

AN ABSTRACT OF THE THESIS OF

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Title: Factors Determining Species Composition of Post-Disturbance
Vegetation Following Logging and Burning of an Old Growth Douglas-fir
Forest

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Abstract approved:_____

Mark V. Wilson

I investigated how the factors that affect the contribution of propagules from the seed bank, bud bank and seed rain influenced the initial vegetation following logging and slash-burning of an old growth Douglas-fir forest at 800 m elevation located in the western Cascades of Oregon.

Permanent field plot data showed species composition and density of establishing vegetation differed greatly between the first and second year after disturbance. This difference was caused by a shift in the relative contribution of propagule sources, which generally differed in species composition. Vegetative propagules of old growth species dominated the first year (67%) and dispersed seed of early successional species dominated the second year (98%).

Seedling emergence from field soil samples placed in a greenhouse showed early successional species dominated the old growth seed bank, which included 88 seeds/m² and 11 species; the disturbed seed bank density was significantly reduced to 18 seed/m² with 6

species.

To further investigate the effect of heat on seed bank density, a laboratory study assessed the effect of experimental heat treatments on the germination of six old growth seed bank species. With one exception all species had the same response to heat treatment: at 50C germination was not reduced; at 100C germination was significantly reduced; and, at 75C, germination was significantly reduced in the wet soil, but not in the dry soil.

Of the pre-disturbance species on the permanent field plots, 89% have the ability to sprout after disturbance. These species constitute the potential bud bank.

Seedling emergence from soil seed traps placed at the field site showed the seed rain of the second year was dominated by early successional species.

To investigate why so few old growth species regenerated from dispersed seed, seed reproduction, seed viability, dispersal rates and emergence rates were examined for three old growth understory species, Berberis nervosa, Linnaea borealis and Gaultheria shallon. Although B. nervosa had the highest cover, it produced no seeds in the year of study. The seed production (227 seeds/m²) of G. shallon was much greater than that of L. borealis (4 seeds/m²). The density of dispersed seed of G. shallon, the only species to disperse seed into the old growth (18 seeds/m²) and into the disturbed site (6 seeds/m²), was much less than the density of seeds produced. None of the three species emerged from seed experimentally sown in the disturbed site. Thus, if similar patterns of low seed production, low seed viability, low dispersal and establishment rates hold for

other old growth understory species, regeneration from dispersed seed will be necessarily slow immediately after disturbance.

Both the low potential of the seed bank and the greater potential of the bud bank contributed to the dominance of old growth species from vegetative propagules in the first year's establishment. The reduction of the bud bank propagules after the first year's establishment, the low regeneration of old growth understory species from dispersed seed and the on-site dispersal of early successional species that colonized the first year contributed to both the greater density of vegetation establishing the second year and the dominance of early successional species.

Factors Determining Species Composition of Post-
disturbance Vegetation Following Logging and Burning of
an Old Growth Douglas-fir Forest

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FACTORS DETERMINING SPECIES COMPOSITION OF POST-
DISTURBANCE VEGETATION FOLLOWING LOGGING AND BURNING OF
AN OLD GROWTH DOUGLAS-FIR FOREST

Chapter 1

INTRODUCTION

DISTURBANCE AND SUCCESSION

Disturbance is a pervasive influence on vegetation throughout the world (Pickett and White 1985, Sousa 1984, Bazzaz 1983, Oliver 1981, White 1979). Both physical processes, such as fire, storms, drought, avalanches, landslides and biological activities, such as predation, herbivory and disease, damage vegetation (Sousa 1984). Humans also cause much disturbance--extensive land clearing, selective harvesting, introduction of alien species, drainage of wetlands, introduction of industrial chemicals into the environment and warfare (Bazzaz 1983).

Because disturbance is ubiquitous, most of the world's vegetation is at one time or another recovering from disturbance. This recovery and the subsequent changes in species composition and other ecosystem characteristics through time constitute succession, a basic concept in plant ecology (Finegan 1984, Connell and Slatyer 1977, West et al. 1981). Although the ecological literature contains many descriptive studies of succession, few address the underlying mechanisms of succession directly, and almost none have done so experimentally (Huston and Smith 1987, Waring and Schlesinger 1985, Finegan 1984, Connell and Slatyer 1977).

Understanding the processes of succession is essential to develop generalities about succession (Pickett et al. 1987, West et al. 1981), for effective conservation and management of natural resources, for preservation of biological diversity and for restoration of land damaged by human activities (Neiring 1987, Jordan et al. 1987, Pickett and White 1985, West et al. 1981).

This review focuses on one successional process, initial establishment of vegetation after disturbance, and the mechanisms, such as pre-disturbance availability, survival of disturbance and establishment, that influence the species composition of this post-disturbance vegetation.

INITIAL ESTABLISHMENT OF VEGETATION AFTER DISTURBANCE

Three major propagule sources for revegetation after disturbance are 1) the seed rain, i.e., dispersed seed, 2) the seed bank, i.e., seed stored in the soil and 3) the bud bank, i.e., sprouts from surviving plant tissues. Other sources for revegetation are serotinous cones, surviving individuals and transported vegetative parts. If the disturbed area is very small, regrowth may simply come from expansion of surrounding plants.

Community characteristics may depend on whether the post-disturbance vegetation regenerates predominately from vegetative propagules or from seeds. Revegetation from vegetative propagules, which may have well-established root systems, is generally more rapid and produces more abundant cover and biomass than regeneration from seed (Gecy and Wilson 1990, Murphy and Lugo 1986a-b, Malanson and O'Leary 1982, Ohmann and Grigal 1981, Uhl et al. 1981, Oliver 1981, Ahlgren 1960). If most species regenerate from vegetative propagules, initial species composition and diversity will be similar to pre-disturbance vegetation (Gimingham et al. 1981, Bell and Koch 1980, Lyon and Stickney 1974) with few changes in the distribution pattern of individuals (Bazzaz 1983), giving a floristic stability (Stocker 1981) and a spatial stability to the community.

The species composition of the post-disturbance vegetation is important because differing initial species composition can produce fundamentally different successional patterns, thus determining the characteristics of mature vegetation (Stickney 1986, McCune and Allen 1985, Drury and Nisbet 1973, Egler 1954). For example, some species

that establish initially may facilitate the establishment of other species, resulting in sequential replacement (relay floristics) (Humphrey 1984, Connell and Slatyer 1977, Egler 1954), or some species may inhibit the establishment of others (Connell and Slatyer 1977). Because most eventual dominants may enter a community in the earliest developmental stages (either as seed or as vegetative propagules) when competitive pressures are low, the failure of a species to establish early reduces its chances for later dominance (Egler 1954, Drury and Nisbet 1973).

The initial species composition also alters other ecosystem processes. For example, fast growing species that establish after fire immobilize nutrients released in the burn, minimizing nutrient losses (Auclair 1985). Invasion of animals and fungi often depends on the species composition of initial vegetation. For example, if only non-mycorrhizal plants establish immediately after disturbance, obligately mycorrhizal fungi die and are unavailable for colonizing plants in later successional stages (Janos 1980).

The species composition of the post-disturbance vegetation will vary depending on the relative contribution of the different propagule sources, assuming that the propagule sources differ in their species composition. For example, in old-field successions, long-lived perennials dominate plots receiving propagules from the bud bank as well as the seed bank and seed rain (Marks and Mohler 1985). These plots also have the most cover. Annuals and short-lived perennials dominate plots receiving propagules from the seed

bank and seed rain only. Establishment of plants in plots receiving propagules from only the seed rain is very slow.

Among similar tropical forests sites in Venezuela (Uhl et al. 1982a, Uhl et al. 1982b, Uhl et al. 1981) tree stump sprouts dominate on cut-over sites. After logging followed by burning, pioneer woody species establishing from seed bank propagules dominate; on burned sites that have been abandoned following short-term agriculture or long-term cattle grazing, grasses and forbs establishing from dispersed seed dominate.

FACTORS INFLUENCING THE CONTRIBUTION OF THE DIFFERENT PROPAGULE

SOURCES

The contribution of propagules from the seed or bud bank to the initial establishment depends on their pre-disturbance availability and the effect of disturbance on their survival and establishment. The contribution of dispersed seeds depends on dispersal rates from on- and off-site sources and the effect of disturbance on establishment.

Pre-disturbance availability of on-site propagules. Ecosystems vary widely in their availability of pre-disturbance seed bank propagules (Leck et al. 1989). Differences in seed bank densities among ecosystems reflect differences in seed bank dynamics-- differences in seed inputs by on- and off-site vegetation (past and present) balanced by seed losses from germination and death.

As vegetation changes through time, seed bank composition and dynamics also change, resulting in seed banks with varying species composition and density (Garwood 1989, Oosting and Humphrey 1940). For example, undisturbed tropical forest seed banks include many tree seeds, secondary regrowth/farm site seed banks are dominated by herbs and older regrowth sites (30-75 yrs) have more tree and shrub seeds (Garwood 1989). As heathland vegetation of Scotland ages, the number of grass and forb seeds in the seed bank declines markedly until seeds of only two ericaceous species remain (Mallik et al. 1984).

Seed banks also change over shorter periods. Some species persist for less than a year forming a transient seed bank; others survive for more than a year forming a persistent seed bank (Thompson

and Grime 1979). In tropical ecosystems where seed production occurs year round, the species composition of the seed bank changes rapidly throughout the year. In a Mexican forest seed bank (Garwood 1989, Guevara and Gomez-Pompa 1972), the tree Robinsonella mirandae was the most abundant species in five of the eight months sampled; three different herbs and shrub species dominated in the other three months. Availability of bud bank propagules depends on the pre-disturbance vegetation. Frequently burned communities generally have many species that sprout after disturbance. Examples include understory species of coniferous forests in North America (Armour et al. 1984, Flinn and Wein 1977, Sobey and Barkhouse 1977, Lyon and Stickney 1974), shrubs and deciduous tree species in boreal forest-tundra (Wein and MacLean 1983), species of Mediterranean-type climates of southern California, South Africa, Australia, Chile, Israel (James 1984, Malanson and O'Leary 1982, Keeley and Zedler 1978, Naveh 1973, Hanes 1971), sagebrush and grasslands species of North America (Wright and Bailey 1982) and heathlands (Mallik and Gimingham 1985). Few studies document the pre-disturbance bud bank or predict which ecosystems are more likely to have a large bud bank.

Post-disturbance availability of seed bank propagules.

Response of seeds to disturbance, particularly fire, is species specific, i.e., some species are unaffected while others are killed (Bell et al. 1987, Mallik and Gimingham 1985, Keeley et al. 1985). For example, seeds of herbaceous chaparral perennials are more heat sensitive than seeds of annuals and suffrutescent perennials (Keeley et al. 1985). For chaparral species with larger seeds, longer

heating at lower temperature is more detrimental than short exposures to high temperature (Keeley 1987).

Several factors determine seed survival of fire. For example, the effect of fire decreases with depth of seed burial (Garwood 1989, Moore and Wein 1977). Seeds with thick, hard seed coats or cuticles survive fires better than seeds with thin, soft seed coats (Parker and Kelly 1989). Seeds that absorb moisture beyond 20% of their dry weight are quite sensitive to heat when imbibed--imbibition reduces both temperature and duration tolerated (Parker and Kelly 1989, Beadle 1940). In one study, seeds were generally intolerant of exposure to post-stratification heat but unaffected or enhanced by pre-stratification heat (Pratt et al. 1984); thus, the season in which fire occurs may determine seed survival.

Post-disturbance availability of bud bank propagules.

Survival of disturbance and subsequent sprouting ability of bud bank propagules are influenced by both plant and disturbance characteristics. Vegetative propagules that are protected belowground or with bark, tillers or other tissues survive fire better than those more exposed or above the surface (Mallik and Gimingham 1985, Johnston and Woodard 1985, Wein and MacLean 1983, Rowe 1983, Gill 1981, Flinn and Wein 1977, Moore and Wein 1977, McLean 1969).

Grasses and other monocots, in contrast to dicots, often recover first after fire (Gill 1981) and sprout much faster (Humphrey 1984). Regrowth of monocots can continue from the damaged leaves, unlike dicots which must develop new leaves (Gill 1981). Heathland

geophytes and hemicryptophytes recover much faster after burning than do sprouting shrubs (Mallik and Gimingham 1983), which must develop adventitious buds from callus tissue at the stem base (Mallik and Gimingham 1983).

Survival of regenerating buds also depends on the fire regime. The depth of heat penetration into the soil depends on duff consumption (Johnston and Woodard 1985, Armour et al. 1984) and moisture content of the soil (Al Nakshabandi and Kohnke 1965), which is related to the time of the year (Wright and Bailey 1982, Ohmann and Grigal 1981).

Sprouting ability is greater if disturbance occurs after seasonal growth is completed and carbohydrate reserves are replenished and available for new growth. But if disturbance occurs when carbohydrate reserves are depleted, then the plant may die or sprout poorly (Flinn and Wein 1988, Garrison 1972, Hough 1968, Wenger 1953). If disturbance occurs during the dormant season, some plant species will not sprout until the normal growing season (Tsiouvaras et al. 1986, Abrahamson 1980, Naveh 1973), whereas others sprout immediately.

After fire, new environmental conditions encourage sprouting and extensive growth by certain formerly minor species in the Mediterranean shrublands (Naveh 1973) and in heathlands (Mallik and Gimingham 1983). These long-lived individuals exhibit a "sit-and-wait" strategy with little aboveground biomass, in that they live for long periods of time until fire releases them from shading or

nutrient limitations; they then sprout and grow extensively (Abrahamson 1980).

Post-disturbance availability of dispersed seed: Seed production from off-site sources is often irregular from year to year. Dispersal onto a site depend on the availability of vectors for animal dispersed seed, physical barriers (e.g., large expanses of forest) for wind-dispersed seed and the distance to the disturbed site (Waring and Schlesinger 1985, Uhl and Jordan 1984, Uhl et al. 1981). If the disturbed area is large, dispersed seed may be available only on the periphery. For example, sparse off-site seed production and restricted dispersal were probably the factors limiting establishment of pre-disturbance species after logging and burning of an old growth Douglas-fir forest (Kellman 1974). In the Amazon basin on sites that are cleared for farming, forbs, grasses and early successional species comprise the post-disturbance vegetation because the seeds of these species are easily dispersed. Regeneration of the primary forest trees is limited because the seeds of these species are large and poorly dispersed (Uhl et al. 1982a-b).

The goal of this research is to understand some of the factors that determine the initial species composition after logging and slash-burning of an old growth Douglas-fir forest. The revegetation patterns--species composition and density (chapter 2)--were examined for two years following disturbance. The relative contribution of propagules from the seed bank, the bud bank and the seed rain were also quantified (chapter 2). The results of the mechanistic

studies--pre-disturbance availability of seed bank and bud bank propagules (chapter 2), their survival of disturbance (chapters 2 and 4), dispersal (chapters 2 and 3) and establishment rates (chapter 3)--were used to explain the revegetation patterns.

Chapter 2

PROPAGULE SOURCES OF REVEGETATION AFTER LOGGING AND
BURNING OF AN OLD GROWTH DOUGLAS-FIR FORESTINTRODUCTION

Although succession is a central concept of ecology (Finegan 1984, West et al. 1981, Connell and Slatyer 1977) and the ecological literature is filled with descriptive studies of succession, few studies address the underlying mechanisms of succession directly (Huston and Smith 1987, Waring and Schlesinger 1985, Finegan 1984, Connell and Slatyer 1977). Understanding the processes and mechanisms of succession is essential in the development of generalities about succession, for effective conservation and management of resources, for preservation of biological diversity and for restoration of land damaged by human activities (Pickett et al. 1987, Niering 1987, Jordan et al. 1987, Pickett and White 1985, West et al. 1981).

One important successional process is the initial establishment of vegetation after disturbance (Walker and Chapin 1987, Pickett et al. 1987, Hibbs 1983). The species composition of this initial revegetation can determine subsequent successional patterns, thus controlling the species composition and other ecosystem characteristics of mature successional vegetation (Humphrey 1984, Connell and Slatyer 1977, Drury and Nisbet 1973). Many of the eventual dominants enter a community early in succession when competitive pressures are low. The failure of a species to establish

in the first few years after disturbance reduces its chances for later dominance (Egler 1954, Drury and Nisbet 1973).

The initial species composition also alters other ecosystem processes and community characteristics. For example, fast growing species that establish after fire immobilize nutrients released in the fire, minimizing nutrient losses (Auclair 1985). Revegetation from vegetative propagules, which may have well-established root systems, is generally more rapid and produces higher cover and biomass immediately after disturbance than revegetation from seed (Halpern 1988, Murphy and Lugo 1986a-b, Mallik et al. 1984, Malanson and O'Leary 1982, Ohmann and Grigal 1981, Uhl et al. 1981). Communities establishing primarily from vegetative propagules will be more similar to pre-disturbance vegetation than communities establishing largely from seed (Gimingham et al. 1981, Bell and Koch 1980, Lyon and Stickney 1974), giving a floristic stability (Stocker 1981) and spatial stability to the community (Bazzaz 1983).

The three major propagule sources of the initial vegetation after disturbance are 1) the seed rain--dispersed seed, 2) the seed bank--seed stored in the soil and 3) the bud bank--vegetative propagules. The relative contribution of these propagule sources depends on their pre-disturbance density and their ability to survive and establish after disturbance.

The goal of this research is to understand some of the factors, particularly pre-disturbance availability and survival of disturbance that determine the initial species composition after logging and slash-burning of an old growth Douglas-fir forest. The specific

objectives were to 1) determine the pre-disturbance availability of propagules in the bud bank and in the seed bank, 2) determine the effects of the disturbance on the species composition and density of seeds in the old-growth seed bank and 3) determine the propagule sources of plants establishing the first two years after disturbance.

METHODS

Study site

Field work for this research was done at the H. J. Andrews Experimental Forest, a NSF Long-Term Ecological Research Site, located in the western Cascade Mountains about 80 km east of Eugene, Oregon. The climate is maritime with mild wet winters and dry summers. The average annual precipitation is approximately 2300 mm (Dyrness et al. 1974).

The 3.2 ha study site (Figure 2.1) is located on a generally westward facing 20-30% slope at 790-825 m elevation. Before disturbance the site was dominated by old growth western hemlock (Tsuga heterophylla) and Douglas-fir (Pseudotsuga menziesii), with some western redcedar (Thuja plicata) (M. W. Wilson, unpublished data). The understory included Berberis nervosa, Linnaea borealis, Vaccinium parvifolium, Rhododendron macrophyllum and Gaultheria shallon. The habitat-type is hemlock/rhododendron/dwarf Oregon grape (Dyrness et al. 1974).

The site was clear-cut logged in late fall 1985 and burned in July, 1986. Slash was left in place and burned with a light intensity fire. (Soil temperatures during burning were <52C-177C at the surface, <39-139C at 2 cm deep, 52C-66C at 4 cm and <52C at 6 cm (M. V. Wilson, unpublished data)). Before burning, a portion of the site was marked with a 10 m x 10 m grid. After slash-burning, five 10 m x 10 m permanent plots were randomly selected from a pool of 10 m X 10 m plots that were as homogeneous as possible with respect to pre-disturbance vegetation and intensity of burn. Within each of

these 10 m x 10 m plots, three 7 m x 2 m plots were marked and one was randomly selected for this study (Figure 2.2).

Objective one

Bud bank. To estimate the species composition of the bud bank, the sprouting ability of each pre-disturbance species growing on the five permanent field plots was determined using a review of the literature.

Seed bank. In late March 1987, 120 soil samples (8 cm in diameter x 10 cm deep from the soil surface) were collected with an auger in the old growth forest surrounding the burned site. The total area sampled was 0.6 m². Care was taken to collect samples from areas with vegetation similar to the pre-disturbance vegetation on the burned site and to collect samples away from the boundary between the old growth forest and the burned site. The vegetation was clipped to the soil surface and the litter layer included in each soil sample. Each seed bank sample was mixed with an equal volume of vermiculite and spread in 17 cm x 13 cm flats placed in an greenhouse. The samples and controls (17 cm x 13 cm flats filled with vermiculite) were kept under greenhouse temperatures and light conditions and watered regularly. To determine the species composition and density of seeds in the seed bank, emergent seedlings were identified and counted weekly (approximately) from each soil sample until early July, 1987. Earlier research using seed bank samples from an old growth Douglas-fir forest (Ingersoll and Wilson

in press) showed that greenhouse conditions yield the best estimate of the soil seed bank.

Objective two

In late March 1987, 120 soil samples (8 cm in diameter x 10 cm deep from the soil surface) were collected with an auger from random locations in the permanent field plots. The total area sampled was 0.6 m².

Species composition and density of seeds in the seed bank were determined by monitoring emergence of seedlings from the soil samples placed under greenhouse conditions, as described in the previous section. Emergence data were collected until early July. Mann-Whitney tests were used to determine if significant differences existed in the density of propagules (total and for each species) between the old growth seed bank as compared to the disturbed seed bank.

Differences in propagule density for species present in the old growth seed bank but not present in the disturbed seed bank were tested using a different approach. I assumed that the number of old growth seed bank samples with no seeds of a particular species present divided by the total number of old growth seed bank samples provided a good estimate of the probability that another single sample of the same size would contain no seeds (q). If the disturbance had no effect on propagule density, then the probability that all of the n samples from the disturbed seed bank contained no seeds of that species would be q^n , that is, $P=q^n$ is the probability of

getting no seeds in samples even though the disturbed seed bank has the same number of seeds as the old growth seed bank. Therefore, if $P=q^n$ is <0.05 , I concluded that propagules of the species were reduced in density in the disturbed soil bank.

Objective three

First year. Propagule sources of establishing vegetation were monitored within a 0.5 m wide strip inside the perimeter of each 7 m x 2 m plot (Figure 2.2). The number of individuals of each species establishing and the propagule source of each individual were recorded from April 1987 until September 1987.

Each seedling was counted as an individual. All sprouts coming from a single aboveground stem such as Acer circinatum and Rhododendron macrophyllum were counted as one individual. For species that sprout from underground stems, such as Berberis nervosa and Gaultheria shallon, each aboveground stem was counted as an individual.

If cotyledons were present, the propagule source was seed. An individual was considered establishing from vegetative propagules if no cotyledons were present and the plant could be traced to established vegetative structures such as the aboveground stems of Rhododendron macrophyllum and the rhizomes of Gaultheria shallon. If no cotyledons were present and the plant could not be traced to established vegetative structures, the propagule source was undetermined.

Each plant was labeled with an aluminum tag and those individuals alive at the end of the growing season were considered to be established.

Second year. Because establishment of vegetation was much more abundant the second year than the first, emergence was measured within a single randomly selected subsample (0.725 m^2) on each of the five $7 \text{ m} \times 2 \text{ m}$ plots (Figure 2.2). Each individual that emerged the second year was identified, marked with colored toothpicks and the propagule source determined using the same criteria as the first summer.

In early August, when new establishment had ceased and before annuals had senesced, all individuals were identified and counted on the entire area (40 m^2 over 5 plots) monitored the summer before. Propagule sources of each of the species on the larger sample area (40 m^2) were assumed to be the same as the propagule sources of the same species growing in the smaller sample area (0.725 m^2).

To distinguish between species establishing the second summer from dispersed seed and those from seed bank propagules, soil seed traps were used to trap dispersed seed. In late March 1987, 60 seed traps ($25 \text{ cm} \times 25 \text{ cm} \times 6 \text{ cm}$ plastic flats filled with potting soil) were randomly placed in the five $10 \text{ m} \times 10 \text{ m}$ permanent field plots but outside of the $7 \text{ m} \times 2 \text{ m}$ observation plot. The total area sampled was 3.75 m^2 . The seed traps were sunk into the ground so that the top edges of the flats were level with the soil surface, thus minimizing wind obstruction. The number of species establishing was recorded through fall of 1987. Flats were removed in spring 1988 and

brought to the Oregon State University greenhouses (under the same conditions as seed bank studies) where new emergence was monitored through summer 1988.

RESULTS

Pre-disturbance availability of on-site propagules

Of the 29 identified pre-disturbance species found on the permanent plots, 26 species (89%) can sprout after disturbance (Table 2.1). These species are assumed to constitute the bud bank.

The old growth soil seed bank samples contained 11 species and an average of 88.6 emergents/m² (Table 2.2). The two most abundant species were Senecio sylvaticus and Epilobium watsonii. Of the 67 seed plant taxa present in the pre-disturbance vegetation census on the site (Tables 2.1 and 2.3, M. V. Wilson, unpublished data), only 7 species were also present in the old growth seed bank (Table 2.2).

The bud bank and the seed bank had only three species in common, Gaultheria shallon, Rhododendron macrophyllum and Rubus ursinus (Tables 2.1 and 2.2).

Post-disturbance availability of seed bank propagules

The post-disturbance seed bank contained six species and an average of 18 emergents/m² (Table 2.2). These values may be an overestimate of the seed bank density immediately after disturbance, because they include any seed inputs after the slash burn in the summer, 1986, until the samples were collected in the spring, 1987. But because the total numbers of species and seeds in the seed bank are small, it is likely that any addition of seed was not large.

The disturbed seed bank samples and old growth seed bank samples had four species in common: Epilobium watsonii, Gaultheria

shallon, Rubus ursinus and Senecio sylvaticus (Table 2.2). Two species found in the disturbed seed bank, Conyza canadensis and Gnaphalium microcephalum, were absent in the old-growth seed bank.

The density of emergents in the disturbed seed bank was significantly lower than that in the old growth seed bank (Table 2.2). The densities of four species were significantly reduced after disturbance; the density of one species was the same in the two seed banks (Table 2.2). Although the low densities of the other species in the old growth seed bank samples prevented the detection of any statistically significant change, the density of each of these six species was less in the disturbed seed bank samples (Tables 2.2).

Dispersed seed

Nineteen species were found in the seed traps (Table 2.4). Because of high mortality of seedlings after removal of the seed traps from the disturbed site to the greenhouse, the number of individuals per species could not be determined.

Propagule sources of plants establishing in the first and second year after disturbance

The first year's vegetation contained 267 individuals/40 m² from 19 taxa (Table 2.5). Twenty-two taxa established the second year (4431 individuals/40 m²) (Table 2.6). Only 10 taxa were common to both years.

Although equal numbers of species established from seed as from vegetative propagules the first and second years (Tables 2.5 and 2.6), more than two-thirds of the individuals established from vegetative propagules the first year (Table 2.5). In the second year, in contrast to the first, most individuals established from seed (Table 2.6).

Four species dominated the first year's vegetation (Table 2.5): Ceanothus velutinus and Senecio sylvaticus, which established from seed, and Berberis nervosa and Gaultheria shallon, which regenerated from vegetative propagules (Table 2.5).

In the second year, 90% of the individuals establishing from seed came from two taxa: Senecio sylvaticus, which had propagules in both the seed bank and the seed rain, and Epilobium paniculatum/Epilobium minutum, which had propagules in the seed rain only (Tables 2.4 and 2.5). Berberis nervosa and Gaultheria shallon contributed most of the individuals regenerating from vegetative propagules (Table 2.6).

Only Epilobium angustifolium established from more than one propagule source (Tables 2.5 and 2.6).

DISCUSSION

Seed bank

The propagule density of this old growth seed bank (88.6/m²) is small even compared to the small seed reserves found in other North American coniferous forests (Ingersoll and Wilson in press, Archibold 1989, Fyles 1989, Morgan and Neuenschwander 1988, Kramer and Johnson 1987, Pratt et al. 1984, Archibold 1979, Whipple 1978, Moore and Wein 1977, Strickler and Edgerton 1976, Kellman 1974, 1970, Livingston and Alessio 1968, Oosting and Humphreys 1940). Thus, the potential of this old growth seed bank to contribute propagules to revegetation after disturbance is low.

One explanation for few seed bank propagules is low seed inputs. Understory species of mature forests characteristically produce fewer seeds and generally regenerate vegetatively more than vegetation of early successional stages (Roberts 1981, Abrahamson 1980, Cook 1980, cf. Bierzychudek 1982). Seed production of understory species declines in mature successional stages because of increased shading and sequestering of nutrients by woody dominants (Bunnell 1990, Barrett and Helenurm 1987, Helenurm and Barrett 1987, Haeussler and Coates 1986, Thompson 1978, Sabhasri 1961).

Conifers, however, produce abundant seed crops, but not every year. These seeds are not generally incorporated into the seed bank (Kramer and Johnson 1987) because they are frequently short-lived (Archibold 1989) and often eaten by insects, birds and rodents (Archibold 1989, Gashwiler 1967, 1970). Few conifer seeds were found in either the old growth or disturbed seed banks (Table 2.2).

Although seven of eleven old growth seed bank species were present in the pre-disturbance vegetation, three early successional species (Senecio sylvaticus, Cirsium sp. and Epilobium watsonii) contributed 57% of the seed bank propagules. In many other studies, seeds of early successional species, not the seeds of the mature forest vegetation, dominate the seed bank (Archibold 1989, Pickett and McDonnell 1989, Livingston and Allessio 1968, Oosting and Humphreys 1940). Seeds of these early successional species were probably incorporated recently from off-site sources rather than during stand initiation (perhaps 500 years ago), especially Senecio sylvaticus which is a recently introduced species. Senecio sylvaticus, Cirsium sp. and Epilobium watsonii produce wind-dispersed seeds (personal observation) from nearby logged sites, and were available for incorporation into the old growth seed bank. Logged sites may increasingly become an important source of dispersed seeds into these old growth forest seed banks (Kellman 1974).

The seed bank density decreased from an already low density of 88/m² in the old growth seed bank to 18/m² after disturbance. This decreased seed density after logging and slash-burning is consistent with that of other ecosystems (Young et al. 1987, Uhl et al. 1981, Ewel et al. 1981).

Bud bank

Of the 29 species present before disturbance on the permanent plots, 89% can sprout after disturbance. The potential of the bud bank to contribute to revegetation after disturbance is much greater

than that of the seed bank. As discussed above, old growth understory species are more likely to regenerate vegetatively than from seeds. Also, many species typical of environments subject to periodic fires survive fire by sprouting (Rowe 1983, Bell and Koch 1980, Lyon and Stickney 1974).

Of the twenty-six species that can sprout, eight actually sprouted either the first or second year after disturbance. Species with buds buried in the soil (e.g., Gaultheria shallon, Berberis nervosa, Xerophyllum tenax) survived better vegetatively than species (e.g., Linnaea borealis) with buds near the soil surface (Mooney and Hobbs 1986, McLean 1969). Species with buds near the surface often spread from unburned plants (personal observation). Given the patchy nature of fire, vegetative regeneration of these species with unprotected buds may be more important for spreading after fire than for survival of fire.

Propagule sources of first and second year's revegetation

The contribution of the three propagules sources to revegetation differed between the first and the second years. In the first year more individuals established from vegetative propagules (67.4%) than from seed. Although no seed trap data were available during the first year, other evidence shows that most first year seedlings emerged from seed in the seed bank. Almost 60% of individuals establishing from seed were by Ceanothus velutinus, which is common in seed banks, stimulated to germinate by heat and has no obvious means of dispersal (Kramer and Johnson 1987, Hauessler and

Coates 1986, Conard et al. 1985, Gratkowski 1962). (Ceanothus velutinus seedlings were patchily distributed on the permanent field plots and thus probably not detected in the disturbed seed bank samples. No seedlings were expected in the old growth seed bank because of no heat stimulation). Thus, because the seed bank was dominated by Ceanothus velutinus, seed bank propagules were more important sources of regrowth in the first year than were dispersed seed. The only other species to regenerate from seed in large numbers was Senecio sylvaticus, present both in the seed bank and the seed rain.

The relative contribution of propagule sources reversed dramatically the second year. Few vegetative propagules established the second year, probably because most propagules sprouted the first year. Not only did the relative contribution of seed sources to the new establishment increase the second year to about 98%, but the absolute number of individuals establishing from seed 50 times greater than the first year. The seed rain probably contributed more than the seed bank to the increase in seedling establishment. The most abundant species establishing from seed, Senecio sylvaticus, was available both in the seed rain and in the seed bank. Propagules in the old growth seed bank were 1.7 seeds per m² so the second year's establishment (68.9 seeds/m²) presumably came from the seed rain. Epilobium paniculatum/Epilobium minutum, the second most abundant taxon, was present in the seed rain only. Furthermore, because Epilobium paniculatum/Epilobium minutum and Senecio sylvaticus both produced copious seed the first year, it is likely that these species

established the second year from on-site dispersed seed rather than off-site dispersed seed.

These shifts in revegetation sources produced remarkably different revegetation patterns between the first and second years. Only ten species were common to both years' establishment, the density of the second year's establishment was 16 times that of the first and old growth species dominated the revegetation the first year in contrast to the second year in which early successional species dominated. These patterns are consistent with other descriptions of the early successional stages of mid-elevation sites of the Cascade mountains (Franklin and Dyrness 1973, Dyrness 1973, Halpern 1988). These studies describe a first year with sparse vegetation consisting of residual species from the original stand with small amounts of invading early successional species. The second year is dominated by invading annual herbaceous species often with Senecio sylvaticus the most abundant species.

Among similar tropical forest sites in Venezuela (Uhl et al. 1982a, Uhl et al. 1982b, Uhl et al. 1981) several patterns of revegetation after disturbance emerge, which can be explained by the contribution of propagule sources. On cut-over sites stump sprouts of primary trees dominate. On sites logged followed by burning, pioneer woody species established from seed bank propagules dominate. On burned sites that have been abandoned following short-term agriculture or long-term cattle grazing, grasses and forbs establishing from dispersed seed dominate. Some of the variation commonly seen in the initial stages of old field succession in the

Northeast United States can also be partially explained by sources of propagules (Marks and Mohler 1985). Long-lived perennials dominate plots receiving propagules from the bud bank as well as the seed bank and the seed rain; these plots are similar to fields abandoned from row crop agriculture after several years of poor weed control.

Annuals and short-lived perennials dominate plots receiving propagules from seed bank and seed rain only; these plots are similar to abandoned fields with more complete weed control through the cropping cycle. Establishment of plants in plots receiving propagules from only the seed rain is very slow, with few plants establishing. In both these systems, the survival of the pre-disturbance propagules of disturbance was an important factor in determining the source of propagules.

In conclusion, the difference in revegetation patterns between year one and year two in this study was caused by the shift in the relative contribution of propagule sources, which generally differed in species composition. Vegetative propagules of the old growth species dominated the first year and dispersed seed of early successional species dominated the second year. This research demonstrates the importance of the following factors in determining the relative contribution of the propagule sources: (1) the biological legacy of the pre-disturbance community in the form of seed bank and bud bank propagules, (2) the influence of disturbance on the survival and establishment of this legacy and (3) the availability of dispersed seed and the influence of disturbance on seedling establishment. Thus, to predict patterns of early

revegetation it is necessary to understand these mechanisms that determine the contribution of the propagule sources.

CORNELL TIMBER SALE
(T. 15 S., R. 5 E., Sec. 33)

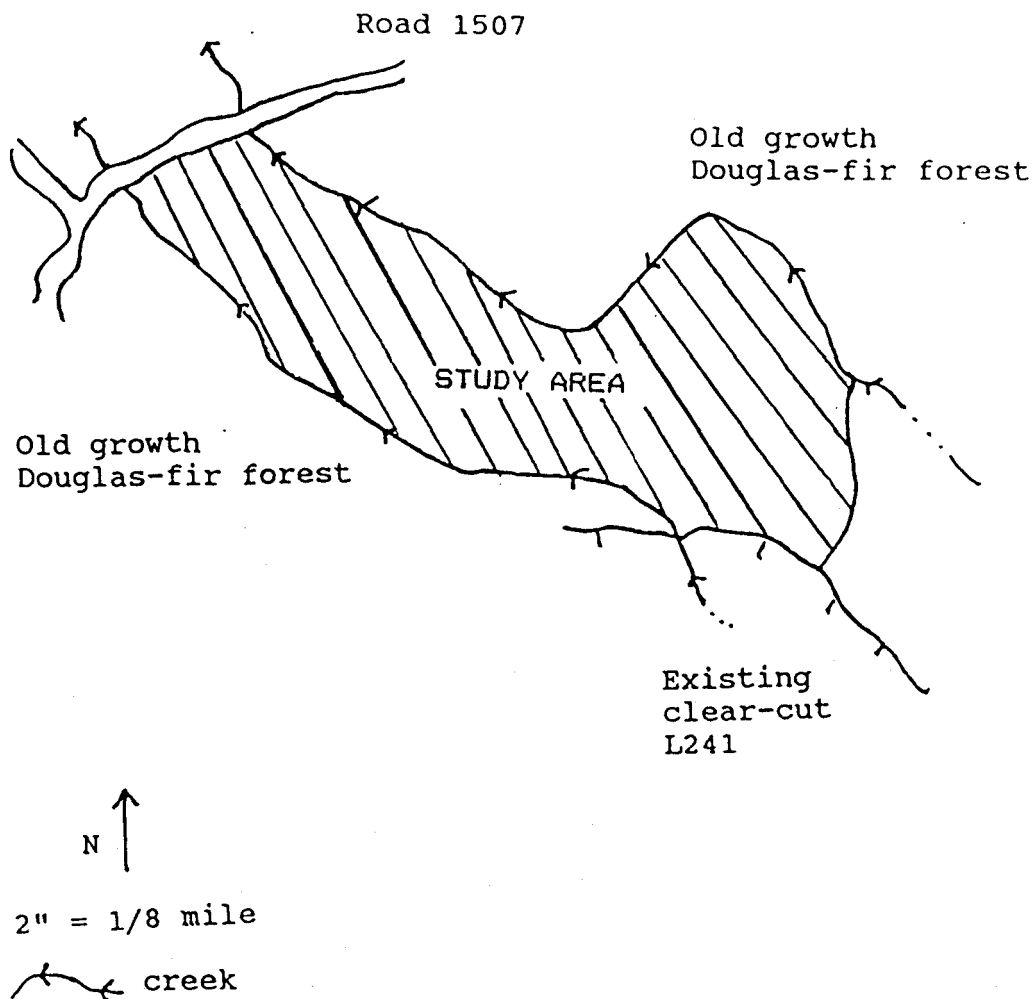


FIGURE 2.1. The study site, 3.2 ha, located at the H.J. Andrews Experimental Forest which is in the western Cascade Mountains about 80 km east of Eugene, Oregon.

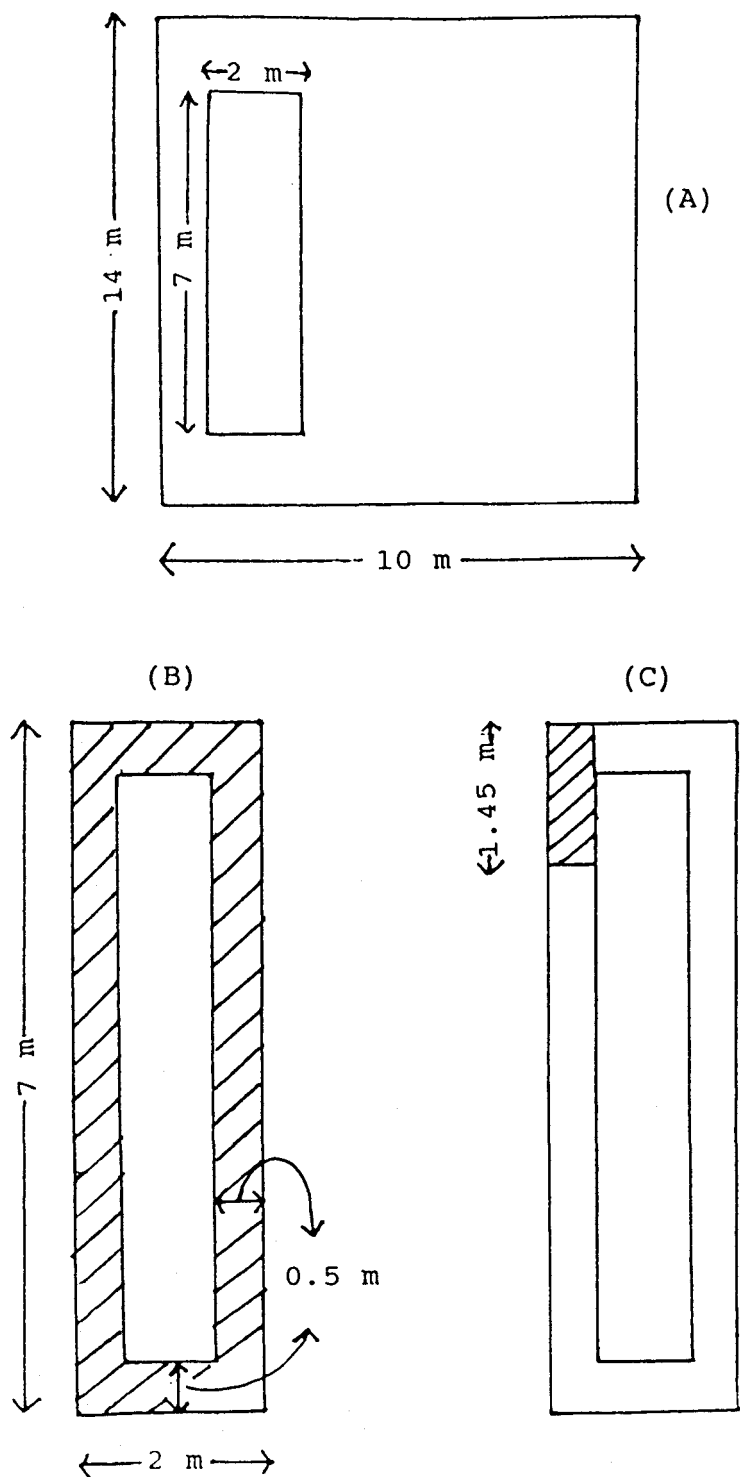


FIGURE 2.2. Permanent field plots. (A) One 7 m x 2 m plot, placed within the 10 m x 10 m plot, was used to monitor propagule sources of post-disturbance vegetation. (B) The shaded area is the area within the 7 m x 2 m plot monitored the first year (C) The shaded area is the area within the 7 m x 2 m plot monitored the second year.

Table 2.1. Species present in the pre-disturbance vegetation of the permanent field plots (M. V. Wilson, unpublished data), their ability to establish from vegetative propagules and whether they actually established in the field from vegetative propagules.

Species	Able to establish vegetatively	Established vegetatively	Reference
<i>Acer circinatum</i>	yes	yes	1
<i>Achlys triphylla</i>	yes	no	2
<i>Anemone deltoidea</i>	yes	no	13
<i>Berberis nervosa</i>	yes	yes	3
<i>Castanopsis chrysophylla</i>	yes	no	1
<i>Chimaphila umbellata</i>	yes	yes	4
<i>Coptis lacinata</i>	yes	no	4
<i>Corallorhiza mertensiana</i>	yes	no	13
<i>Galium triflorum</i>	yes	no	5
<i>Gautheria shallon</i>	yes	yes	6
<i>Goodyera oblongifolia</i>	yes	no	7
Graminae sp.	unknown	no	-
<i>Hieracium albiflorum</i>	yes	no	4
<i>Linnaea borealis</i>	yes	no	4
<i>Listera caurina</i>	unknown	no	-
<i>Polystichum munitum</i>	yes	no	6
<i>Pseudotsuga menziesii</i>	no	no	8
<i>Pyrola asarifolia</i>	yes	no	13
<i>Rhododendron macrophyllum</i>	yes	yes	3
<i>Rubus ursinus</i>	yes	yes	3
<i>Taxus brevifolia</i>	yes	no	9
<i>Thuja plicata</i>	yes*	no	14
<i>Tiarella trifoliata</i>	yes	no	4
<i>Trientalis latifolia</i>	yes	no	1
<i>Trillium ovatum</i>	yes	no	10
<i>Tsuga heterophylla</i>	no	no	8
<i>Vaccinium membranaceum</i>	yes	no	11
<i>Vaccinium parvifolium</i>	yes	yes	12
<i>Viola sempervirens</i>	yes	no	4
<i>Xerophyllum tenax</i>	yes	yes	3
Unknown	-	-	-
TOTALS:			
29 identified species	26	8	

References: (1) Volland and Dell 1981, (2) K. Merrifield, personal communication, (3) personal observation, (4) Ingersoll and Wilson, in press, (5) Crane and Fischer 1986, (6) Haeussler and Coates 1986, (7) McLean 1969, (8) Fowells 1965, (9) Sudworth 1908, (10) K. Chambers, personal communication, (11) Minore 1978, (12) Stewart 1978, (13) Antos and Zobel 1985, (14) Minore 1983 (* by layering or root branching)

Table 2.2. Average density (emergents/m²) of propagules in old growth and in disturbed seed bank samples. P is the probability that the disturbed seed bank density is the same as the old growth seed bank. (No comparisons were made between old growth and disturbed seed bank densities for Conyza canadensis and Gnaphalium microcephalum.) f is the number of samples with seeds of that species present. $n = 120$ samples.

Species	Old growth <u>seed bank</u>		Disturbed <u>seed bank</u>		P
	mean	f	mean	f	
Carex deweyana	5.0	2	0	0	0.13
Cirsium sp.	8.3	5	0	0	0.01
Conyza canadensis	0	0	1.7	1	
Epilobium angustifolium	1.7	1	0	0	0.37
Epilobium watsonii	20.0	11	1.7	1	0.003
Gaultheria shallon	8.3	4	8.3	4	1
Gnaphalium microcephalum	0	0	3.3	2	
Juncus effusus	3.3	2	0	0	0.13
Rhododendron macrophyllum	5.3	3	0	0	0.13
Rubus ursinus	10.0	6	1.7	1	0.056
Senecio sylvaticus	21.7	12	1.7	1	0.001
Thuja plicata	1.7	1	0	0	0.37
Tsuga heterophylla	3.3	2	0	0	0.13
TOTAL	88.6		18.4		<0.001

Table 2.3. Species present in the pre-disturbance vegetation but not found in the permanent field plots.

<i>Abies amabilis</i>	<i>Equisetum</i> sp.
<i>Acer macrophyllum</i>	<i>Habenaria unalascensis</i>
<i>Adenocaulon bicolor</i>	<i>Lysichitum americanum</i>
<i>Alnus rubra</i>	<i>Mitella ovalis</i>
<i>Anaphalis margaritacea</i>	<i>Oxalis oregana</i>
<i>Arctostaphylos columbiana</i>	<i>Petasites frigidus</i>
<i>Asarum caudatum</i>	<i>Prunus</i> sp.
<i>Asplenium trichomanes</i>	<i>Pyrola picta</i>
<i>Blechnum spicant</i>	<i>Rosa gymnocarpa</i>
<i>Boykinia elata</i>	<i>Rubus parviflora</i>
<i>Carex</i> sp.	<i>Rubus spectabilis</i>
<i>Chimaphila menziesii</i>	<i>Salix</i> sp.
<i>Circaea alpina</i>	<i>Stachys cooleyae</i>
<i>Clintonia uniflora</i>	<i>Symphoricarpos</i> sp.
<i>Cornus canadensis</i>	<i>Thelypteris ovalifolium</i>
<i>Cornus nutallii</i>	<i>Vaccinium ovalifolium</i>
<i>Corylus cornuta</i>	<i>Vancouveria hexandra</i>
<i>Disporum smithii</i>	<i>Viola glabella</i>
<i>Dryopteris austriaca</i>	<i>Whipplea modesta</i>
<i>Epilobium angustifolium</i>	

Table 2.4. Species composition
of seed traps.

Anaphalis margaritacea
Cirsium sp.
Conyza canadensis
Epilobium angustifolium
Epilobium minutum
Epilobium paniculatum
Epilobium watsonii
Gnaphalium sp.
Gaultheria shallon
Graminae
Hieracium albiflorum
Lactuca serriola
Senecio sylvaticus
Sonchus asper
Tsuga heterophylla
Viola sp.
unknown 1
unknown 2
unknown 3

Table 2.5. Number of individuals (per 40 m²) establishing the first year from each propagule source.

Species	Propagule sources		
	Seed	Vegetative	Undetermined
<i>Acer circinatum</i>		4	
<i>Berberis nervosa</i>		95	
<i>Ceanothus velutinus</i>	44		
<i>Coptis lacinata</i>	1		
<i>Chimaphila umbellata</i>		1	
<i>Epilobium angustifolium</i>	1	13	
<i>Epilobium paniculatum</i>	4		
<i>Epilobium watsonii</i>	4		
<i>Galium</i> sp.	1		
<i>Gaultheria shallon</i>		41	
<i>Rhododendron macrophyllum</i>		19	
<i>Rubus nivalis</i>			1
<i>Rubus ursinus</i>		3	
<i>Sambucus</i> sp.	1		
<i>Senecio sylvaticus</i>	20		
<i>Trientalis latifolia</i>			8
<i>Vaccinium parvifolium</i>			1
<i>Xerophyllum tenax</i>		4	
unknown			1
Total	76	180	11
Percentage of total emergents	28.5	67.4	4.1

Table 2.6. Number of individuals (per 40 m²) establishing the second year from seed, vegetative propagule or undetermined propagule source. (a) Number of individuals of species found in both the seed bank and the seed rain; (b) Number of individuals of species found in the seed rain only; (c) Number of individuals of species with undetermined seed source.

Species	Propagule sources				
	Seed			Vege-	Undeter-
	(a)	(b)	(c)	tative	mined
<i>Berberis nervosa</i>				25	
<i>Cirsium</i> sp.	33				
<i>Conyza canadensis</i>	28				
<i>Epilobium angustifolium</i>	11			4	49
<i>Epilobium paniculatum</i> and <i>Epilobium minutum</i>		1129			
<i>Epilobium watsonii</i>	217				
<i>Gaultheria shallon</i>				14	
<i>Gnaphalium</i> sp.	1				
<i>Hieracium albiflorum</i>		53			
<i>Lactuca serriola</i>		86			
<i>Pseudotsuga menziesii</i>			2		
<i>Rhododendron macrophyllum</i>				5	
<i>Rubus ursinus</i>				1	
<i>Senecio sylvaticus</i>	2757				
<i>Tsuga heterophylla</i>	3				
<i>Trientalis latifolia</i>					4
<i>Vaccinium parvifolium</i>				2	
unknown 1				1	
unknown 2				1	
unknown 3					1
unknown 4				1	
unknown 5				3	
Totals	3050	1268	2	57	54
Percentage of total emergents	68.8	28.6	0.1	1.3	1.2

Chapter 3

FACTORS LIMITING REGENERATION OF OLD GROWTH UNDERSTORY
SPECIES FROM SEED AFTER DISTURBANCEINTRODUCTION

At one time or another most of the world's vegetation is recovering from disturbance. This recovery and the subsequent changes in species composition are called succession, a basic concept in plant ecology. Although many studies describe successional changes, few address the underlying mechanisms (Huston and Smith 1987, Waring and Schlesinger 1985, Finegan 1984, Connell and Slatyer 1977). Understanding these mechanisms is important to develop generalities about succession, to effectively conserve and manage natural resources, to preserve biological diversity and to restore land damaged by human activities (Pickett et al. 1987, Neiring 1987, Jordan et al. 1987, Pickett and White 1985, West et al. 1981).

One important successional process is the initial establishment of vegetation after disturbance (Walker and Chapin 1987, Pickett et al. 1987). The species composition of this initial revegetation can determine subsequent successional patterns, thus controlling the species composition and other ecosystem characteristics of mature successional vegetation (Humphrey 1984, Connell and Slatyer 1977, Drury and Nisbet 1973). The relative contribution of the major propagule sources--seed bank, seed rain and bud bank--determine the species composition of this initial establishment (Chapter 2, Marks and Mohler 1985, Uhl et al. 1982a-b, Uhl et al. 1981). For example,

during the first year after logging and slash-burning of an old growth Douglas-fir forest, most regeneration was from vegetative propagules, i.e., the bud bank (Chapter 2). Even though the site was surrounded by old growth forest, virtually no old growth understory species regenerated from seed. To determine why three dominant understory species, Berberis nervosa, Gaultheria shallon and Linnaea borealis, did not regenerate from seed, I investigated their seed production, seed viability, seed dispersal, and rate of seedling establishment.

METHODS

Study site

Field work for this research was done at the H. J. Andrews Experimental Forest, a Long-Term Ecological Research Site, located in the western Cascade Mountains about 80 km east of Eugene, Oregon. The 3.2 ha study site is located on a north-facing slope at 790-825 m elevation, with a fairly uniform 20-30% slope. Before disturbance, the vegetation was dominated by old growth western hemlock (Tsuga heterophylla) and Douglas-fir (Pseudotsuga menziesii) with some western redcedar, (Thuja plicata). The understory included Gaultheria shallon, Berberis nervosa, Linnaea borealis, Vaccinium parvifolium and Rhododendron macrophyllum. The habitat-type is hemlock/rhododendron/dwarf Oregon grape (Dyrness et al. 1974). The site was clear-cut logged during fall, 1985, and burned in early July, 1986. Slash, except for very large pieces, was left in place and burned with a light intensity fire. Soil temperatures during burning were <52C-177C at the surface, <39-139C at 2 cm deep, 52C-66C at 4 cm and <52C at 6 cm (M. V. Wilson, unpublished data).

Study species

Berberis nervosa (dwarf Oregon grape): This evergreen shrub is typically 20 cm - 50 cm tall and spreads with underground stems, which can sprout after disturbance (Hitchcock and Cronquist 1981). The long flower stalks produce showy yellow flowers in early spring. The blue fleshy fruits contain several hard-coated seeds for which the germination requirements are unknown.

Gaultheria shallon (salal): This evergreen shrub generally grows 1 to 2 meters tall and also sprouts after disturbance. Each fleshy purplish "fruit" (capsule) contains an average of 126 tiny seeds (Sabhasri 1961) that germinate easily (Kruckeberg 1982) and appear to have no dormancy requirements.

Linnaea borealis (twinline): This creeping herb-like shrub with 1-2 cm evergreen leaves spreads from aboveground runners (Antos and Zobel 1984). The two fruits per stem are small, dry, indehiscent (Kruckeberg 1982) and contain one seed each, for which the germination requirements are unknown.

Seed production

In late August 1988, a total of twenty-two 3 m x 3 m plots were randomly selected in four locations in the old growth forest surrounding the disturbed site. On these plots, plant cover and number of fruits of each study species was measured. In plots with dense cover of Linnaea borealis, only 1.5 m x 1.5 m of the plot was sampled.

Forty-three randomly selected fruits of Gaultheria shallon were collected from the 3 m x 3 m plots, the number of seeds counted for each fruit and the average number of seeds per fruit calculated. (No fruits of Berberis nervosa were found. The average ground cover and the average number of seeds per m² of cover were calculated for each species.

Viability

Fruits of Linnaea borealis and Gaultheria shallon were randomly collected from the same field plots used to determine seed production. Germination tests were used to determine viability of Gaultheria shallon seeds. Tests were conducted at 20/15 C (with light), with six repetitions of 100 seeds each. The seeds were placed on moist filter paper in petri dishes and germination monitored until none occurred for 14 days. Because of the difficulty in germinating Linnaea borealis seeds, robustness of seeds was used to determine viability. One hundred seventy Linnaea borealis fruits were cut and examined; any plump filled seeds were considered viable.

Dispersal

For seed traps, a 9-cm diameter plastic petri dish lid with a hole drilled in the center was lined with filter paper (Werner 1975). A large nail was inserted through both the filter paper and the hole in the petri dish lid. These units were placed in the field by pushing the nail firmly into the soil until the trap bottom was level with the ground. The filter paper was covered with Tanglefoot, a non-drying sticky material (Tanglefoot Co., Grand Rapids, Mich.) that binds any seeds contacting it.

In July, 1988 ten traps were placed in the disturbed site, 1 m apart along each of five randomly chosen 9 m transects (total area = 0.32 m²). Similarly in the old growth, ten seed traps were placed along eight transects (total area = 0.51 m²). Until October the filter papers in the traps were replaced whenever they filled with

seeds and debris. Filter papers were then examined under a dissecting microscope for presence of Linnaea borealis, Berberis nervosa and Gaultheria shallon seeds. For each species, the number of dispersed seeds per m² was calculated.

Seedling establishment

Seeds of Berberis nervosa, Linnaea borealis and Gaultheria shallon were collected throughout the disturbed and old growth site in late summer, 1988 and stored at room temperature until sown in late October 1988. I pooled the seeds for each species and then selected robust seeds for the experimental sowing. For Berberis nervosa and Linnaea borealis I sowed 25 seeds of each species into each of 20 randomly chosen 30 cm x 30 cm plots located on the disturbed site. For Berberis nervosa I sowed 20 seeds into each of 20 randomly chosen 30 cm x 30 cm plots. Because Berberis nervosa seeds appeared to have hard seed coats, the seeds in 10 plots were scarified by sanding and the seeds in the others were not. Twenty control plots were also randomly selected. In May 1989, the plots were observed for any seedlings of the three species.

RESULTS

Seed production and viability

Berberis nervosa, which had the most abundant cover of the three species within my plots, produced no seeds on the plots (Table 3.1). Gaultheria shallon and Linnaea borealis had similar cover, but Gaultheria shallon produced 227 seeds/m² (standard error = 87) and Linnaea borealis, only 3 seeds/m² (s.e. = 2) (Table 3.1).

The viability of Gaultheria shallon seeds was twice that of Linnaea borealis (Table 3.1).

Dispersal and Establishment

The seed traps contained only one of the species under investigation, Gaultheria shallon. The average density of seeds trapped in the old growth and in the disturbed site did not differ significantly (Table 3.1) (Mann-Whitney test, $P = 0.77$), but both are much less than the density of seeds produced. No seedlings were observed in the experimentally sown plots for any of the three species.

DISCUSSION

One process, common to all three species, that limited regeneration from seed in this study was emergence. None of species studied established from experimentally sown seeds, although all three grow well as adults on disturbed sites (Halpern 1988, Dyrness 1974). Other studies also show Gaultheria shallon does not establish from seed on open sites (Tappeiner and Zasada 1988). Previous work at this site showed that even though Gaultheria shallon is present in the seed bank and the seed rain, it did not emerge on the disturbed site from seed (Chapter 2). However, Gaultheria shallon does emerge from seed bank samples and soil seed traps when the samples are grown under greenhouse condition (Chapter 2), suggesting the lack of appropriate conditions for emergence in the field.

Fire affects the post burn microenvironment, including chemical and physical properties of the soils, which could strongly affect seedling survival and establishment (De Bano et al. 1979). Both the maximum soil temperature and the range of soil temperatures can increase due to blackened soil and these temperatures are often lethal to seedlings (Heinselman 1981). These factors possibly limited safe-sites at my research site.

Even if environmental conditions were suitable for establishment, regeneration of these understory species would be limited by other processes. Seed production was low for Berberis nervosa and Linnaea borealis during the year of measurement. Because seed production of woody perennials may vary considerably (Davies 1976), long-term data are needed to determine variability in seed

production. Seed production by Gaultheria shallon is greater (1926 seeds/flowering stalk, Sabhasri 1961) than by Linnaea borealis (approximately 2 seeds/flowering stalk) but still small compared to early successional species such as Senecio sylvaticus and Epilobium angustifolium, which produce 8,564 cypelas/plant (West and Chilcote 1968) and 20,000 - 80,000+ seeds/live stem (Haeussler and Coates 1986) respectively. Low seed viability in Linnaea borealis would further limit regeneration from seed.

One explanation for low seed production of these species is that understory species of mature forests generally regenerate vegetatively (Antos and Zobel 1984, Roberts 1981, Abrahamson 1980, Cook 1980, cf. Bierzychudek 1982). One study suggested that Linnaea borealis and other understory species that have extensive vegetative spread rarely establish from seedlings (Antos and Zobel 1984). Increased shading and sequestering of nutrients by woody dominants can limit seed production of understory species (Bunnell 1990, Barrett and Helenurm 1987, Helenurm and Barrett 1987, Haeussler and Coates 1986, Sabhasri 1961). For example, Gaultheria shallon does not fruit under canopies with greater than 30% closure (Bunnell 1990, Haeussler and Coates 1986). However, when stress, e.g., shading, is removed, many of these forest understory species, including Gaultheria shallon, increase seed production (Haeussler and Coates 1986, Sabhasri 1961). The most abundant fruit production of Gaultheria shallon in this study appeared to be on the plots receiving the most light (personal observation).

Two possible explanations for the difference between the number of Gaultheria shallon seeds produced and the number in the seed traps are (1) dispersal agents such as birds and mammals (Sabhasri 1961, USDA 1974), were lacking, so seeds remained on the plant until later in the winter or (2) pre- or post-dispersal mortality (e.g., by mammals) was high. If seed production is generally low (and possibly coupled with high pre-or post-dispersal mortality) seeds of all three species are not likely to be incorporated into the seed bank in great numbers. This is consistent with the low densities of seed bank propagules at this site (Chapter 2, Ingersoll and Wilson in press).

Similar mechanisms limiting regeneration from seed are found in other systems. Low seed production, limited dispersal distance and short-lived seeds cause poor regeneration of pre-disturbance species after logging of an 100-year old Douglas-fir forest in British Columbia (Kellman 1974). Poorly dispersed seeds and lack of seed bank propagules limit regeneration of primary trees of tropical forests in Venezuela after logging and burning coupled with farming (Uhl et al. 1982a-b, Uhl et al. 1981). Few seedlings of understory species established under the intact forest canopy the first four years following the eruption of Mount St. Helens, Washington (Antos and Zobel 1985). Colonization of the deforested terrain on Mount St. Helens was also limited; poor seedling establishment and poor dispersal of available seed were the restricting factors (Wood and del Moral 1987). Recovery of pre-disturbance species is slower in many of these ecosystems because regeneration was primarily from

slowly dispersed off-site seed (Kellman 1974, Uhl et al. 1982a-b, Wood and del Moral 1987).

The patterns of non-establishment, low seed production and low dispersal rates shown by Berberis nervosa, Gaultheria shallon and Linnaea borealis, which are common and often dominant understory species of old growth Douglas-fir forests, may indicate similar patterns for the other understory species. If so, regeneration of understory species from seed will be necessarily slow in the first years after disturbance. Because many of these old growth understory species are capable of regenerating vegetatively, the bud bank rather than the seed bank or dispersed seed is crucial in forest regeneration immediately after disturbance.

Table 3.1. Factors influencing regeneration of Berberis nervosa, Gaultheria shallon and Linnaea borealis from seed after disturbance. The number of Gaultheria shallon seeds dispersed into the old growth does not differ significantly from the seed rain on the disturbed site.

	<u>Berberis</u> <u>nervosa</u>	<u>Gaultheria</u> <u>shallon</u>	<u>Linnaea</u> <u>borealis</u>
Cover (percent) (s.e.)	18 (4)	4 (1)	4 (2)
Seed production (mean/m ²) (s.e.)	0	227 (87)	3 (2)
Viability (percent) (s.e.)		36 (5)	18 (2)
Seed rain: old growth (mean/m ²) (s.e.)	0	18 (11)	0
Seed rain: disturbed site (mean/m ²) (s.e.)	0	6 (4)	0
Seedling establishment: experimental sowing (percent)	0	0	0
Seedling establishment: field studies (Chapter 2) (mean/m ²)	0	0	0

Chapter 4

EFFECTS OF HEAT TREATMENTS ON SEEDS FROM AN OLD GROWTH

DOUGLAS-FIR FOREST SEED BANK

INTRODUCTION

The initial establishment of vegetation after disturbance is important (Walker and Chapin 1987, Pickett et al. 1987, Hibbs 1983) because the species composition can initiate fundamentally different successional patterns, thus determining the characteristics of mature vegetation (McCune and Allen 1985, Humphrey 1984, Connell and Slatyer 1977, Drury and Nisbet 1973, Egler 1954).

The species composition and abundance of the post-disturbance vegetation depends on the relative contribution of the major propagule sources--seed bank, seed rain and bud bank (Chapter 2, Marks and Mohler 1985, Uhl et al. 1982a-b, Uhl et al. 1981). Thus, to predict patterns of early revegetation, one must understand the mechanisms that determine the contributions of the propagule sources. In particular, the contribution of seed bank propagules to regrowth after disturbance will depend in part on their survival of disturbance.

The survival of seed bank propagules after fire depends on its severity. Severe fires consume more organic matter and produce a greater degree and duration of heat than less intense fires (Rowe 1983); thus, fewer seed bank propagules will survive (Moore and Wein 1977). The depth of heat penetration into the soil depends on duff consumption (Johnston and Woodard 1985, Armour et al. 1984) and

moisture content of the soil (Al Nakshabandi and Kohnke 1965), which is related to the time of the year (Wright and Bailey 1982, Ohmann and Grigal 1981). Seed characteristics also influence post-fire seed availability. Seeds found deeper in the soil are more protected from fire (Garwood 1989, Moore and Wein 1977). Seeds with thick, hard seed coats or cuticles survive fires better than seeds with thin, soft seed coats (Parker and Kelly 1989). The season in which fire occurs may determine seed survival because seeds are generally intolerant of heat after stratification but survival is unaffected or enhanced by pre-stratification heat (Pratt et al. 1984). Moist seeds are more susceptible to heat than dry seeds (Parker and Kelly 1989, Salisbury and Ross 1985).

The goal of this study was to understand, by using experimental heat treatments, the effect of fires of varying intensities on the availability of seeds of several species found in the seed bank of an old growth coniferous forest.

METHODS

The species selected for this research were Gaultheria shallon, Cirsium vulgare, Epilobium angustifolium, Senecio sylvaticus, Carex deweyana, and Rhododendron macrophyllum. These species contributed 57% of the seeds in the seed bank of an old growth coniferous forest located in the western Cascades at the H.J. Andrews Experimental Forest, Oregon, a NSF Long-Term Ecological Research Site (Chapter 2).

The site, at 790-825 m elevation, is dominated by old growth western hemlock (Tsuga heterophylla) and Douglas-fir (Pseudotsuga menziesii), with some western redcedar (Thuja plicata) (M. V. Wilson, unpublished data). The understory included Berberis nervosa, Linnaea borealis, Vaccinium parvifolium, Rhododendron macrophyllum and Gaultheria shallon. The habitat-type is hemlock/rhododendron/dwarf Oregon grape (Dyrness et al. 1974). Seeds were gathered at this site during the summer of 1988 and stored dry at 4C until experimental treatment in early 1990.

The six experimental treatments were: seeds were heated in dry soil at three temperatures--50C for one hour, 75C for 15 min and 100C for 15 min, and seeds were heated in moist soil at the same three temperatures for the same durations. For each heat treatment two test tubes (2.5 cm diameter x 15 cm) per species were placed in a water bath. Each tube was filled with 20 seeds mixed with approximately 15 cm³ dry soil; 10 ml of water was added to the second tube which then sat for 3 minutes before being placed in the water bath. (For Cirsium 10 seeds were used for each test tube). This

procedure was repeated five times for a total of five replications per experimental treatment.

In preliminary tests thermistors were placed in a test tube filled with soil at four locations: the surface, the center, the bottom and along the side between the soil and the glass. Temperatures were recorded during each of the six experimental treatments. These tests showed that (1) the temperature of the soil was the same as the temperature of the water bath at equilibrium, with the exception of the dry soil at the 100C treatment, which was 98C, (2) the soil temperature was uniform throughout the test tube during each treatment, and (3) it took approximately 7-10 minutes for the soil in the test tubes to equal the temperature of the water bath.

After each heat treatment with dry soil the contents of each test tube were emptied into a petri dish. After the wet treatments for all species, residues in the test tubes were rinsed with distilled water, filtered, dried and added to the appropriate petri dish. Five controls (no heat treatment) using the same extraction procedure following the dry soil treatment were run for each species.

The petri dishes were placed in a controlled environment with 14 hours of light at the appropriate germination temperature and moistened with distilled water as needed. Preliminary tests showed that Gaultheria shallon, Senecio sylvaticus and Rhododendron macrophyllum germinated best with alternating temperatures of 20/15C. The other species germinated best at alternating temperatures of

30/20C. The number of germinating seeds was counted until no new germination occurred for at least 14 days. Seeds were considered germinated when the shoot could be seen.

RESULTS AND DISCUSSION

Germination percentages were not significantly affected at 50C with either the wet or dry treatments with the exception of Epilobium angustifolium in the wet soil (Table 4.1). At 75C germination was eliminated with wet soil, while in the dry soil 75C produced results similar to 50C (Table 4.1). Germination percentages were reduced for all species at 100C with both the wet and dry treatments (Table 4.1).

It is not clear why there was a difference between the wet and dry soil treatments at 75C. Preliminary tests showed that the temperature between the dry and wet soils never varied more than 0.9C for the 75C treatment. These tests also showed that the temperature throughout the soil was uniform for both the wet and dry soil treatments. The wet treatments probably retained heat longer after removal from the water bath (personal observation); thus, more seeds could have been killed with the longer heat duration. The seeds in the wet soil possibly imbibed more water than those in the dry soil. Seeds, particularly those of herbaceous species, that absorb moisture beyond 20% of their dry weight are quite sensitive to heat when imbibed (Parker and Kelly 1989). Imbibition reduces both the maximum temperature and duration tolerated (Parker and Kelly 1989), possibly because enzymes are more susceptible to heat denaturation when hydrated than when dry (Salisbury and Ross 1985).

Comparisons with other studies of laboratory heat treatments are difficult to make because the duration of temperature varies between studies and it is not always clear if the reported

temperature and duration were actually experienced by the seed. For example, preliminary tests in this study showed that equilibrium of the soil temperature with the water bath temperature was reached in about 7-10 minutes; thus, the duration of the treatment temperature was less than the total time in the water bath. Other studies probably show similar patterns.

Nevertheless, comparisons of these results with those of other studies are useful. In this study, germination percentages of each species were significantly reduced after heating to 100C; no seeds germinated in wet soil. In contrast, other studies show that seeds of several species can survive temperatures greater than 100C (Keeley et al. 1985, Strickler and Edgerton 1976). Some species not only survive the higher temperatures but increase the percent of germination (Boone 1986, Keeley et al. 1985, Mallik and Gimingham 1985, Gratkowski 1962).

Although seeds of early successional annuals, herbaceous perennials and old growth species were tested, the germination responses to the temperature and moisture treatments were similar for all species except Epilobium angustifolium (Table 4.1). Other studies, in contrast, report a diversity of responses by seeds within an ecosystem to heat treatments (Bell et al. 1987, Mallik and Gimingham 1985, Keeley et al. 1985). For example, seeds of herbaceous perennials in chaparral are more heat sensitive than seeds of annuals and suffrutescent perennials (Keeley et al. 1985). Longer heating at a lower temperature is more detrimental for chaparral species with large seeds than short durations at high temperature

(Keeley 1987). Thus, with a diversity of responses to heat, generally some seed bank species will survive and be available for establishment after a particular fire intensity. In this study, however, the response of the old growth seed bank species is "all-or-nothing"; i.e., either all the species survive a particular fire intensity or none do. In ecosystems in which seed bank species have a diversity of survival abilities, there may be a greater potential for varied revegetation patterns than in a region where the seed bank species all respond similarly.

The mean seed bank densities for experimental species except Gaultheria shallon were less on a logged and burned site than on an old growth forest site (Chapter 2). The results of this experimental study are consistent with the hypothesis that high temperatures during burning reduced seed bank densities.

Combining these experimental results with soil temperature data recorded during the low-intensity fire following logging of the old growth site indicates that seeds located within 2 cm of the soil surface probably did not survive even the relatively cool temperatures of this fire. Temperatures (M. V. Wilson, unpublished data) at the top of the mineral soil ranged from $<52^{\circ}\text{C}$ to 177°C , temperatures at 2 cm from $<39^{\circ}\text{C}$ to 139°C . Both of these ranges extend into the lethal temperatures for seeds ($>75^{\circ}\text{C}$) found in this study. Those seeds buried deeper probably survived because of decreased temperatures (52°C - 66°C at 4cm and $<52^{\circ}\text{C}$ at 6 cm). But deeper burial may also decrease the chance of seedling emergence and subsequent establishment of all except the large seeded species. Thus, few seed

bank seeds would have been available for establishment after fire, even one of low intensity. The post-disturbance vegetation would, therefore, depend on vegetative propagules or dispersed seed. This prediction is consistent with the revegetation patterns observed immediately after logging and burning--vegetative propagules contributed 67% of the individual establishing in the first year; in the second year, 98% of the individuals established from dispersed seed (Chapter 2).

Table 4.1. Mean seed germination percentages of six old growth coniferous forest understory species following seven experimental heat treatments. The treatments were as follows: W50, 50C for 60 min in wet soil, W75, 75C for 15 min in wet soil, W100, 100C for 15 min in wet soil, D50, 50C for 60 min in dry soil, D75, 75C for 15 min in dry soil, D100, 100C for 15 min in dry soil and (CON) control. n=5

\bar{P} is the probability that the treatment mean is the same as the control mean for each species.

SPECIES	TREATMENTS						
	W50	W75	W100	D50	D75	D100	CON
<i>Carex deweyana</i>	85.0	0.0**	0.0**	89.0	89.0	0.0**	89.0
<i>Cirsium vulgare</i>	34.0	0.0**	0.0**	44.0	32.0	6.0*	62.0
<i>Epilobium angustifolium</i>	0.0**	0.0**	0.0**	26.0	30.0	0.0**	20.0
<i>Gaultheria shallon</i>	21.0	0.0**	0.0**	20.0	10.0	1.0**	17.0
<i>Rhododendron macrophyllum</i>	37.0	0.0**	0.0**	33.0	48.0	2.0**	41.0
<i>Senecio sylvaticus</i>	72.0	0.0**	0.0**	72.0	76.0	29.0**	87.0

* $\bar{P} < 0.05$

** $\bar{P} < 0.01$

Chapter 5

CONCLUSIONS

The revegetation patterns differed remarkably between the first and second years (Chapter 2): only ten species were common to both years' establishment, the density of the second year's establishment was about 16 times that of the first, and old growth species dominated the first year's establishment in contrast to the dominance of early successional species the second year. Understanding such mechanisms as pre-disturbance availability of seed bank and bud bank propagules (Chapter 2) , their survival of disturbance (Chapter 2 and 4), and dispersal (Chapters 2 and 3) help explain the causes of these revegetation patterns (Figure 5.1).

Old growth understory species generally established from bud bank propagules only (Chapters 2 and 3). Because most vegetative sprouting will take place immediately after disturbance or during the first growing season after disturbance, few vegetative propagules will sprout the second year; thus, few old growth species established the second year (Chapter 2).

The density of the old growth seed bank was low and was dominated by propagules of early successional species--only 7 of the 67 pre-disturbance old growth species were present (Chapter 2). Low seed production and low seed viability of the old growth understory species (Chapter 3) may explain their low representation into the seed bank. Thus, the potential of the seed bank to contribute

propagules to the regeneration of old growth understory species is low.

Similar patterns of low seed production, low seed viability and low dispersal shown by Berberis nervosa, Linnaea borealis and Gaultheria shallon, three common and often dominant old growth understory species (Chapter 3), may explain why few old growth understory species were present in the second year seed rain (Chapter 2). The failure of these three species to emerge from experimental sowing on the disturbed site (Chapter 3) also indicates that even if seeds were available in the seed bank or seed rain, lack of establishment will limit regeneration of old growth understory species from seed. Thus, because of the general lack of propagules of old growth understory species in the seed rain and the seed bank (Chapters 2 and 3) and the greater availability in the bud bank (Chapter 2), old growth species established primarily in the first year.

In contrast to the old growth species, early successional species established primarily the second year (Chapter 2). Although early successional species dominated the old growth seed bank (Chapter 2), the potential of the seed bank to contribute propagules to the first year's vegetation was low, particularly after loss of seed from heating (Chapters 2 and 4). Seed rain propagules were either absent the first year or were unable to establish. In the second year, however, seed rain propagules of early successional species were abundant, particularly those of Senecio sylvaticus, Epilobium paniculatum and Epilobium minutum (Chapter 2). This

greater abundance was probably caused by copious on-site seed production of the few individuals establishing the first year. This abundant seed availability also contributed to the greater density of individuals establishing the second year compared to the first (Chapter 2). Thus, a relatively rare event of a few individuals establishing one year from seed can have important consequences for the species composition and density of revegetation in following years.

This research demonstrates that the early post-disturbance vegetation established over more than one year, and that timing of establishment is closely related to the species' method of regeneration (seed or vegetative), which is in turn closely related to whether the species were early or late successional species. For example, old growth species generally established only in the first year and primarily from vegetative propagules. In contrast, early successional species generally established only in the second year and primarily from seed. Thus, initial revegetation patterns can be interpreted in terms of the propagule sources and how the relative importance of these sources varies with time. The following mechanisms are important in determining the contribution of these propagules sources: (1) the biological legacy of the pre-disturbance community in the form of seed bank and bud bank propagules, (2) the influence of disturbance on the survival and establishment of this legacy and (3) the availability of dispersed seed and the influence of disturbance on seedling establishment.

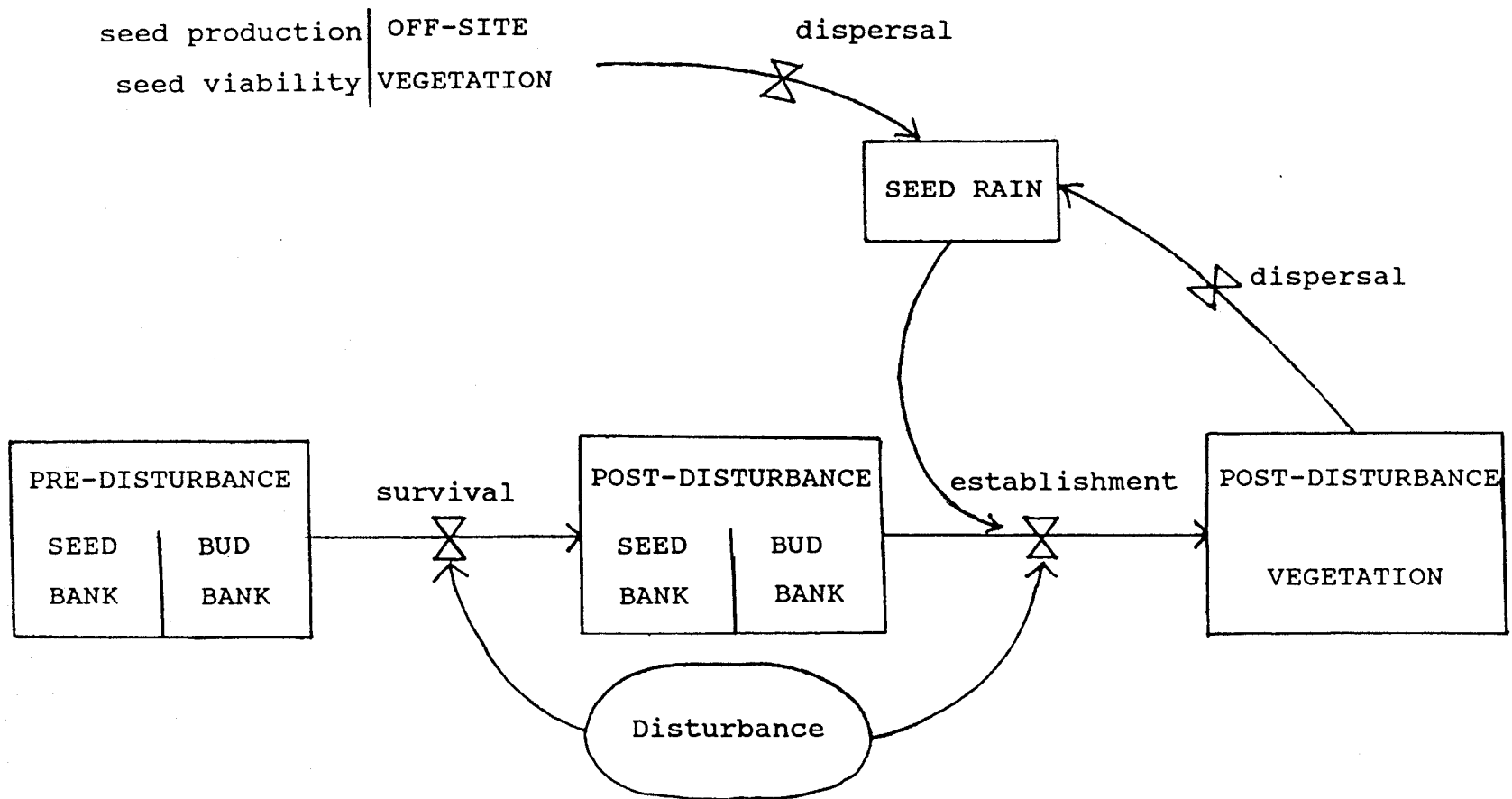


FIGURE 5.1 Factors influencing post-disturbance vegetation

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