). Examples of minor disturbances include surface fires, lightning strikes, snow avalanches, insects, and diseases (Oliver 1981). These types of disturbances create gaps in the canopy which allow the recruitment of subcanopy trees into the main canopy (Aplet et al. 1988, Veblen et al. 1991). Disturbances of any scale may eliminate seed sources and thus influence species availability (Veblen et al. 1991).

The temporal scale and the nature of disturbances in a given landscape is governed by endogenous factors in the plant community as well (White 1979). For example, stand age, composition, and structure affect fire potential and fire behavior. Stand conditions also promote the initiation and spread of insect outbreaks. Another concept essential for understanding the role of natural disturbances in forest ecosystems is that disturbances are also a function of topography, soils, and other site characteristics (White 1979). Thus, explanations of vegetation patterns and dynamics in forest ecosystems should account for the effect of multiple disturbances, the relationship between these disturbances, and how the state of the vegetation influences disturbance.

The following discussion describes how fire and other disturbances acting alone, or through their interactions, can influence aspen, lodgepole pine, and spruce-fir successional pathways and contribute to the development of intermountain spruce-fir communities. This discussion applies to sites on the Daniel Forest and other subalpine forests of similar latitudes and elevations. Different successional dynamics apply in other areas. For example, at lower elevation forests, Douglas-fir and disturbances associated with these species would be more important.

The Aspen Pathway

Aspen, if present, commonly colonizes sites after stand-replacing fire in the spruce-fir zone due to its ability to resprout (Lotan 1976). Engelmann spruce and subalpine fir required a relatively long time to establish under aspen on the Daniel Forest. This might reflect the inability of quaking aspen to adequately moderate environmental extremes during the first phases of stand initiation. Once established, however, Engelmann spruce and subalpine fir grew faster beneath aspen than in either lodgepole pine pathway (Figures 2, 3). This may be due to higher organic matter and soil nutrients or the fact that leaf area indexes are lower in aspen than in lodgepole pine (Kaufmann et al. 1982) and lower transpiration rates in aspen provide more soil moisture (Jones et al. 1985). Also, when subjected to water stress, quaking aspen cease transpiration sooner than lodgepole pine and extract less soil water (Kaufmann 1982, Jones et al. 1985). In the early spring, vegetation in the understory of aspen stands have high rates of photosynthesis, but not in the understory of lodgepole pine stands (Kaufmann et al. 1982).

During all stages of stand development, aspen typically has low flammability (Jones and DeByle 1985). Fuels primarily consist of dead herbaceous material, fallen leaves, downed timber, and shrubs or young conifers and these fuels may propagate fire of low to moderate intensity in dry weather conditions (Jones and DeByle 1985). On the Daniel Forest, and in many other forests of the Intermountain West, grazing has reduced fine fuels necessary for fire spread (Wadleigh and Jenkins 1996). Additionally, Engelmann spruce and subalpine fir height growth analyses (Figures 4, 5) indicate that following their establishment beneath aspen, these species require 70–80 years to provide ladder fuels that would increase fire intensity and the potential for crown fires.

Aspen are extremely sensitive to fire, however, and a fire event of low to moderate intensity during this stage of stand development would be sufficient to kill overstory trees and promote resprouting (Jones and DeByle 1985). As stands mature, decays, root and butt rots, and cankers make aspen more susceptible to wind and snow damage (Jones and DeByle 1985). Broken and uprooted trees contribute to the 1000-hour fuel loads and, combined with an increased density of shrubs and young conifers in the understory, create an arrangement of fuels favoring more intense fire with rapid spread (Jones and DeByle 1985).

In the absence of low to moderate fires, our data indicate that understory Engelmann spruce and subalpine fir approximately 4 meters tall would overtop the aspen in approximately 30 years and eventually dominate the site. Newly germinated conifer seedlings would reach the main canopy in about 90 years (Figures 4, 5). Individual tree mortality caused by fungal diseases including aspen heart rot (*Phellinus tremulae* ([Bond.]) Bond. & Boriss.) and other damaging agents may hasten the replacement of aspen by understory Engelmann spruce and subalpine fir by reducing competition for available resources.

The Lodgepole Pine Pathway

With an available seed source, lodgepole pine will quickly colonize burned sites (Lotan 1976). We found that Engelmann spruce and subalpine fir establishment in the lodgepole pine and lodgepole pine-surface fire pathways was generally the same, although we had hypothesized that low-intensity surface fires in lodgepole pine might have served to accelerate the establishment of Engelmann spruce and subalpine fir by creating canopy gaps and mineral seedbeds. It appears that seed sources for Engelmann spruce and subalpine fir might not have been available at the time of these fires.

The peak fire susceptibility of lodgepole pine stands occurs about 25 years after colonization due to the lack of early self-pruning and the presence of standing fire-killed snags (Brown 1975). Fires occurring prior to the maturity of a sufficient number of seed-producing trees may eliminate lodgepole pine from the site resulting in a persistent meadow (Wellner 1970). In approximately 60 years, lodgepole pine begins to self-prune and fire-killed snags begin to fall. During this time, lodgepole pine stands become moderately fire resistant (Brown 1975).

Our data indicate that in about 20 years after a stand-replacing fire, Engelmann spruce and subalpine fir began to establish beneath lodgepole pine. During this period of stand development the fuels configuration and arrangement are conducive to low-intensity surface fire. This type of fire would kill young Engelmann spruce and subalpine fir while causing little damage to the lodgepole pine overstory. The reestablishment of Engelmann spruce and subalpine fir requires another 20 years following such a low-intensity surface fire. The occurrence of a high-intensity, stand-replacing crown fire will also be delayed for approximately 125 years in the absence of extreme fire weather.

In the absence of surface fires, understory Engelmann spruce and subalpine fir continue to grow, and after 40 years, become tall enough to provide vertical continuity into the lodgepole pine canopy. Newly germinated seedlings would provide the vertical fuel needed for crown fire in about 125 years. Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engel.) infests lodgepole pine throughout the Intermountain West and dwarf mistletoe brooms contribute to ladder fuel development (Hawksworth and Johnson 1989). These conditions increase the likelihood of a stand-replacing fire that would perpetuate lodgepole pine on the site. In the absence of a stand-replacing fire Engelmann spruce and subalpine fir will eventually dominate the site, although scattered, lodgepole pine often persist in developing spruce-fir communities due to the slow rates of succession and recurring surface fires (Habeck and Mutch 1973, Lotan and Critchfield 1990).

Lodgepole pine mortality caused by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins Coleoptera:Scolytidae) can hasten succession to spruce and fir. This insect tends to attack lodgepole pines greater than 20 centimeters in diameter, over 80 years of age, and growing on midelevation sites (Amman et al. 1977). Damage caused by low-intensity surface fires has been related to tree selection and colonization by mountain pine beetles (Geiszler et al. 1980). Fire-damaged tissue provides entry courts for decay fungi that gradually weaken the tree. Stressed trees are preferentially attacked by mountain pine beetle (Geiszler et al. 1980) and as beetle populations increase they can cause extensive lodgepole pine mortality (Gara et al. 1984).

Tree mortality caused by mountain pine beetle outbreaks also increases the probability of high-intensity fire. A stand-replacing fire would delay succession to Engelmann spruce and subalpine fir and serve to reinitiate the lodgepole pine cycle.

The Spruce-Fir Pathway

Engelmann spruce and subalpine fir gradually replace seral communities in the spruce-fir zone. Our results support other findings (Wright and Bailey 1982) that the replacement of early successional, shade-intolerant communities by Engelmann spruce and subalpine fir requires many years.

Although harsh postfire environmental conditions including temperature extremes, intense solar radiation, and desiccating winds generally deter the establishment of Engelmann spruce and subalpine fir (Wardle 1968, Hellmers et al. 1970, Ronco 1970, Daly and Shankman 1985, Alexander 1987), these two species colonized large burned areas of the Daniel Forest (Wadleigh-Anhold 1988). The successful postfire colonization by Engelmann spruce and subalpine fir on these sites might have been due to the absence of aspen and the unavailability of lodgepole pine seed sources. Surviving Engelmann spruce and subalpine fir, or trees growing in adjacent stands, may have provided an adequate seed source following fire and standing dead trees may have moderated postfire environmental extremes creating suitable microsites for seedling establishment (Stahelin 1943, Oliver 1981, Pickett et al. 1987).

Burned sites on the Daniel Forest as described above are conducive to the recolonization and subsequent growth of the late successional species and allowed for the fastest return to climax Engelmann spruce-subalpine fir communities. The lack of competition from overstory aspen and lodgepole pine for light, nutrients, and water likely contributed to faster height growth of Engelmann spruce and subalpine on these sites versus height growth observed in all other pathways.

In fire-initiated Engelmann spruce and subalpine fir stands, our data indicate that these two species approach maximum height and stand density in about 100 years (Figures 4, 5). In mature spruce-fir stands, more shade-tolerant subalpine fir comprised the highest proportion of regeneration in the understory. Fewer Engelmann spruce seedlings might reflect their inability to establish in dry, heavy duff (Alexander 1974, Knapp and Smith 1982, Aplet et al. 1988). The fungus *Geniculodendron pyriforme* Salt (Ascomycetidae, Pezizales), the imperfect stage of *Caloscypha fulgens* (Pers.) Bouldier (Ascomycetidae, Pezizales), also commonly infects and kills Engelmann spruce seeds that overwinter on duff seedbeds (Daniel and Schmidt 1972, Paden et al. 1978, Wicklow-Howard and Skujins 1980). These factors do not affect subalpine fir seed or seedlings.

As the canopy begins to thin, subalpine fir will be primarily recruited into the main canopy and will dominate the stand for about 200 years (Veblen 1986, Aplet et al. 1989). In mature stands, subalpine fir experiences a higher rate of windthrow which is consistent with its shorter life span and susceptibility to root disease (Veblen 1986). A reinitiation phase for Engelmann spruce follows as these small-scale disturbances open gaps in the canopy and provide suitable microsites of upturned mineral soil and downed logs for seedling establishment (Shea 1985, Aplet et al. 1989). With increasing stand age Engelmann spruce dominates the main canopy due to its longevity and subalpine fir continues to persist in the subcanopy.

Spruce beetle outbreaks have the most dramatic impact on the development of postfire spruce-fir communities (Holsten et al. 1991). The principle host of this insect in the central Rocky Mountains is Engelmann spruce, although spruce beetles frequently attack blue spruce (*Picea pungens* Engel.) and during epidemics may kill lodgepole pine (Schmid and Frye 1977). Large outbreaks cause extensive spruce mortality; however, single-tree and small group mortality account for much of the loss of spruce saw timber annually (Schmid and Frye 1977). Spruce beetles typically inhabit the well-shaded surfaces of downed spruce (Schmid and Frye 1977). During epidemics, spruce beetles attack mature, living spruces, preferring stressed, large-diameter trees. The most susceptible stands are those comprised of 65% spruce, with a basal area greater than 35 meters squared per hectare, and an average stand diameter of 40 centimeters or more.

Figure 6 shows a conceptual model we have developed to illustrate the interactions between fire and other important disturbances that influence vegetative dynamics in Engelmann spruce-subalpine communities. Any disturbance that produces downed host material can potentially contribute to the rapid increase of spruce beetle populations. Spruce beetles have reportedly increased to outbreak levels in windthrown trees following blowdown, or in logging slash (Miller 1970, Schmid and Hinds 1974, Werner et al. 1977, Schmid 1981).

Infrequent, large snow avalanches also produce significant quantities of downed host material, although few studies have documented their influence on spruce beetle population dynamics. The importance of understanding the relationship between winter disturbances and spruce beetle outbreaks is that the season when downed host material becomes available for colonization by spruce beetles may strongly relate to its suitability for brood production and larval survival. Thus, the timing of disturbance would determine the necessity of treatments, influence choice of treatments, and dictate when application of treatments would be most effective for reducing spruce beetle populations.

Spruce beetle mortality modifies stand structure and species composition by removing large, overstory

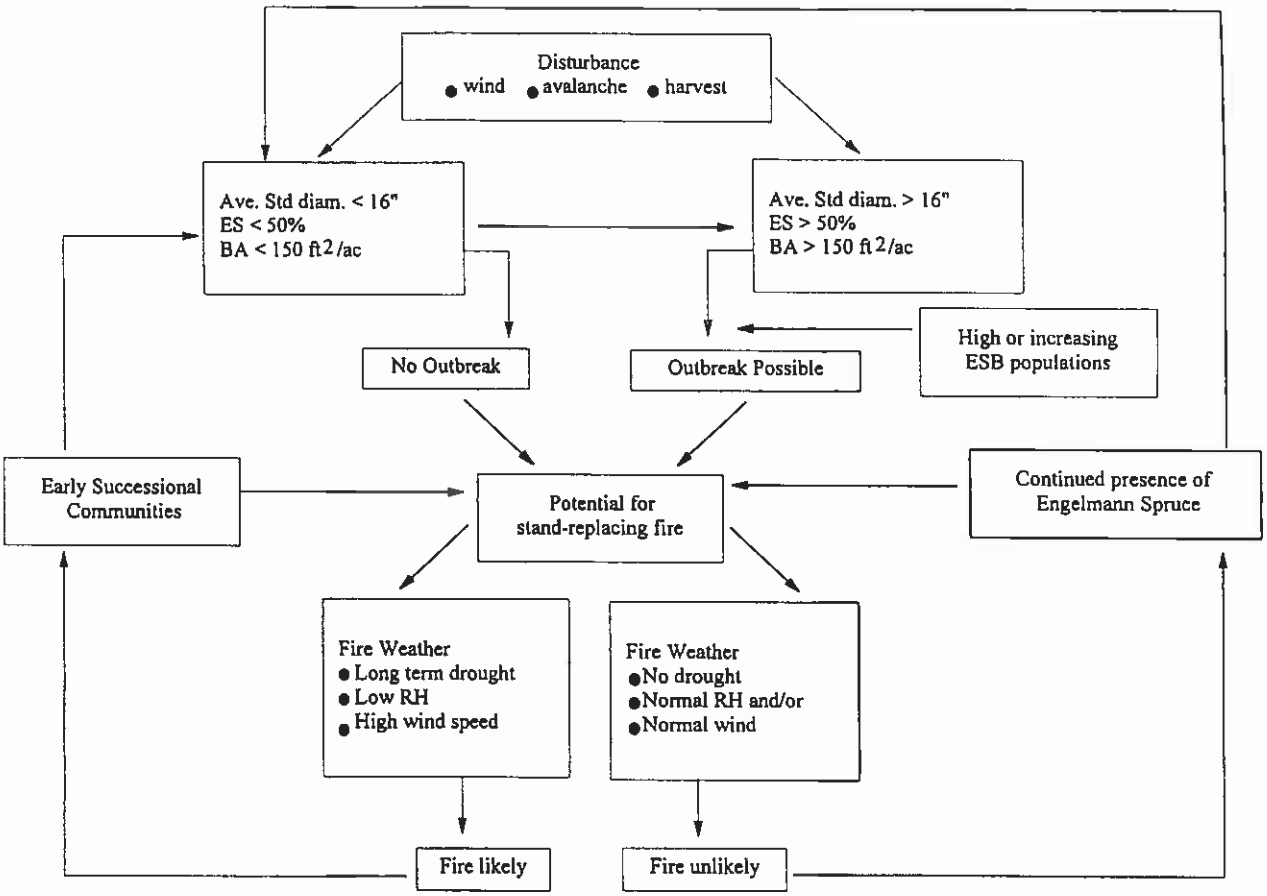

Fig. 6. Conceptual model of the relationship between fire, spruce beetle outbreak and other disturbances in the spruce-fir zone, and their influence on the development of spruce-fir communities (16" = 40 cm; 150 ft²/ac = 34.44 m²/ha). ES=Engelmann spruce, BA=basal area, ESB=Engelmann spruce beetle, RH=relative humidity.

spruce (Schmid and Frye 1977, Veblen et al. 1991). Stands affected by past spruce beetle outbreak generally have a scarcity of spruce older than 140 years, and nonhost species are typically stand dominants (Veblen et al. 1994). The incredible amount of understory release increases the density of post-outbreak stands often resulting in uneven-aged, multistoried stands (Miller 1970, Baker and Veblen 1990, Long 1994).

Mortality caused by spruce beetles also increases fuel loads and stand-replacing fires are possible under the appropriate weather conditions (Schmid and Frye 1977). The accumulation of dead downed and standing woody fuel and the presence of advance regeneration in the understory make stands susceptible to high-intensity fire when fire weather is extreme (Heinselman 1973). After high-intensity fires in spruce-fir stands succession will proceed via early successional communities as described (Figure 1). However, in the climate characteristic of the subalpine zone fire weather is seldom suitable for large fire since the snow-free period can be as short as 2 months. Long-term drought is required to dry large diameter fuels as a prerequisite for high-intensity, stand-replacing fires. Without fire, spruce will be retained on the site and stands will be susceptible to another spruce beetle outbreak in less than 100 years although small outbreaks may occur where large diameter trees persist.

Management Implications

During the 20th century, forest management has used suppression of wildfires as the primary means of addressing perceived negative effects of fire. Forest managers currently recognize the importance of fire for maintaining biological diversity and ecosystem vitality. The exclusion of fire also has resulted in unnaturally high fuel accumulations increasing the potential for large, intense fire in forest communities. Where appropriate, prescribed fire can be used to attain land and resource management objectives including the restoration of historic landscapes, removing hazardous fuels, and increasing the resistance of stands to disease and insect outbreaks (Bradley et al. 1992).

For example, in subalpine forests throughout the Intermountain West, the suppression of fire and other disturbance mechanisms has led to the decline of seral aspen communities and subsequently resulted in the loss of critical wildlife browse and habitat, water yield, visual quality, and recreational opportunities (Loope and Gruell 1973, Jones and DeByle 1985, Bradley et al. 1992). Application of a prescribed fire regime consistent with historic fire behavior would remove decadent aspen and mixed aspen-conifer stands, deter encroachment by late successional species, and promote aspen regeneration with the eventual restoration of aspen to the landscape.

On sites where lodgepole pine is a valuable seral component, prescribed fire has been used successfully in site preparation to promote regeneration following harvest and for fuels reduction (Bradley et al. 1992). Hawksworth and Johnson (1989) suggested using prescribed fire to control lodgepole pine dwarf mistletoe in infested stands. Also, prescribed fire can create a mosaic of varying age classes, and compositional and structural diversity within the landscape that increases the resistance of lodgepole pine stands to mountain pine beetle attack. The patchy mortality in affected stands would not propagate highly destructive fires; thus, moderating insect-fire interaction cycles (Cole 1978).

In spruce-fir communities, the effects of fire suppression on vegetative patterns and dynamics have not been ecologically significant due to the length of the fire-return interval relative to the length of the suppression era. However, spruce beetle outbreaks, windfall, competition-induced mortality, and slow rates of decomposition contribute to naturally heavy loads of downed and dead woody fuels in mature stands (Habeck and Mutch 1973, Bradley et al. 1992). During drought, the large amount of woody fuel combined with deep duff can result in hot, smoldering fire capable of killing Engelmann spruce and subalpine fir. Severe injury to boles and root systems also predisposes spruce and fir to windthrow and windbreak, insect attack, and disease (Alexander 1987). The presence of a dense understory, low tree crowns, and persistent dead branches create fuel ladders that spread fire into tree crowns increasing the likelihood of large, destructive fires (Bradley et al. 1992, Long 1994).

The maintenance of vegetative diversity does not require frequent fires at subalpine elevations (Habeck and Mutch 1973). Prescribed fire can sanitize spruce-fir stands and remove woody fuels, which reduces the fire hazard, although its use necessitates implementing strict control measures to avoid crown scorch and lethal cambium heating and to prevent the loss of regeneration, seed source, and site fertility (Bradley et al. 1992). The goals of perpetuating viable climax spruce-fir communities and providing protection from catastrophic fire may be best accomplished through silvicultural practices rather than prescribed fire. Variations of group selection and shelterwood methods closely simulate the effects of minor canopy disturbances typical in climax spruce-fir communities and are most successful for regeneration. These methods can also create desired age-class, compositional, and structural diversity within stands (Long 1994).

The mechanical removal of dead, woody fuels can reduce immediate fire potential on specific sites. However, long-term programs of fuel management may encompass larger landscapes and mechanical treatments may prove costly, and labor intensive. Perhaps the most ecologically appropriate, inexpensive, and efficient means of fuel management at broader landscape levels is through the prevention of extensive mortality caused by spruce beetle outbreaks.

Spruce beetle control strategies often involve silvicultural treatments, such as thinning, to maintain stand conditions outside the range of spruce beetle susceptibility and to enhance tree vigor. Following harvest, cull logs and tops are scattered or destroyed to eliminate host material (Schmid and Frye 1977). Other strategies include the use of chemical treatments and trap trees (Shea et al. 1988, Johnson 1996).

Perhaps the most important component of spruce beetle management programs is the development of hazard rating systems. Hazard or risk-rating schemes are commonly used to identify variables predisposing stands to bark beetle attack. Utilizing this information provides forest managers with the means to evaluate stand conditions, make predictions of when and where outbreaks are likely to occur, and initiate management practices to prevent outbreaks or decrease mortality.

CONCLUSIONS

The return to Engelmann spruce and subalpine fir dominated communities in the Intermountain spruce-fir zone occurs most rapidly with immediate colonization of the site by these two species after stand-replacing fire. Due to the infrequent occurrence of stand-replacing fire in the spruce-fir zone, disturbances such as low-intensity surface fire, spruce beetle outbreaks, wind, and snow avalanches have primarily influenced vegetative structure, species composition, and successional dynamics in the spruce-fir zone. While fire drives secondary succession back to an earlier stage, disturbances which remove overstory trees, such as bark beetles, can hasten succession by releasing understory Engelmann spruce and subalpine fir.

The development and implementation of prescribed fire regimes for spruce-fir communities requires a more complete understanding of the ecological role of fire and other important disturbances that influence successional pathways in the Intermountain spruce-fir zone and should consider the appropriateness of prescribed fire for achieving desired management objectives and possible ecological outcomes. Understanding these relationships can also be useful for predicting fire potential after a stand-replacing fire.

The perpetuation of viable climax spruce-fir communities protected from catastrophic fire may be best accomplished through silvicultural practices rather than the application of prescribed fire. Spruce beetle management programs may prevent extensive mortality associated with outbreaks and curb the accumulation of dead, woody material in spruce-fir stands providing an ecologically appropriate alternative to prescribed fire and mechanical treatments of these fuels.

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