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Post-Fire Succession and Disturbance Interactions on an Intermountain Subalpine Spruce-Fir Forest

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POST-FIRE SUCCESSION AND DISTURBANCE INTERACTIONS ON AN

INTERMOUNTAIN SUBALPINE SPRUCE-FIR FOREST

by

Christopher A. Dicus

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ABSTRACT

Post-Fire Succession and Disturbance Interactions on an

Intermountain Subalpine Spruce-Fir Forest

by

Christopher A. Dicus, Master of Science

Utah State University, 1995

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Department: Forest Resources

Four general post-fire successional pathways leading to a climax Engelmann

spruce (Picea engelmannii Parry)/subalpine fir (Abies lasiocarpa [Hook] Nutt.) forest

were identified operating on the T.W. Daniel Experimental Forest in northern Utah.

These included initial colonization by seral quaking aspen (Populus tremuloides

Michx.), seral lodgepole pine (Pinus contorta Dougl. ex Loud.), colonization by

lodgepole pine followed by a low intensity surface fire, and immediate colonization by

late successional Engelmann spruce and subalpine fir.

Post-fire establishment of the late successional species occurred earliest in the

Engelmann spruce/subalpine fir pathway followed by the lodgepole pine and lodgepole

pine ground fire pathways, and the quaking aspen pathway. The late successional species

grew fastest in the Engelmann spruce/subalpine fir pathway followed by the quaking aspen, lodgepole pine, and lodgepole pine ground-fire pathways.

Conceptual models were presented showing how perturbations by fire, insect epidemics, and disease could interact to influence succession and shape the subalpine landscape. The subalpine forest changes through time to facilitate different types of disturbance that have varying effects on succession. In the continued suppression of fire, species and age class diversity will be reduced and disturbances may occur that are larger and more intense than those that have occurred historically.

(69 pages)

ACKNOWLEDGMENTS

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Introduction

The Engelmann spruce (Picea engelmannii Parry)/subalpine fir (Abies

lasiocarpa [Hook] Nutt.) forest type is widely distributed from west central British

Columbia to northern California on the Pacific Coast and from southwest Alberta to

northern Arizona and New Mexico in the Rocky Mountains (Alexander 1980). In the

Intermountain region of northern Utah, southern Idaho, and western Wyoming, these

2 species compose the climax forest found on the cool, moist sites found above 2285

m up to timberline near 3355 m (Schimpf et al. 1980, Mauk and Henderson 1984).

These areas characteristically have a high yearly precipitation, generally in the form

of snow, with a July mean temperature of 31°C and a mean January temperature of -

10°C (Alexander 1980). Below 3200 m, lodgepole pine (Pinus contorta Dougl. ex

Loud.) and quaking aspen (Populus tremuloides Michx.) are common seral associates,

and at the lower elevations and drier sites of the Engelmann spruce/subalpine fir

range, Douglas-fir (Pseudotsuga menziesii [Mirb] Franco) may be found intermixed

with this type (Mauk and Henderson 1984). The T.W. Daniel Experimental Forest,

located in northwestern Utah, with an elevation of 2377 m to 2651 m, serves as an

excellent example of an Intermountain subalpine Engelmann spruce/subalpine fir

forest.

The Intermountain subalpine forest is a dynamic area where natural

successional turnover drives the landscape through time to a stable climax community

of shade-tolerant Engelmann spruce and subalpine fir. Natural perturbations such as

snow avalanches, insect and pathogen outbreaks, wind events, and fire drive the system in a variety of ways. Fire has directly or indirectly shaped the majority of current vegetation in the Intermountain West (Billings 1969, Loope 1971, Romme and Knight 1981, Peet 1988).

In subalpine forests, fires are generally large, long return interval, high-intensity crown fires (Billings 1969, Loope 1971, Arno 1980, Romme 1980). Lightning commonly strikes trees in the subalpine zone, but because of the characteristic low temperatures and high moisture found at this elevation, it is common for a fire to be limited to a single tree or small group of trees, causing little effect on the landscape level (Gabriel 1976, Arno 1980, Romme 1980).

The same climatic conditions that deter fire indirectly prepare stands for a large stand-replacing fire. In subalpine forests, decomposition proceeds at a slower rate than does litter accumulation (Lotan et al. 1978), thereby causing fuel buildup through time. In prolonged drought periods, with associated high temperatures and low relative humidity, the potential exists for a high-intensity stand-replacing fire.

The frequency of stand-replacing fires in subalpine forests is controlled primarily by the time needed to create a suitable fuel complex to sustain a conflagration (Romme 1982), and is a function of many factors, including elevation and site potential (Romme 1980). In the absence of other types of disturbance, lower elevation sites support a longer growing season and subsequently accumulate high fuel loads in shorter time than do the upper elevations, which may be limited to a growing season of 1 mo a year (Wardle 1968).

Mean fire-return intervals are the average time between fires on a given parcel of land. Arno (1980) found a mean fire-return interval of 22-150 yr on lower elevation, high-production subalpine sites in the northern Rockies, while Romme (1982) estimated a mean fire-return interval of 300-400 yr in a higher, less productive area in Yellowstone National Park. Some high-elevation sites may experience no fire at all for several thousand years due to lack of fuels and an environment that is not conducive to fire spread (Billings 1969). Wadleigh and Jenkins (in press) estimated a presettlement mean fire-return interval on the T.W. Daniel Experimental Forest of 39 yr in the lodgepole pine forest type, 156 yr in the quaking aspen forest type, and no fire in the Engelmann spruce/subalpine fir type. However, because fire in the quaking aspen and Engelmann spruce/subalpine fir forest types rarely leaves physical evidence due to total tree consumption, the mean fire-return intervals for these 2 forest cover types on the Daniel Experimental Forest required further study.

A lightning ignition may occur directly in the subalpine forest, but often starts in the drier, lower elevation, montane Douglas-fir forest, and then increases in intensity and spreads into the subalpine zone.

Successional Pathways

Schimpf et al. (1980) suggested 3 alternative successional pathways initiated by a disturbance, commonly fire, which may lead to an Engelmann spruce/subalpine fir-dominated forest in the Intermountain subalpine zone (Figure 1). Pathway 3 represents Engelmann spruce and subalpine fir colonization on a burned site without
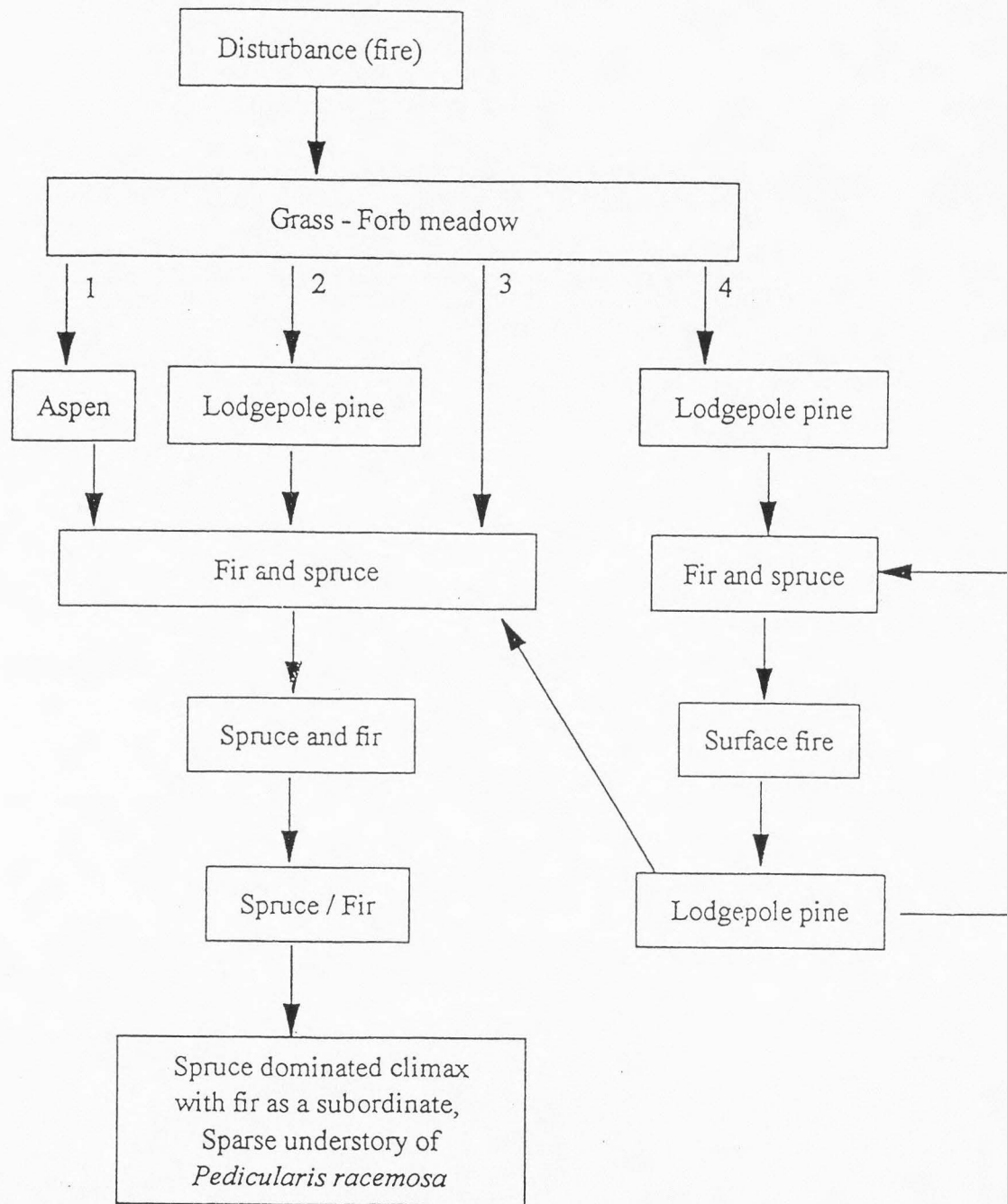
Figure 1. Post-fire successional pathways operating on the T.W. Daniel Experimental Forest. Modified from Schimpf et al. 1980.

facilitation by a seral stand of quaking aspen, pathway 1, or lodgepole pine, pathway 2.

These successional pathways assume that all disturbance by fire reinitiates secondary succession. However, in lodgepole pine stands, low-intensity surface fires may consume understory Engelmann spruce and subalpine fir while leaving little residual damage to the overstory (Loope and Gruell 1973, Arno 1976, Gabriel 1976). This successional scenario creates a different environment for eventual Engelmann spruce and subalpine fir germination on the T.W. Daniel Experimental Forest (Wadleigh and Jenkins in press) and should be included as a separate successional pathway, hereafter referred to as the lodgepole pine groundfire successional pathway, pathway 4 (Figure 1). Schimpf et al. (1980) also described a successional pathway in which fire has played no significant role and is therefore not included in the post-fire successional pathways model (Figure 1). This pathway, where quaking aspen invades a long persisting meadow through suckering, will be referred to as pathway 5.

The very characteristics of a fire (size, severity, timing, etc.) initially affect succession (Pickett et al. 1987a). The environment created after stand-consuming fires in the subalpine zone of the Intermountain West generally inhibits colonization by late successional Engelmann spruce and subalpine fir. Subalpine fir is better able to withstand the harshness of a newly burned site than Engelmann spruce because of its ability to establish a more hardy root system (Knapp and Smith 1982, Alexander et al. 1984).

Pathway 3 of the conceptual successional model (Figure 1) represents post-fire colonization of the site by the late successional species, Engelmann spruce and subalpine fir, but this is rare. The 3 requirements for natural regeneration of a tree species are 1) adequate seed supply, 2) suitable seedbed, and 3) an environment conducive to both germination and survival (Roe et al. 1970). Some Engelmann spruce and subalpine fir may survive a fire due to variability in fire behavior and provide a seed supply for the fire-created ash seedbed, which does not deter Engelmann spruce and subalpine fir regeneration (Woodard and Cummins 1987). However, the post-fire environment would hinder Engelmann spruce and subalpine fir establishment through competition with pioneering herbs and shrubs (Alexander 1974). Post-fire site conditions deter immediate colonization of Engelmann spruce and subalpine fir by many environmental means, including temperature extremes (Hellmers et al. 1970, Alexander 1974, 1984), intense solar radiation, which inhibits the photosynthetic mechanism (Ronco 1970), and nighttime frost and freezing damage (Wardle 1968, Alexander 1984, Alexander and Shepperd 1990). Also, canopy removal by fire reduces shade and promotes desiccating winds, which indirectly increase water loss from the soil and seedlings (Alexander 1984, Daly and Shankman 1985).

Engelmann spruce and subalpine fir can regenerate under such conditions, however, if adequate woody material remains after a fire to create a protective microsite (Schimpf et al. 1980). Subalpine fir tolerates a wider range of site conditions than Engelmann spruce and is more likely to immediately establish on a

post-fire site (Fowells 1965). However, Engelmann spruce have colonized sites in small numbers immediately after a fire on extremely harsh south slopes near timberline (Day 1972, Shankman 1984). The ability to regenerate on such sites can be attributed to the presence of favorable microsites created by standing dead trees that provided shelter by reducing light intensity, lowering soil surface temperature, and conserving soil moisture (Alexander 1974).

The environment for Engelmann spruce and subalpine fir establishment is often ameliorated by a seral stage of quaking aspen or lodgepole pine that buffers the environmental extremes that deter the late successional species. A seral stand of quaking aspen or lodgepole pine reduces incoming solar insolation and subsequent high soil temperatures, prevents desiccating winds, minimizes temperature extremes, and reduces vapor pressure deficits.

Pathway 1 of the conceptual successional model represents initial colonization by quaking aspen after fire (Figure 1). Quaking aspen is the most widely distributed tree in North America (Harlow et al. 1979) and is found throughout the T.W. Daniel Experimental Forest in both pure and mixed stands with conifers (Wadleigh-Anhold 1988). Quaking aspen is noted for its ability to sucker, especially after a disturbance such as fire. Most even-aged quaking aspen stands in the West are the direct result of fire (Jones and Debyle 1985). Almost any segment on a quaking aspen root, except newly formed root parts, can sucker (Sandberg 1951). Although quaking aspen does not readily burn, even a light surface fire can kill quaking aspen because of its extremely thin bark (Jones and Debyle 1985). A fire intense enough to kill the

quaking aspen overstory will stimulate abundant suckering. Up to 120,000 suckers/ha were produced after burning sites in western Wyoming (Bartos 1979). A new quaking aspen stand is commonly regenerated after a high-intensity fire even in stands where quaking aspen is a minor component of a conifer stand (Patton and Avant 1970, Jones and Trujillo 1975). When a healthy quaking aspen component is present, it will monopolize a site after a stand-replacing fire through prolific suckering (Stahelin 1943).

Fire suppression policies since the early 1900's caused a dramatic decline in the abundance of quaking aspen in the western United States and Canada. Although seed production is generally adequate, the exacting seedling survival requirements of quaking aspen are such that, in the West, the species cannot establish by seed. Therefore, quaking aspen relies primarily on suckering after fire to perpetuate its existence on a site (McDonough 1985). Fire frequency in the quaking aspen forest type was generally 50-100 yr (Hendrickson 1972). However, because quaking aspen does not readily burn, few extensive fires in this forest type have occurred since the fire suppression era began (Heinselman 1981). Ryan (1976) noted that in a 14-yr period on National Forests in Colorado, only 0.28% of the total quaking aspen acreage annually burned. On the Daniel Experimental Forest, there have not been extensive fires since 1903 (Wadleigh and Jenkins in press). In Utah, quaking aspen matures in 60-80 yr, followed by a rapid decline in vigor and increased susceptibility to disease (Schier 1975). Mueggler (1989) found that almost 66% of the aspen stands in the Intermountain West exceed 95 yr of age. Aspen clones that are replaced by

conifers or that are represented only by scattered, overmature trees are lost (Loope 1971, Houston 1973). With the virtual elimination of natural fire in the quaking aspen forest type, loss of this species in many parts of the West is possible.

Pathway 2 of the conceptual successional model represents colonization by lodgepole pine (Figure 1). Where quaking aspen is not present and a supply of lodgepole pine seed is available, lodgepole pine is often the initial colonizer on a burned site because of cone serotiny, a condition in which cones do not open at maturity due to a resinous bond between cone scales (Lotan and Critchfield 1990). Lodgepole pine seeds may be stored for many years in serotinous cones, and when the heat from a fire breaks the resinous bond, millions of seeds per hectare may be released (Spurr and Barnes 1980). The level of cone serotiny varies and many stands have very low percentages of serotinous cones (Lotan and Critchfield 1990). However, even in areas of low cone serotiny such as the Daniel Experimental Forest, lodgepole pine is able to successfully regenerate after a fire due to its germanitive energy, early rapid growth, and ability to withstand many different microsite conditions (Lotan 1976). Lodgepole pine is very intolerant of shade and best germination occurs in full sunlight on sites free of competing vegetation (Lotan and Critchfield 1990). Fire frequency and intensity will often determine how long lodgepole pine remains on a site. After a post-fire lodgepole pine stand is established, a second fire within 25 yr may prohibit reestablishment and create a persistent meadow in the absence of quaking aspen because there may not be adequate time for lodgepole pine seed to be produced (Wellner 1970). If the frequency

between fires is too long, late successional, shade-tolerant Engelmann spruce and subalpine fir will establish in the understory, and eventually dominate the site, forming a climax community at the expense of the shade-intolerant lodgepole pine. High-intensity fires that occur before complete successional turnover to Engelmann spruce and subalpine fir would generally facilitate a subsequent lodgepole pine stand due to cone serotiny and the aggressive pioneering nature of lodgepole pine.

Pathway 4 of the conceptual successional model (Figure 1) represents the scenario in which a high-intensity fire initiates a lodgepole pine stand and is followed by a low-intensity surface fire that destroys the understory of late successional Engelmann spruce and subalpine fir while causing little damage to the existing lodgepole pine overstory. Regular, low-intensity surface fires may indefinitely prolong the existence of a mature lodgepole pine overstory on a site due to the elimination of competition by the shade-tolerant species and by breaking the vertical and horizontal continuity of fuels needed for a high-intensity stand-replacing fire. Periodic low-intensity fires have been shown to prevent the establishment of Engelmann spruce and subalpine fir on a site (Gabriel 1976). A lodgepole pine stand that has experienced a low-intensity surface fire may exist for many years before the fuel necessary to sustain a high-intensity stand-replacing fire is produced (Muraro 1971). In the absence of fire, Engelmann spruce and subalpine fir will eventually dominate the site as the stable climax forest.

Pathway 5, not included in the post-fire successional pathways model (Figure 1), represents the successional scenario in which a long persisting meadow exists and

is invaded on its fringes by quaking aspen, which is subsequently invaded by late successional shade-tolerant Engelmann spruce and subalpine fir. Meadows experience higher soil temperatures than do adjacent forested stands due to the greater amount of incoming solar insolation striking the meadow floor. Unshaded soil temperatures have been found to be over 50°C higher than adjacent shaded soils (Alexander 1984). A higher soil temperature may cause a few quaking aspen suckers to annually arise from a fringe clone, which would extend the boundaries of the clone into the long persisting meadow (Zasada and Schier 1973). Schimpf et al. (1980) found that on the T.W. Daniel Experimental Forest, quaking aspen extended its boundaries into long persisting meadows at a mean rate of 19 cm/yr and in 20 yr was subsequently invaded by the late successional conifers, which assumed dominance on the site in 100-150 yr. This successional pathway allows quaking aspen to persist under the lengthened fire-return intervals of the fire suppression era.

There is much debate as to what will occur on a site over time in the absence of a large-scale fire once Engelmann spruce and subalpine fir have excluded quaking aspen and lodgepole pine from a site through natural successional turnover. Commonly in a mature Engelmann spruce/subalpine fir forest, Engelmann spruce is represented by fewer, but larger and older trees than subalpine fir (Oosting and Reed 1952). Engelmann spruce characteristically forms the majority of the main upper canopy while subalpine fir dominates the subcanopy and understory (Mauk and Henderson 1984).

Subalpine fir has less demanding site requirements and a much greater understory representation than Engelmann spruce, and some believe that it will eventually displace Engelmann spruce from a site in the absence of a stand-replacing fire (Daubenmirer and Daubenmirer 1968, Day 1972, Peet 1981). Others concluded that due to Engelmann spruce longevity, it will dominate a site over time (Alexander 1974). It is unlikely, however, that a large enough period of time free of a large-scale disturbance will ever occur in the Intermountain subalpine zone to test either hypothesis (Peet 1981).

Current thought is that Engelmann spruce and subalpine fir are able to coexist indefinitely in the climax state (Shea 1985, Aplet et al. 1988, 1989). As Engelmann spruce and subalpine fir initially come to dominance in a stand following either immediate post-fire colonization or after a seral quaking aspen or lodgepole pine stage (Figure 1), Engelmann spruce enters into a state of recruitment exclusion, which subalpine fir does not experience (Aplet et al. 1988). Subalpine fir commonly has a greater representation in all size and age classes at this time, and the species enters into a period of dominance in the stand during this Engelmann spruce exclusion phase (Aplet et al. 1989).

An Engelmann spruce reinitiation phase follows in which small-scale disturbances, usually due to subalpine fir mortality, open gaps in the stand that provide a suitable microsite for Engelmann spruce establishment (Aplet et al. 1989). The Engelmann spruce reinitiation phase generally coincides with heavy mortality of subalpine fir caused by either old age or by other small-scale perturbations (Aplet et

al. 1989). Although subalpine fir can germinate in most understory conditions, Engelmann spruce is often able to exclude establishment of subalpine fir on the upturned mineral soil caused by tree fall (Shea 1985).

Engelmann spruce, the longer lived species, matures and grows to the large size characteristically found in old growth stands. Subalpine fir continues to persist on the site by reproducing in the understory and by being released upon the death of dominant or codominant trees. The death of a dominant or codominant tree consequently provides new microsites for Engelmann spruce establishment. Over time, the 2 late successional species are able to coexist due to the greater longevity of Engelmann spruce, subalpine fir's less demanding site requirements, and small-scale disturbance, which perpetuate Engelmann spruce establishment.

Subalpine Disturbance Regime

The subalpine forest of the Intermountain West is a dynamic system with numerous perturbations, including fire, insects, avalanches, diseases, wind events, and others, which advance mortality in individual or stands of trees. While these disturbances are detrimental to the individuals affected, they individually and collectively shape the landscape into a diverse mosaic and thereby insure ecosystem stability. Disturbances are a natural part of ecosystems and in the subalpine forest have varying effects dependent of the size, intensity, frequency, and hierarchal level being examined (Pickett et al. 1989). Small disturbances such as tree windthrow create small patches that provide microsites for new tree regeneration. Large-scale

disturbances such as conflagration forest fires shape the landscape into a mosaic of species and age classes.

In subalpine forests, the type of disturbance can be more important than the size (Veblen et al. 1991a). On the landscape level, only a conflagration fire that consumes stands of trees acts to completely reinitiate secondary succession (Veblen et al. 1989, 1991a). All other disturbances in subalpine forests generally affect only the overstory species, not the shade-tolerant understory Engelmann spruce and subalpine fir.

For example, quaking aspen are frequently subject to heart rot disease, most commonly Phellinus tremulae ([Bond.] Bond. & Boriss.). In one study, which encompassed five national forests in Colorado (Davidson et al. 1959), 53% of the aspen sampled were infected with bole decay. This disease is common in most stands on the Daniel Experimental Forest. The disease will weaken the overstory quaking aspen and hasten the stand's mortality, which subsequently releases the shade-tolerant Engelmann spruce and subalpine fir.

A similar situation would occur in a lodgepole pine stand if the overstory is attacked by the mountain pine beetle (Dendroctonus ponderosae Hopkins) (Coleoptera: Scolytidae). Lodgepole pine trees, located at low to mid elevations within the subalpine zone, over 80 yr of age, and greater than 20 cm diameter at breast height (1.37 m) tend to be most susceptible to the mountain pine beetle (Amman et al. 1977). The vast majority of lodgepole pine stands located on the Daniel Experimental Forest lie within the range of high susceptibility.

In old growth Engelmann spruce and subalpine fir stands, disturbance other than fire serves to perpetuate the existence of Engelmann spruce and subalpine fir. Windthrow, typically a frequent, low-intensity disturbance, becomes more important as trees get older (Veblen 1991a). Subalpine fir, which already has a greater susceptibility to windthrow than Engelmann spruce (Veblen 1986), is further susceptible when weakened by the annosum root disease (Heterobasidion annosum [Fr.] Bref.), common on the Daniel Experimental Forest. When trees fall due to windthrow, the abundant subalpine fir is released and new microsites for Engelmann spruce germination are provided.

These disturbances act only as a release mechanism for the shade-tolerant Engelmann spruce and subalpine fir and therefore serve to hasten succession rather than reinitiate it (Veblen et al. 1989). The species in the understory will quickly dominate the site after all disturbances except for a large stand-replacing fire (Veblen et al. 1991b). However, all disturbances that hasten succession also facilitate successional reinitiation by a stand-replacing fire through deposition of large amounts of fuel in short amounts of time.

In subalpine forests, a disturbance seldom acts alone. Rather, a particular disturbance modifies the environment so as to make a site susceptible to other forms of disturbance. For example, wind events can be detrimental to overstory trees by the breaking of limbs and boles. During storms, small quaking aspen roots may be broken through twisting and bending and thereby provide an entrance corridor for

subsequent root pathogens (Basham 1958). These same root pathogens then work to further tree susceptibility to future windthrow.

In some lodgepole pine forests, there exists a relationship between fire, root pathogens, and the mountain pine beetle (Gara et al. 1984a). Low-intensity surface fires in the lodgepole pine forest type scar trees, which thereby promotes fungal entry. Trees that have root damage caused by smoldering logs are more susceptible to the pathogens than are those with a typical tapering bole scar (Gara et al. 1986). In time, trees with fires scars, regardless of diameter, are preferentially attacked by the mountain pine beetle (Geiszler et al. 1980). Those with both a fire scar and root pathogen are particularly susceptible (Gara et al. 1984a, 1984b). If there are enough damaged trees, beetle populations may become epidemic and destroy vast acreage of the lodgepole pine forest and consequently provide the fuel needed for another fire to repeat the cycle (Gara et al. 1984a, Geiszler et al. 1984).

In an old growth Engelmann spruce/subalpine forest, a major windthrow event could occur in which large numbers of trees are affected. Engelmann spruce bark beetle (D. rufipennis Kirby), which are attracted to weakened trees, may become epidemic and destroy all Engelmann spruce larger than 10 cm diameter at breast height over thousands of hectares (Schmid and Frye 1977). Because subalpine fir often has a greater representation in the understory, there will be a quick shift to an subalpine fir-dominated forest (Veblen et al. 1991b). The Engelmann spruce bark beetle also serves as an agent to facilitate the buildup of fuel necessary for a conflagration fire.

A fire may enhance or deter an epidemic beetle population depending on its intensity. If a fire is able to damage many trees but not consume them, the damaged trees may be the focal point of an initial bark beetle epidemic much in the same way as the lodgepole pine example. However, stand-replacing fires act as a mechanism to limit beetle infestations by creating stands of younger Engelmann spruce on the landscape which are not affected by beetle epidemics, thereby insuring species survival. A fire-induced landscape then can inhibit insect epidemic populations by providing a diversity of species and age classes.

All disturbances in subalpine forests that act as a mechanism to remove standing trees from steep slopes also create conditions that enhance snow avalanches (McClung and Schaerer 1993). Avalanche zones, like fire and insect epidemics, act as a source for diversity in the landscape and once a path is created, avalanches often occur yearly (Veblen et al. 1994). Avalanche zones act as a fire break by keeping these areas free of fuel by periodically removing large plant life. Avalanches can also facilitate insect epidemics by creating a large debris pile of slash, which provides bark beetles and engraver beetles (Ips sp.) (Coleoptera: Scolytidae) with a favorable environment in which to breed. Epidemic populations may then attack healthy trees outside the avalanche zone. However, small trees that survive in the avalanche zone would not be affected by a beetle epidemic because they would be killed before they grow large enough to be attractive to the beetles (Veblen et al. 1994).

The types, sizes, and frequencies of disturbances in the subalpine zone are greatly affected by stand elevation and topography. Both stand-replacing and low-

intensity surface fires occur most frequently at lower elevations, except in bottoms, due to shorter fuel accumulation periods, higher temperatures, and lower relative humidities (Romme 1980, 1982). The mountain pine beetle, which hastens succession while simultaneously depositing fuels for subsequent fires, is more important at the lower elevations and will not exist at all in the upper elevation where there is no host (Amman et al. 1977). Wind events become much more important at the higher elevations where trees come to exist only in a krumholz form. At high elevations where the forest is not continuous, fire can indirectly adjust wind patterns through tree removal. Subsequent changes in snow drifts can kill trees not directly affected by the fire and create tundra conditions that can last for centuries (Billings 1969).

Disturbances in the subalpine forest, then, rarely act alone. Rather, there are complex interrelationships involved between the timing and type of disturbances, and in the absence of disturbance the landscape is modified to facilitate future perturbations by fire, insects, or disease, thereby maintaining a diverse patchwork mosaic.

Policy Concerns

Disturbance, particularly fire, has shaped the Intermountain subalpine landscape. Lightning has served as a natural ignition in the past (Komarek 1967, Taylor 1971, Heinselman 1981) and the historical role of anthropogenic ignitions on forest communities is documented (Lewis 1973, Barrett and Arno 1982, Pyne 1984). However, for many reasons, including fear surrounding catastrophic wildfires that

occurred in the late nineteenth and early twentieth centuries, fire became regarded as an unnecessary evil to be suppressed at all cost (Lotan 1979). While suppression has helped protect human life and property, complete fire exclusion through time has not allowed natural landscape development and therefore has had many negative effects.

Landscapes have lost diversity through natural successional processes, although the upper elevations of the subalpine zone may have experienced less of an impact of fire exclusion due to the extremely slow growth found there (Fahnestock 1976, Romme 1982). Because of a lack of diversity, forest communities have become more susceptible to massive insect epidemics covering areas far larger than most fire boundaries would attain. Fire suppression has also led to a buildup of fuels (Dodge 1972), allowing fires which do occur to become larger and more expensive to contain (Mutch 1994). Total fire exclusion, then, has served to deteriorate forest health over much of the Intermountain West.

Ecosystem management is the current philosophy of federal land management agencies on public lands. Ecosystem management requires that land mangers account for cultural, social, biological, and economical aspects in any management decision. It has forced land managers to become aware of the natural role of perturbations on landscape dynamics and forest health and allows fire to play a more active role in natural systems. While the role of natural fire has been lauded recently, many public land managers are still unwilling to take the potential political risks involved in using fire as a tool. Meanwhile, though, ecosystem diversity and forest health continue to decline.

The implementation of a management option called prescribed natural fire within national parks and designated wilderness areas has been a positive step in restoring fire's natural role. This management option allows fires started from a natural ignition to burn under strict prescription parameters. The subalpine zone has been called on as a starting point to implement a prescribed natural fire policy because fuel accumulation is slower over time and large geographical areas of relatively untouched landscape remain.

In areas outside of designated wilderness and parks, the use of manager-ignited fires to create landscape diversity and reduce unnaturally high, dangerous fuel loads is a management option. Manager-ignited fires, however, should be implemented on the landscape level instead of the traditional stand-by-stand approach and should coincide with natural fire regimes (Mutch 1994).

Where prescribed fire is not an acceptable management option due to smoke, water quality, timber values, visual impairments, or other concerns, different types of land use techniques such as small logging operations could be used to mimic natural fire processes. Also a current management option that is being utilized more frequently is fire containment rather than total fire control during suppression efforts. This allows for more ecosystem diversity as well as lowering suppression costs.

Lodgepole pine and quaking aspen are fire dependant species and much more attention has been directed to their relationship with fire than the effects of fire on the late successional subalpine fir and Engelmann spruce. Lodgepole pine and quaking aspen stands are initiated soon after a disturbance. These species are more convenient

to study during early secondary succession than Engelmann spruce and subalpine fir, which require longer post disturbance intervals to become established on a site.

In any land management decision, a solid foundational knowledge is paramount. Less is known about subalpine forests than other areas in the Intermountain West due to lack of commercial importance, short field seasons due to snow, and little access from roads due to terrain or political boundaries. The decision by land management agencies to allow fire to play a more natural role requires additional knowledge of fire effects and exclusion in the subalpine forest.

INTRODUCTION

The subalpine Engelmann spruce (Picea engelmannii Parry)/subalpine fir (Abies lasiocarpa [Hook] Nutt.) forest type is widely distributed from west central British Columbia to northern California on the Pacific Coast and from southwest Alberta to northern Arizona and New Mexico in the Rocky Mountains (Alexander 1980). In the Intermountain West, these 2 species compose the climax forest found on cool, moist sites above 2285 m to timberline near 3355 m (Schimpf et al. 1980, Mauk and Henderson 1984). Below 3200 m, lodgepole pine (Pinus contorta Dougl. ex Loud.) and quaking aspen (Populus tremuloides Michx.) are common seral associates, and at the lower elevations and drier sites of the Engelmann spruce/subalpine fir range, Douglas-fir (Pseudotsuga menziesii [Mirb] Franco) may be found intermixed with this type (Mauk and Henderson 1984).

The Intermountain subalpine forest is a dynamic system where natural successional turnover drives the landscape through time to a stable climax of shade-tolerant Engelmann spruce and subalpine fir. Natural perturbations by insects, disease pathogens, wind, snow avalanches, and fire influence the system in a variety of ways. Fire, directly or indirectly, has shaped the majority of current vegetation in the West (Billings 1969, Loope 1971, Romme and Knight 1981, Peet 1988).

In the Intermountain subalpine zone, fires are generally large, long return interval, high-intensity crown fires (Billings 1969, Loope 1971, Arno 1980, Romme 1980). There are 4 general post-fire successional pathways that may follow such an

event, each with differing successional dynamics. These include initial colonization by a seral stage of either quaking aspen or lodgepole pine, or immediate post-fire colonization by the late successional species, each leading toward shade-tolerant, late successional Engelmann spruce and subalpine fir (Schimpf et al. 1980) (Figure 1). In addition, low intensity surface fires may occur under a lodgepole pine canopy, which temporarily delays natural turnover to the late successional species by consuming understory Engelmann spruce and subalpine fir while leaving little residual damage to the overstory (Loope and Gruell 1973, Arno 1976, Gabriel 1976).

Fire suppression policies implemented in the early 1900's have been effective at protecting human life and property. However, complete fire exclusion has had many negative effects through time, particularly loss of landscape diversity that may facilitate other types of disturbance such as insect epidemics (Amman et al. 1977).

Ecosystem management is the current philosophy of federal land management agencies on public lands (Robertson 1992). This philosophy has focused attention on the natural role of disturbance in natural systems on the landscape scale. Less is known about disturbance regimes of the subalpine zone than other areas in the Intermountain West, and increased knowledge of fire effects and the impacts of fire exclusion in the subalpine zone is needed.

The objective of this study was to investigate succession following stand-replacing fires in subalpine Engelmann spruce/subalpine fir forests by determining the timing of establishment and growth of late successional Engelmann spruce and

subalpine fir. The effects of varying fire regimes and the interrelationships of other

perturbations on natural succession were also examined.

METHODS

Study Site

The study was conducted on the T.W. Daniel Experimental Forest located approximately 40 km east of Logan, Utah. The Daniel Forest is a typical Intermountain subalpine forest with an elevation from 2377 m to 2651 m. The site annually receives over 100 cm of precipitation, usually in the form of snow, with drifts remaining in scattered pockets until late June. Average monthly temperatures range from a January low of -11°C to an August high of 17°C (Hart and Lomas 1979).

The Daniel Forest contains stands of late successional Engelmann spruce and subalpine fir scattered with subalpine meadows and seral stands of quaking aspen and lodgepole pine. The habitat type on most of the Daniel Forest is <u>Abies lasiocarpa/Pedicularis racemosa</u> (ABLA/PERA) (Schimpf et al. 1980) and all data were collected in this type.

For purposes of this study, 4 successional pathways following stand-replacing fires were defined (Figure 1). Pathways 1 and 2 represent post-fire colonization by seral quaking aspen and lodgepole pine, respectively, followed by shade-tolerant, late successional Engelmann spruce and subalpine fir. Pathway 3 represents immediate post-fire colonization by the late successional species. Pathway 4 represents initial post-fire colonization by lodgepole pine followed in time by a low-intensity surface

fire that consumes understory Engelmann spruce and subalpine fir while leaving little residual damage to the lodgepole pine overstory.

Wadleigh and Jenkins (*in press*) produced a fire history and stand map of the Daniel Forest and their data were used to find sites for the present study. Appropriate study sites consisted of stands of quaking aspen, lodgepole pine, or Engelmann spruce and subalpine fir that 1) were initiated by a stand-replacing fire between 1890 and 1903 and 2) displayed the characteristics of a single post-fire successional pathway (Figure 1). Two lodgepole pine stands initiated by a stand-replacing fire in 1847 and 1860 and that experienced a light surface fire between 1890 and 1903 were also examined. One quaking aspen stand sampled was not within Wadleigh and Jenkins' (*in press*) study area, so a fire history was conducted of that stand using methods described by Arno and Sneck (1977).

Sampling

Three to four 1/25 ha plots were randomly established in each of 2-3 stands for each of the 4 post-fire successional pathways. Four plots in each stand were established in 1993, but upon further statistical consultation the number was reduced to 3 plots in each stand during the 1994 field season. Three stands each of fire-initiated Engelmann spruce and subalpine fir, quaking aspen, and lodgepole pine were examined, while only 2 stands of older lodgepole pine that experienced a surface fire between 1890 and 1903 were examined due to lack of stands of this type found on the Daniel Forest.

At each plot center, a 3.5 basal area factor prism was used to insure that at least 80% of the surrounding overstory basal area represented the intended successional pathway to be examined. Aspect, slope, and basal area by species were determined at each plot to assist in accounting for variability between plots. Tree height and diameter at breast height (DBH) (1.37 m) were measured for every tree within each plot. Trees under 20 cm, however, were not tallied because of the high mortality experienced by Engelmann spruce trees younger than 5 yr (Alexander 1984) and therefore data were generally limited to the first 80 yr after a fire.

All Engelmann spruce and subalpine fir trees large enough to be sampled by an increment borer were cored at stump height and their cores were glued to storage boards for later aging under a microscope. Cross sections of all Engelmann spruce and subalpine fir not large enough to be cored were obtained by clipping or sawing at stump height and stored for later aging. Seral quaking aspen and lodgepole pine stands generally result from stand-replacing fires and are, therefore, even aged (Loope 1971). A subsample of 10 overstory trees in each plot representing these types of stands was aged to insure the plot was within a desired fire boundary. Age of lodgepole pine trees was determined by cores taken at stump height. Age of quaking aspen trees was determined by cores taken at breast height with 5 yr added to the ring count (Jones 1967) due to the abundance of heart rot often found low in the bole.

RESULTS

Data for each post-fire successional pathway were pooled after preliminary analysis showed little difference between stands of the same pathway. The timing of Engelmann spruce and subalpine fir establishment differed between the 4 post-fire successional pathways. Figures 2 and 3 show the years required for post-fire establishment of Engelmann spruce and subalpine fir, respectively, in each successional pathway. In the Engelmann spruce/subalpine fir pathway, both species established in large numbers within 30 yr after a fire, then tapered off dramatically as trees grew and limited available space. Engelmann spruce and subalpine fir in the lodgepole pine and lodgepole pine ground fire pathways established in fairly consistent numbers through time, but there were greater numbers of the late successional species present in the lodgepole pine pathway. In the quaking aspen pathway, however, Engelmann spruce and subalpine fir establishment was delayed until later in the stand's life. Establishment of both species in the quaking aspen pathway was very low until 15 yr after a fire and both species established in large numbers around 70 yr after a fire.

The difference in years required for post-fire establishment of Engelmann spruce and subalpine fir is expressed by a cumulative frequency distribution of the percent of current Engelmann spruce and subalpine fir that had germinated in successive 5-yr periods following a fire (Figures 4 and 5). For example, in the Engelmann spruce/subalpine fir pathway, 50% of the late successional species

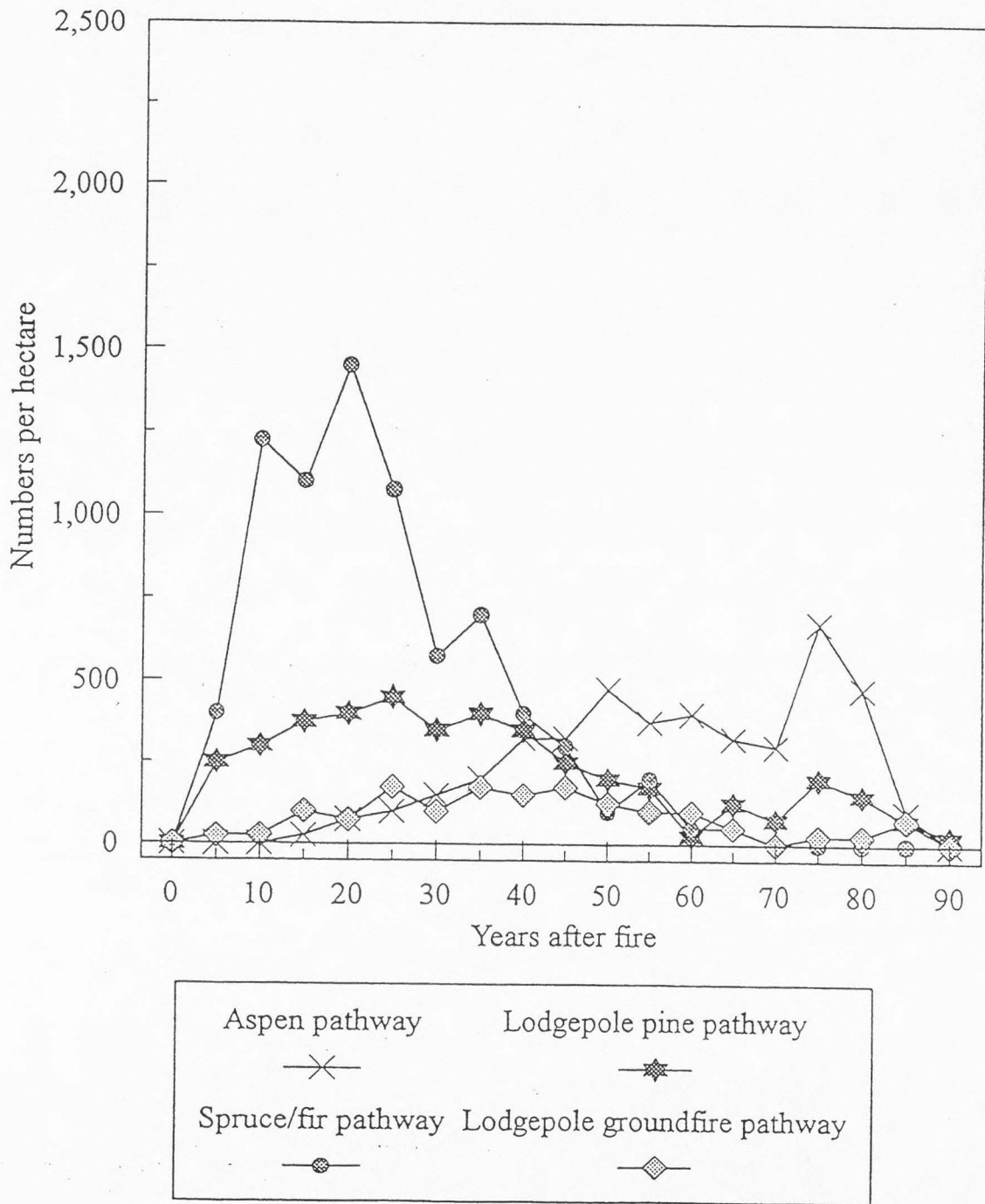Figure 2. Engelmann spruce establishment in each 5-yr period following fire.
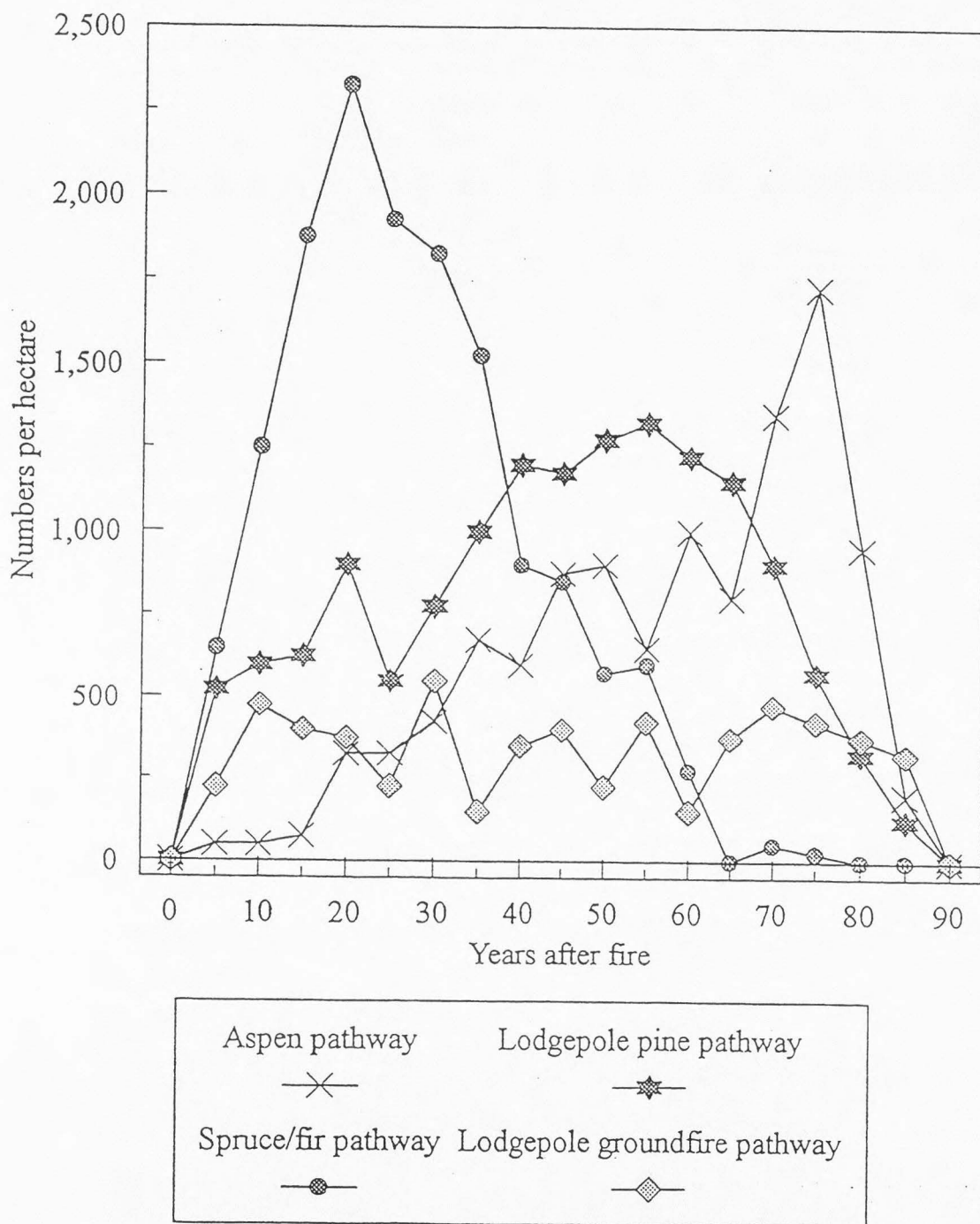
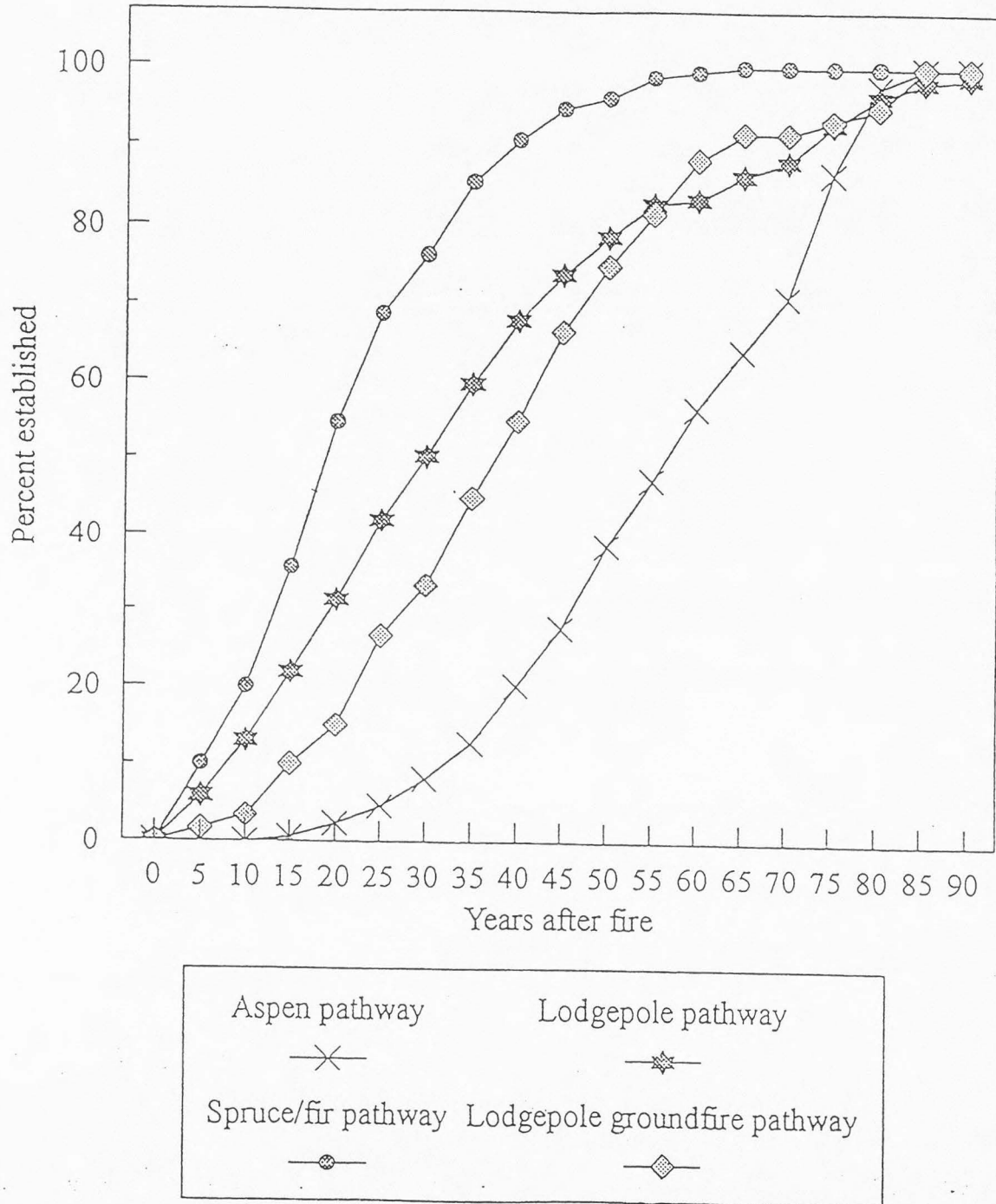Figure 3. Subalpine fir establishment in each 5-yr period following fire.

Figure 4. Cumulative frequency distribution of percentage of current Engelmann spruce established in 5-yr periods following fire.
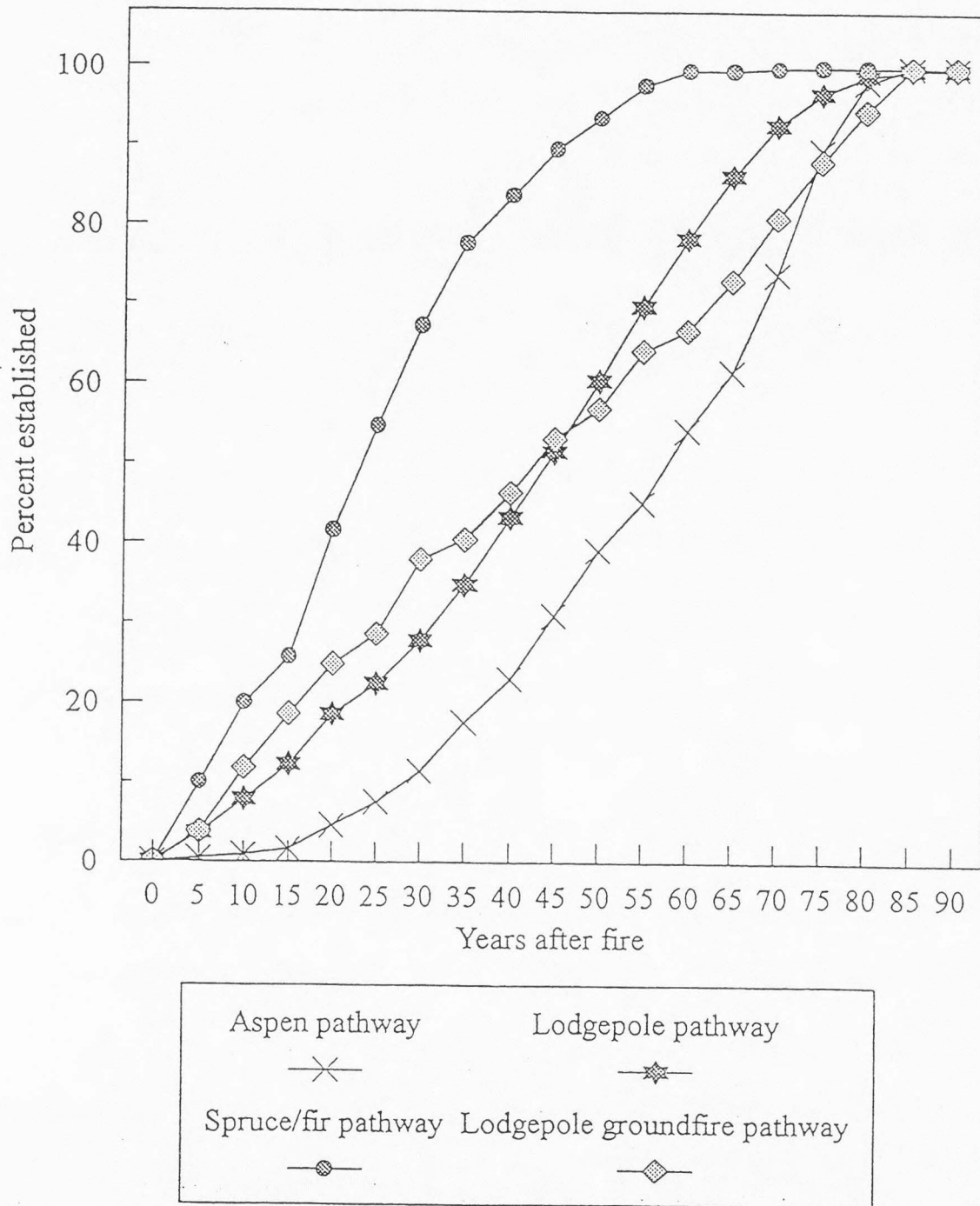
Figure 5. Cumulative frequency distribution of percentage of current subalpine fir established in 5-yr periods following fire.

currently present germinated by 20 yr after a stand replacing fire while in the quaking aspen pathway it took 55-60 yr until 50% of Engelmann spruce and subalpine fir currently present had germinated.

Regression analysis of Engelmann spruce and subalpine fir height as a function of age for each of the 4 post-fire pathways yielded results shown in Figures 6 and 7, respectively. For both species, height at any age after germination was generally greatest in the Engelmann spruce/subalpine fir pathway followed by the quaking aspen pathway, lodgepole pine pathway, and the lodgepole pine ground fire pathway.

The greatest number of late successional species was found in the Engelmann spruce/subalpine fir pathway followed by the lodgepole pine, quaking aspen, and lodgepole pine ground fire pathways (Figure 8), with subalpine fir represented by 2-5 times more trees/ha than Engelmann spruce in each pathway. In the Engelmann spruce/subalpine fir pathway there existed for both late successional species a good height distribution between 1-20 m and a good DBH distribution between 2-26 cm. In the seral pathways, however, most late successional trees were less than 2 m high and 2 cm DBH.

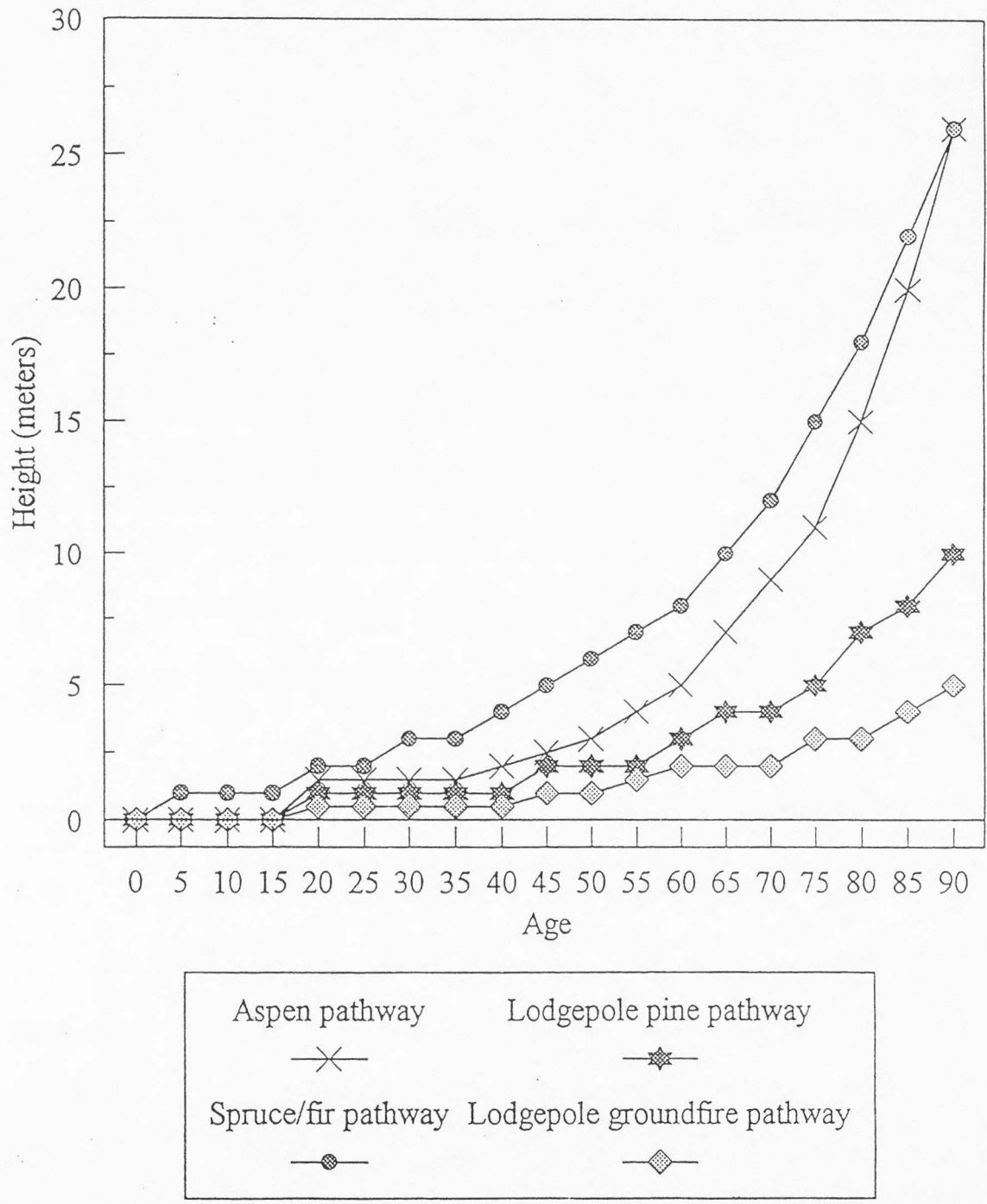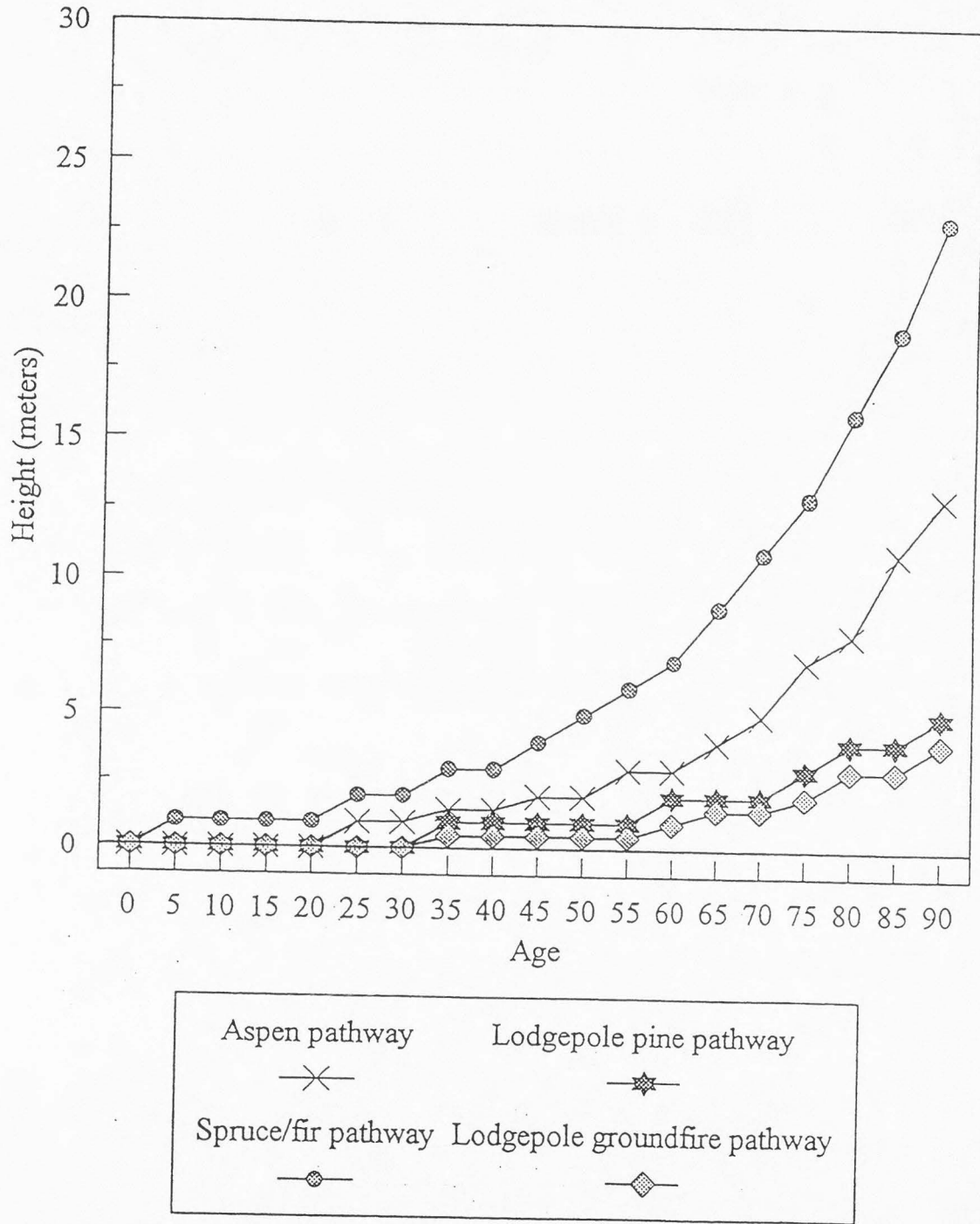Figure 6. Engelmann spruce height growth after germination.

Figure 7. Subalpine fir height growth after germination.
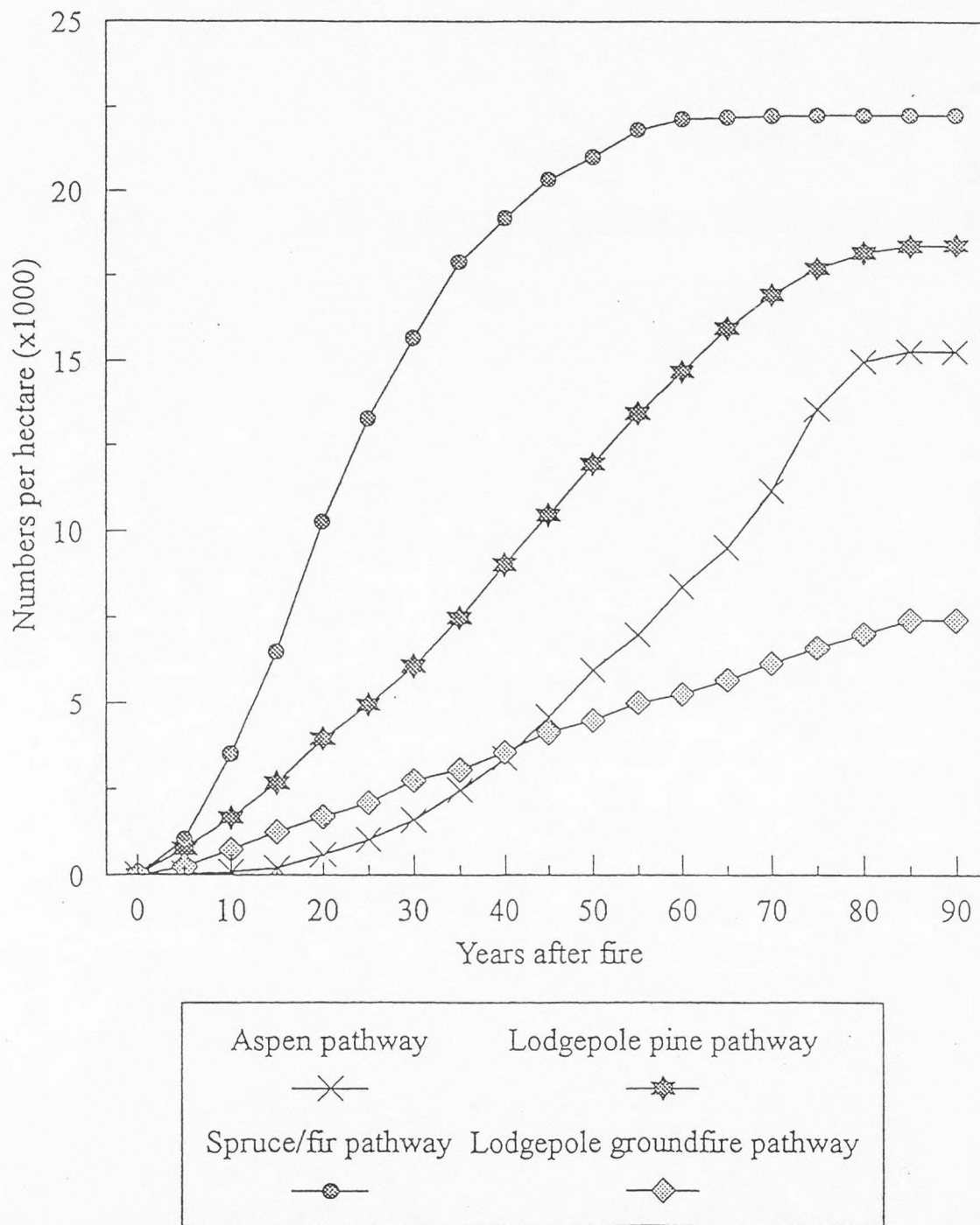
Figure 8. Total accumulation of Engelmann spruce and subalpine fir following fire.

DISCUSSION

Post-Fire Establishment and Growth of Late
Successional Species

Common colonizers after a stand-replacing fire in the subalpine zone are
quaking aspen, due to its ability to propagate by sprouting after a major disturbance,
and lodgepole pine, due to its germanitive energy, early rapid growth, and ability to
withstand many different microsite conditions (Lotan 1976).

Immediate post-fire colonization of Engelmann spruce and subalpine fir is
often deterred due to a harsh post-fire environment, which includes temperature
extremes (Hellmers et al. 1970, Alexander 1974, 1984), intense solar radiation, which
inhibits the photosynthetic mechanism (Ronco 1970), nighttime frost and freezing
damage (Wardle 1968, Alexander 1984, Alexander and Shepperd 1990), and
desiccating winds, which increase water loss from the soil and seedlings (Alexander
1984, Daly and Shankman 1985). It was somewhat unexpected, then, to discover that
Engelmann spruce and subalpine fir were able to immediately colonize large areas on
the Daniel Forest after a stand-replacing fire (Wadleigh-Anhold 1988).

Where Engelmann spruce and subalpine fir post-fire colonization occurred, it
was assumed that 1) there were no aspen present on the site, 2) lodgepole pine seed
was unavailable due to either distance from the burn sites or cone crops did not
coincide with the burns, 3) adequate Engelmann spruce and subalpine fir seed were
available either from fire survivors or adjacent fringe stands, and 4) adequate
microsites created by standing dead trees existed, which reduced the post-fire

environmental extremes (Stahelin 1943, Oliver 1981, Pickett et al. 1987b).

It was expected that Engelmann spruce and subalpine fir would establish most rapidly after a fire in the Engelmann spruce/subalpine fir post-fire successional pathway (Figures 4 and 5). If the site did not need facilitation by a seral nurse crop, Engelmann spruce and subalpine fir would be able to exploit these sites first if a seed source existed.

When the 2 lodgepole pine pathways were compared, Engelmann spruce and subalpine fir establishment patterns were generally the same through time in both pathways although it was expected that understory establishment would occur sooner on sites that only experienced a light surface fire because an existing overstory would have immediately provided the necessary shelter for the late successional species. One possible explanation for this is that in the lodgepole pine stands that experienced a surface fire, any Engelmann spruce or subalpine fir present in the stand were likely destroyed due to the extreme fire intolerance of these species and a suitable seed source for subsequent understory establishment was thereby lost.

The relatively long time needed for Engelmann spruce and subalpine fir to establish under a quaking aspen overstory could be explained by an inability of quaking aspen to adequately reduce the environmental extremes during the first phases of stand initiation. Stand leaf area and subsequent solar interception increase through time as stand basal area increases, but because the leaf area of quaking aspen trees is inherently lower than subalpine conifers, a post-fire quaking aspen stand would require longer time to sufficiently buffer harmful incoming solar radiation (Kaufmann

et al. 1982). The sharp drop in numbers 75 yr after a fire is attributed to not sampling trees under 20 cm.

Engelmann spruce and subalpine fir growth was highest in the Engelmann spruce/subalpine fir post-fire successional pathway because most trees sampled grew unhindered by competition for light, nutrients, and water from an existing overstory. However, the few trees sampled underneath the Engelmann spruce/subalpine fir overstory showed severely retarded growth. Had a separate pathway existed for trees that existed beneath a canopy of Engelmann spruce and subalpine fir, growth would be more similar to that found in the lodgepole pine pathways.

Where Engelmann spruce and subalpine fir existed in the understory of a seral canopy, growth was faster in the quaking aspen pathway than in the 2 lodgepole pine pathways. This could be explained in a number of ways. Quaking aspen stands have lower leaf area indexes than stands of lodgepole pine (Kaufmann et al. 1982), which allows more understory photosynthesis to occur. More soil moisture is available for Engelmann spruce and subalpine fir under quaking aspen stands because quaking aspen stands transpire less on an annual basis than lodgepole pine stands (Jones et al. 1985). Also, under water stress, quaking aspen stands cease transpiration at a much higher soil moisture level than stands of lodgepole pine, which leads to less soil water extraction under quaking aspen stands (Kaufmann 1982). Finally, Engelmann spruce and subalpine fir are allowed a period of high photosynthesis early in the spring beneath a quaking aspen canopy before leaf flush, which is not available in the understory of lodgepole pine stands.

Disturbance Interactions

Results of this study can be used to project succession and fire potential through time after a stand-replacing fire. For example, knowledge of establishment patterns and growth of Engelmann spruce and subalpine fir in the lodgepole pine pathway can be used to determine when these species will become adequately stocked in the understory, when they will form ladder fuels into the overstory canopy, and when they will eventually begin to shade out light-intolerant lodgepole pine.

The potential for a stand-replacing fire on the T.W. Daniel Experimental Forest currently exists in the stands that followed the Engelmann spruce/subalpine fir post-fire successional pathway. These species are extremely susceptible to fire due to their compact growth form, poor self-pruning, and associated heavy fuel loads on the site (Despain and Sellers 1977, Wadleigh-Anhold 1988).

In quaking aspen stands, a stand-replacing ground fire could also burn at any time although fine fuels needed for fire spread have been reduced by grazing (Wadleigh and Jenkins in press). Although quaking aspen is easily killed by fire, it does not readily burn and there are few Engelmann spruce and subalpine fir over 4 m to increase fire intensity. In the absence of fire, the quaking aspen canopy will be shaded out beginning in about 30 yr by the late successional species currently 4 m tall and in about 90 yr by newly germinated seedlings.

The lodgepole pine type could experience a low-intensity surface fire, but it is doubtful a crown fire could occur except under prolonged extreme drought conditions and high winds because most understory trees are less than 4 m tall and do not

provide ladder fuels into the overstory. Vertical fuel continuity will be attained by existing understory Engelmann spruce and subalpine fir currently 4 m tall in about 30 yr when they attain a height of 60% of the current lodgepole pine height. In about 105 yr newly germinated seedlings will also create vertical fuel continuity. In the absence of other disturbance, lodgepole pine stands on the Daniel Forest will begin to succeed to an Engelmann spruce/subalpine fir forest in 60 yr and completely dominate the site in about 120 yr.

In the lodgepole pine stands that have experienced a low-intensity surface fire, there is little chance of a stand-replacing crown fire due to lack of ladder fuels into the canopy. It will take about 40 yr for an existing understory tree 4 m tall and about 125 yr for newly germinated seedlings to reach a height that will provide the vertical fuel continuity needed for a stand-replacing crown fire. In the absence of other disturbances, these stands will begin to succeed to an Engelmann spruce/subalpine fir forest in about 50-140 yr.

It should be noted that all of these scenarios assume the absence of other types of disturbance. However, in the Intermountain subalpine zone other disturbances such as insects, avalanches, diseases, and wind events regularly play roles in forest dynamics. Figures 9-11 are conceptual models showing how different disturbance types might interact to shape the Daniel Forest.

Figure 9 displays how succession might progress if Engelmann spruce and subalpine fir are able to colonize a site after a stand-replacing fire. If the site is conducive to immediate Engelmann spruce and subalpine fir germination, these
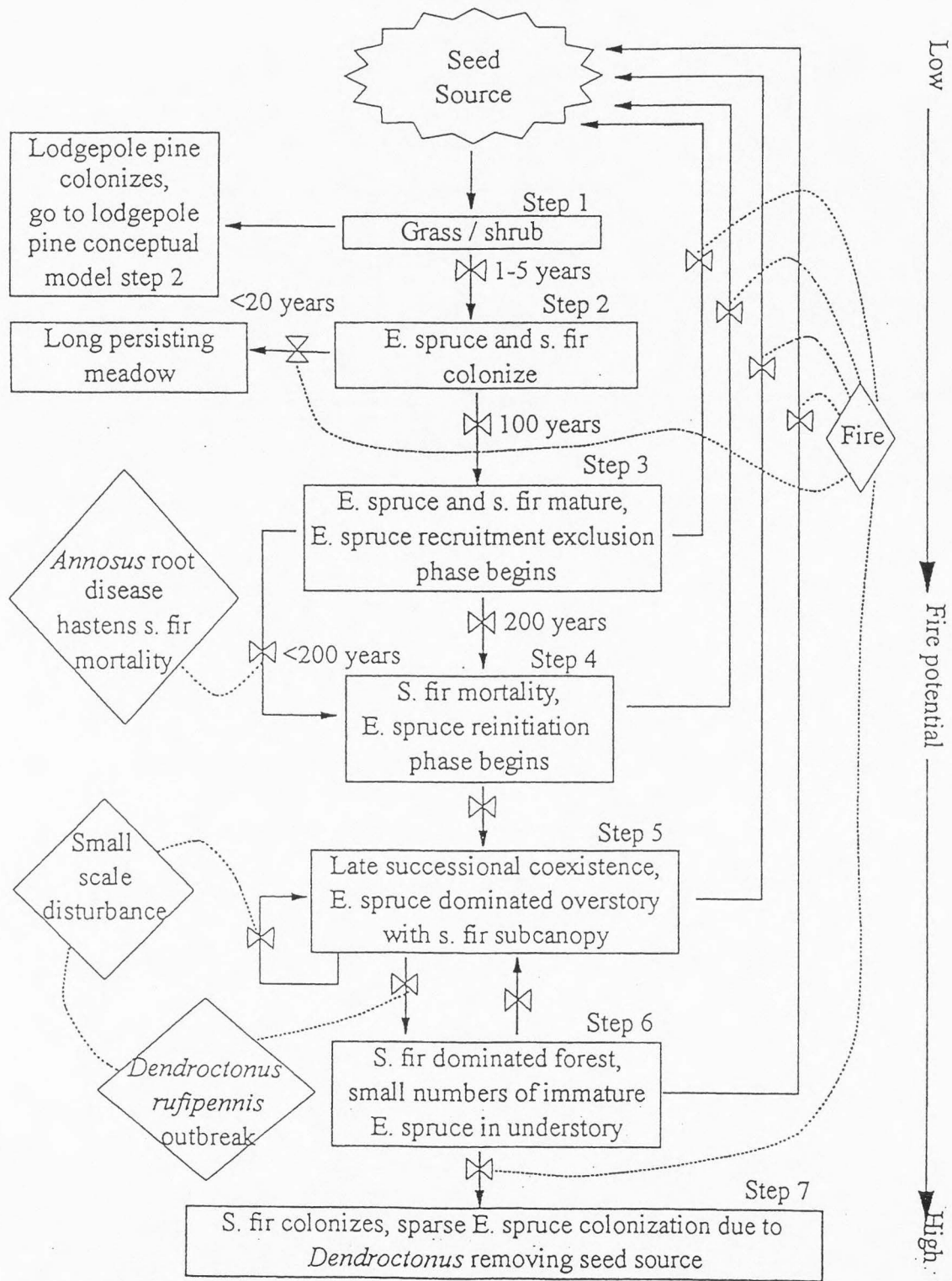
Figure 9. Conceptual model of Engelmann spruce/subalpine fir post-fire pathway successional dynamics.
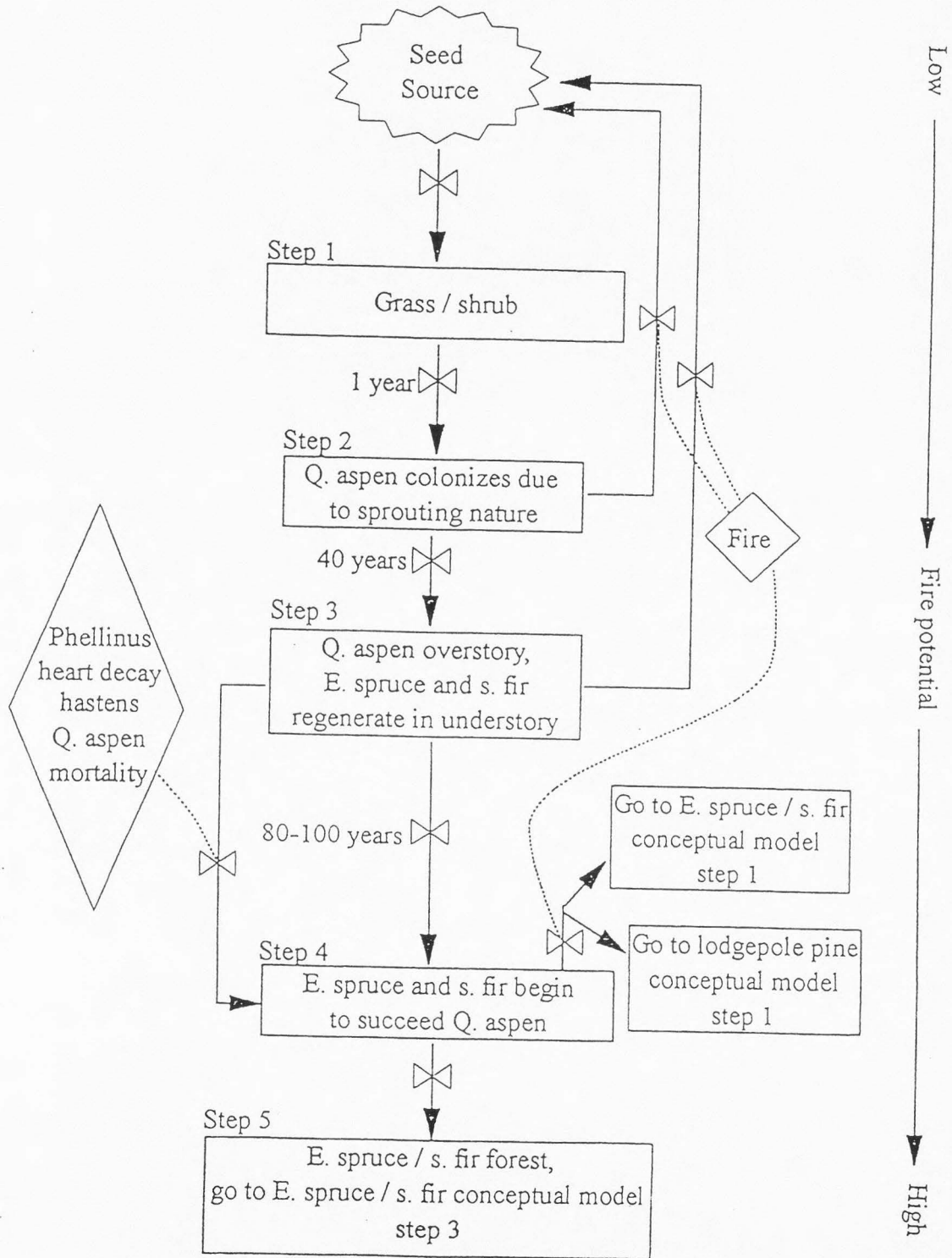
Figure 10. Conceptual model of quaking aspen post-fire pathway successional dynamics.

Figure 11. Conceptual model of lodgepole pine post-fire pathway successional dynamics.

species will begin to establish in significant numbers in the length of time needed for a good seed crop, generally every 2 to 4 yr on the Daniel Forest (Cameron 1987). As Engelmann spruce and subalpine fir mature in about 100 yr, Engelmann spruce enters into a state of recruitment exclusion due to an inability to establish in heavy duff related to the poor moisture retention of duff and shallow root penetration by Engelmann spruce seedlings (Alexander 1974, Knapp and Smith 1982, Aplet et al. 1988). Also, Engelmann spruce seeds that overwinter on duff seedbeds on some sites in the Intermountain West, including the Daniel Forest, may experience mass mortality caused by the fungus Geniculodendron pyriforme Salt (Ascomycetidae, Pezizales), the imperfect state of Caloscypha fulgens (Pers.) Boudier (Ascomycetidae, Pezizales) (Daniel and Schmidt 1972, Paden et al. 1978, Wicklow-Howard and Skujins 1980). Subalpine fir does not experience the recruitment exclusion phenomenon and therefore enters into a period of stand dominance for about 200 yr (Aplet et al. 1989).

An Engelmann spruce reinitiation phase follows in which small-scale disturbances open gaps in the stand and provide suitable microsites of upturned mineral soil and rotten logs in which Engelmann spruce is often able to exclude subalpine fir (Shea 1985, Aplet et al. 1989). This successional phase generally coincides with subalpine fir approaching its life expectancy (Aplet et al. 1989). On the Daniel Forest, subalpine fir is often subject to the annosum root disease (Heterobasidion annosum [Fr.] Bref.), which can hasten this process. Subsequent

small-scale disturbances such as windthrow or lightning strikes perpetuate Engelmann spruce establishment of the site.

Because they are the longer lived species, existing Engelmann spruce trees mature and in time grow to the large size commonly found in old growth stands while subalpine fir trees continue to persist in the subcanopy due to the ability to establish in most understory conditions. Through time, the 2 late successional species coexist due to the greater longevity of Engelmann spruce, the less demanding site requirements of subalpine fir, and small-scale disturbance that perpetuate Engelmann spruce establishment.

As Engelmann spruce increase in age and grow to the large sizes common in old growth stands, the spruce beetle (Dendroctonus rufipennis Kirby) (Coleoptera: Scolytidae) becomes attracted to them. Endemic populations of spruce beetle may selectively attack older and weakened trees. A large disturbance such as a major avalanche or wind event could occur where large numbers of Engelmann spruce are killed or damaged. These damaged trees could become the focal point for a spruce beetle epidemic, which could potentially destroy all Engelmann spruce larger than 10-15 cm diameter at breast height over thousands of hectares (Schmid and Frye 1977). However, a fire-induced landscape, which would contain a diversity of species and age classes, could limit the potential for bark beetle outbreaks. Because subalpine fir often has a greater representation in the understory, there will be a quick shift to a subalpine fir-dominated forest after a spruce beetle outbreak (Veblen et al. 1991b). Any fire occurring after an outbreak could potentially limit future Engelmann spruce

establishment due to a lack of a seed source caused by the spruce beetle killing the trees large enough to produce a good seed crop.

However, if the landscape has a rich age class diversity, fringe stands of Engelmann spruce not large enough to be attacked by the bark beetles would be able to provide a seed source for future stands. In the absence of fire, Engelmann spruce not destroyed by bark beetles will grow and provide seed, thereby ensuring the coexistence of both late successional species.

An examination of the quaking aspen conceptual successional model (Figure 10) shows that quaking aspen may colonize the site immediately after a fire due to its sprouting nature. After about 40 yr, Engelmann spruce and subalpine fir begin to establish in significant numbers (Figure 10) and grow for 80-100 yr until they reach into the quaking aspen overstory and begin to shade out the shade-intolerant species. Any fire occurring before this time will naturally regenerate quaking aspen. At some point, Engelmann spruce and subalpine fir will dominate the site through natural turnover, and quaking aspen will be lost from the site (Loope 1971, Houston 1973).

The successional turnover to Engelmann spruce and subalpine fir may be hastened if quaking aspen is infected with a decay fungi. Quaking aspen trees are frequently subject to the heart rot disease Phellinus tremulae ([Bond.] Bond. & Boriss.) which is commonly observed in most stands on the Daniel Forest. The disease will weaken the overstory quaking aspen and hasten the stand's mortality by making it more susceptible to windthrow or other disturbances. This would subsequently release the shade-tolerant Engelmann spruce and subalpine fir and result

in a rapid change to the climax forest.

An examination of the lodgepole pine conceptual successional model (Figure 11) shows that after a stand-replacing fire, lodgepole pine could quickly colonize the site in the first few years if a seed source existed, especially if there is a high presence of serotinous cones (Lotan 1976). Fire susceptibility of lodgepole pine stands peaks about 25 yr after colonization due to lack of early self-pruning and existence of standing fire-killed snags (Brown 1975). After a post-fire lodgepole pine stand is established, a second fire within 20 yr may prohibit reestablishment as there may not be adequate time for lodgepole pine seed to be produced and could create a persistent meadow in the absence of quaking aspen (Wellner 1970). As lodgepole pine begins to self-prune and fire-killed snags begin to fall, stands enter into a period of moderate fire resistance near age 60 until understory Engelmann spruce and subalpine fir grow and provide vertical fuel continuity into the lodgepole pine crown (Brown 1975).

About 20 yr after a stand-replacing fire, Engelmann spruce and subalpine fir begin to establish in the lodgepole pine understory. After lodgepole pine enters into a period of moderate fire resistance described earlier, a fire will likely be a low-intensity surface fire that would destroy the understory of late successional Engelmann spruce and subalpine fir while causing little damage to the existing lodgepole pine overstory. A fire of this type would break the vertical and horizontal continuity of fuels and therefore delay a high-intensity stand-replacing crown fire for many years.

If such a fire did occur, it would take about 20 yr for subalpine fir and Engelmann spruce to become established in the existing understory and another 125 yr before the subsequent understory would provide the ladder fuels needed for a crown fire. Other surface fires could occur and prolong the existence of lodgepole pine on the site until it reaches its life expectancy, around 400 yr (Lotan and Critchfield 1990).

In the absence of a surface fire, the understory Engelmann spruce and subalpine fir would provide the ladder fuels needed for a stand-replacing fire in about 125 yr after germination. Any crown fire at this point would perpetuate lodgepole pine existence on the site due the energetic colonizing properties inherent to this species.

After about 125 yr in the absence of a surface fire or 150 yr after the most recent surface fire, understory Engelmann spruce and subalpine fir will begin to reach into the upper canopy and begin to shade out the lodgepole pine and eventually succeed to a climax coexistence.

However, this time frame could be significantly reduced if the lodgepole pine overstory was attacked by the mountain pine beetle (D. ponderosae Hopkins). Lodgepole pine trees, located at low to mid elevations within the subalpine zone, over 80 yr of age, and greater than 20 cm in diameter tend to be most susceptible to the mountain pine beetle (Amman et al. 1977). The vast majority of lodgepole pine trees located on the Daniel Forest lie within the range of high susceptibility and could

support a mountain pine beetle outbreak, thereby hastening succession through the release of Engelmann spruce and subalpine fir.

Interestingly, lodgepole pine trees that are scarred by a low-intensity surface fire promote fungal entry and after a delay of 30-100 yr are preferentially attacked by the mountain pine beetle (Geiszler et al. 1980). If there are enough fire-damaged trees, beetle populations may increase and destroy vast acreage of the lodgepole pine forest (Gara et al. 1984a). While this hastens successional turnover to Engelmann spruce and subalpine fir, it also provides large amounts of fuel needed for a high-intensity stand-replacing fire, which would reinitiate the cycle.

After Engelmann spruce and subalpine fir dominate the site, lodgepole pine could be eliminated indefinitely. However, a diverse fire-induced landscape would include scattered stands of lodgepole pine, which would provide a seed source once the site burned again. After coming to dominance through the lodgepole pine pathways, Engelmann spruce and subalpine fir would exist in a similar way as other climax Engelmann spruce/subalpine fir forests.

Fuel loads and subsequent fire potential continually increase through time after a stand-replacing fire in the Engelmann spruce/subalpine fir and quaking aspen successional models (Figures 9 and 10). However, in the lodgepole pine successional model (Figure 11), fire potential peaks at 25 yr after a stand-replacing fire and decreases until overmaturity. In the high elevation forests of the Intermountain West, fuel accumulation proceeds faster than decomposition (Heinselmann 1981). Through time as trees grow, deposit litter, and eventually die, fuel loads continually increase

and in most subalpine forests it is but a matter of time before fire again plays its ecological role.

It should be noted that the general successional models (Figures 9-11) apply to the T.W. Daniel Experimental Forest and other subalpine forests of similar latitudes and elevations and that different successional dynamics would appear in other areas. For example, at lower elevation forests, Douglas-fir and associated disturbances particular to this species would play a much larger role, and at higher elevations, lodgepole pine, quaking aspen, and their associated successional dynamics would not exist. Also at lower elevations, fire frequencies tend to be shorter, while at extreme high elevations, a site may not experience fire for thousands of years (Billings 1969).

Management Implications

Fire exclusion in the West has caused landscapes to lose much of their diversity through natural successional processes, although the upper elevations of the subalpine zone may have experienced less of an impact due to the extremely slow growth found there (Fahnestock 1976, Romme 1982). Because of a lack of diversity, forest communities have become more susceptible to other types of disturbance such as insect outbreaks covering areas far larger than most fire boundaries would attain. Fire suppression has also led to a buildup of fuels (Dodge 1972), allowing fires that do occur to become larger and more expensive to control (Mutch 1994). Total fire exclusion, then, has served to deteriorate forest health over much of the Intermountain West.

Ecosystem management is the current philosophy of federal land management agencies on public lands and requires that land mangers account for cultural, social, biological, and economical aspects in any management decision. It has forced land managers to recognize the natural role of perturbations on landscape dynamics and forest health and to allow fire to play a more active role in natural systems. While the role of natural fire has been lauded recently, many public land managers are still unwilling to take the potential political risks involved in using fire as a tool. Meanwhile, though, ecosystem diversity and forest health have declined.

The implementation of a management option called prescribed natural fire within national parks and designated wilderness areas has been a positive step in restoring fire's natural role. Because fuel growth is slower over time and large geographical areas of relatively untouched landscape remain, the subalpine zone is an exemplary site to implement a prescribed natural fire policy.

In areas outside of designated wilderness and parks, the use of manager-ignited fires to create landscape diversity and reduce unnaturally high, dangerous fuel loads is another management option. Manager-ignited fires, however, should be implemented on the landscape level instead of the traditional stand-by-stand approach and should coincide with natural fire regimes (Mutch 1994). Another management option that could be utilized more frequently is modified suppression where fire containment rather than total fire control is used during suppression efforts. This allows for more ecosystem diversity as well as lowering suppression costs.

Where prescribed fire is not an acceptable management option due to smoke, water quality, timber values, visual impairments, or other concerns, different types of land use techniques such as logging operations that are spatially and temporally comparable to historical fires could be used to mimic natural fire processes.

CONCLUSION

Of the 4 post-fire successional pathways, the Engelmann spruce/subalpine fir pathway was most beneficial for the late successional species. Engelmann spruce and subalpine fir establishment occurred soonest on those sites where there was no need for facilitation of the post-fire environment by a seral nurse crop. Also, growth was enhanced there by lack of competition of resources from an existing overstory.

Where Engelmann spruce and subalpine fir existed in the understory of a post-fire nurse crop, the quaking aspen pathway seemed most advantageous to the late successional species. Although establishment of Engelmann spruce and subalpine fir was delayed under quaking aspen stands, growth of the late successional species was augmented by greater amounts of sunlight and water than under stands of lodgepole pine.

It is clear that disturbance continually drives succession in the subalpine forests in both directions. Conflagration fires drive secondary succession to an earlier stage while most other disturbances hasten natural succession by acting as a release mechanism for understory Engelmann spruce and subalpine fir. Disturbances that hasten successional turnover also work indirectly to reinitiate succession by depositing large amounts of fuel necessary for high-intensity fires in short amounts of time. Perturbations rarely act alone in the Intermountain subalpine zone; rather there are complex interrelationships between disturbance agents that need further exploration.

Disturbance, then, is a monumental force in the natural shaping of forested landscapes. A change in the types, intensities, and frequencies of disturbances can have a profound effect on whole ecosystems. On the T.W. Daniel Experimental Forest, the exclusion of fire in the last 90 yr has allowed succession to proceed toward a climax forest of Engelmann spruce and subalpine fir (Wadleigh and Jenkins *in press*), and in the continued absence of fire, landscape diversity will be minimized while the potential for unusually large and intense fires will continually increase.

The absence of fire has threatened lodgepole pine existence by making large tracts of land susceptible to the mountain pine beetle and has threatened quaking aspen existence through mass successional turnover. This situation is mirrored throughout the Intermountain West where overall forest health has deteriorated. Land managers should implement current ecosystem management philosophy and allow fire to play a more natural role or utilize management techniques that mimic natural fire effects. If not, landscapes may become modified to support fire events and other disturbances on a scale much larger than occurred historically.

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