AN ABSTRACT OF THE THESIS OF

Christopher R. Keyes for the degree of Doctor of Philosophy in Forest Resources presented on August 10, 2001. Title: Recruitment of Ponderosa Pine Seedlings Beneath Partial Overstories.

Abstract approved: ______________________________
Douglas A. Maguire

The objective of this project was to investigate the fate of ponderosa pine regeneration from seed to established seedling, and to determine the relative influences of several important stand elements on those fates. The project was carried out in a series of observational and experimental recruitment studies in central Oregon.

In an analysis of the temporal and spatial patterns of seedfall during one season, viable seeds accounted for 62-73 percent of all seeds, and seed density averaged more than 1 million per hectare. More than half of all viable seeds fell within the first 30 days. Seedfall occurred more rapidly at the more mesic site. The less mesic site produced more seed, and the denser stand within each site yielded more seed. Seedfall patterns within each stand were not spatially uniform. At the two stands of moderate densities, the relationship of seed density to distance from trees followed a negative binomial distribution.

In an observational study of germinant emergence and survival, about 3 percent of viable seed resulted in emergents. A small fraction of germinants

survived the first summer, with most mortality occurring immediately after emergence. Most emergents were from caches, and germinants from caches remained a substantial portion of the cohort after two seasons. Mineral soil substrates produced fewer emergents and were associated with higher mortality rates than litter substrates. Understory cover produced fewer germinants than open locations, but mortality rates were lower. After one year, most survivors were beneath understory cover.

In a seed-sowing experiment, less than 30 percent of seeds sown in fall resulted in live germinants the following spring, and just 5 percent resulted in live germinants by the following fall. Shrubs had no effect on germinant emergence rates, but germinants under shrubs succumbed to desiccation more slowly. Nearly 4 of 5 germinants that survived the first summer were beneath shrubs. Shrubs reduced solar radiation and reduced soil temperatures, especially during midday, but did not affect relative humidity or air temperature. Shallow burying of seeds to mimic rodent caching greatly improved emergence rates, with nearly 90 percent of all germinants emerging from buried seed.

Recruitment of Ponderosa Pine Seedlings Beneath Partial Overstories

by

Christopher R. Keyes

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APPROVED:

Major Professor, representing Forest Resources

Head of Department of Forest Resources

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Christopher R. Keyes, Author

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CONTRIBUTIONS OF AUTHORS

Steven A. Acker and Sarah E. Greene were co-authors of a paper that was an earlier draft of Chapter 3. All data were collected and managed by Sarah Greene. The analysis was conducted by Christopher Keyes with assistance from Steven Acker. The paper has been published as:

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CHAPTER 1

INTRODUCTION

PONDEROSA PINE SEEDLING RECRUITMENT

In silivicultural systems that depend on natural regeneration, the recruitment of a cohort of seedlings is the first and most critical process following harvest. The spatial and temporal patterns of seedling recruitment set the stage for all subsequent stand developmental patterns; hence, the seedling recruitment stage is the first step in determining future silvicultural options. In large part this critical stage determines the success or failure of the entire silvicultural system. An understanding of the natural regeneration process, and the stand elements that have bearing on those processes, is vital to attaining stand goals under silvicultural systems that rely on natural regeneration.

In ponderosa pine forests of central Oregon, the relationship of stand elements – overstory trees, understory shrubs, forest floor, and animal communities – have particularly strong bearing on the patterns of tree seedling recruitment relative to more productive sites. In this region, ponderosa pine forests experience a harsh climate with cold winters and hot, dry summers. Annual precipitation is limited and a regular period of drought occurs throughout much of the growing season (Table 1.1). These climatic conditions are exacerbated by the relatively young, poorly developed, mineral deficient, and

TABLE 1.1. Climatic conditions in the area covered by this project (data from NOAA climate station at Bend, Oregon). Note summertime high temperatures and scarce precipitation (shaded).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Mean Temp (C)													
Max	5.3	7.9	10.6	14.2	18.4	23.1	27.5	27.2	22.8	17.3	9.2	5.4	15.7
Min	-5.6	-4.2	-3.4	-1.6	1.4	5.1	7.2	7.0	3.0	-0.4	-2.7	-5.3	0.1
Mean	-0.1	1.9	3.6	6.3	9.9	14.1	17.3	17.1	12.9	8.4	3.2	0.1	7.9
Extreme Temp (C)													
Max	19.4	21.1	25.0	30.0	33.3	35.6	36.7	38.9	35.0	32.2	23.3	18.9	38.9
Min	-31.1	-27.2	-20.6	-12.8	-10.6	-5.0	-2.8	-2.8	-8.9	-16.1	-23.3	-31.1	-31.1
Precipitation (mm)													
Monthly	46.5	24.6	23.4	15.2	19.6	21.8	12.4	14.7	11.9	16.5	39.9	50.5	297.2
Extreme 24-hour	47.5	38.9	23.1	32.0	20.6	39.4	32.5	20.8	29.7	15.5	48.3	57.4	57.4
Snowfall (cm)													
Monthly Mean	25.5	9.8	10.5	5.0	0.8	0.0	0.0	0.0	0.0	0.5	14.3	24.1	88.3

highly porous volcanic soil types that dominate the region. Together, climatic and soil conditions present environmental challenges to tree survival, growth, and regeneration. These conditions make seedlings more susceptible to influence by other biotic stand elements. But which elements?

Previous studies of regeneration in this region have provided indications of the primary factors driving ponderosa pine recruitment processes. But in some cases these findings conflict. Do shrubs promote or disfavor tree regeneration? Do they facilitate seedling survival by ameliorating the harsh climate, or are they important competitors for the highly-restricted below-ground resources? Do their effects change over the course of seedling establishment and growth? Most studies have targeted only a single stage of seedling recruitment, sometimes resulting in conflicting and hence confusing advice for forest managers. The situation is not unique to ponderosa pine. A review of tree seedling recruitment research by Clark et al. (1999) revealed that most studies were geographically limited, short in duration, and restricted to a single stage of regeneration.

The goal of this project was to quantitatively determine the relative impact of stand elements on regeneration in a series of studies that addressed the fate of individuals from seed to established seedling. The studies were designed to characterize the temporal patterns of important regeneration processes – such as the spatial and temporal patterns of seedfall or germinant mortality – and determine how those patterns differed under different stand conditions. They were also constructed to quantify spatial patterns – patterns of seedling attraction or repulsion by overstory trees and understory shrubs. By incorporating different stages of seedling recruitment in a single comprehensive project, it was intended that these analyses would provide a better, more quantitative basis for understanding ponderosa pine regeneration dynamics, and possibly reconcile past discrepancies over the impact of trees and shrubs on ponderosa pine recruitment.

STUDY AREAS

The studies in this project represent the initial findings from a long-term project, and were based on data collected from a subset of study sites (Keyes and Maguire 2000). For that long-term project, study sites were located in 19 stands at 3 sites in central Oregon (Figure 1.1). These three sites included Warm Springs (the Warm Springs Indian Reservation; 7 stands), Pringle Falls (Pringle Falls Experimental Forest, and the Bend Ranger District of the Deschutes National Forest; 8 stands), and Fort Rock (the former Fort Rock District of the Deschutes National Forest; 4 stands). Most of the stands were subjected to operational regeneration harvests performed within the past 20 years, but retained a range in overstory density from zero to approximately 80 percent crown closure. Other stands had been thinned to specific density levels for other studies of growth, yield, and stand dynamics (e.g., Levels of Growing Stock (LOGS) sites). In addition to variation in overstory retention levels, the stands were selected to represent a range of site qualities and shrub communities.

During the summer 1998, grids of circular 50 m^2 and 10 m^2 plots were installed and permanently monumented in each stand. The plots were distributed

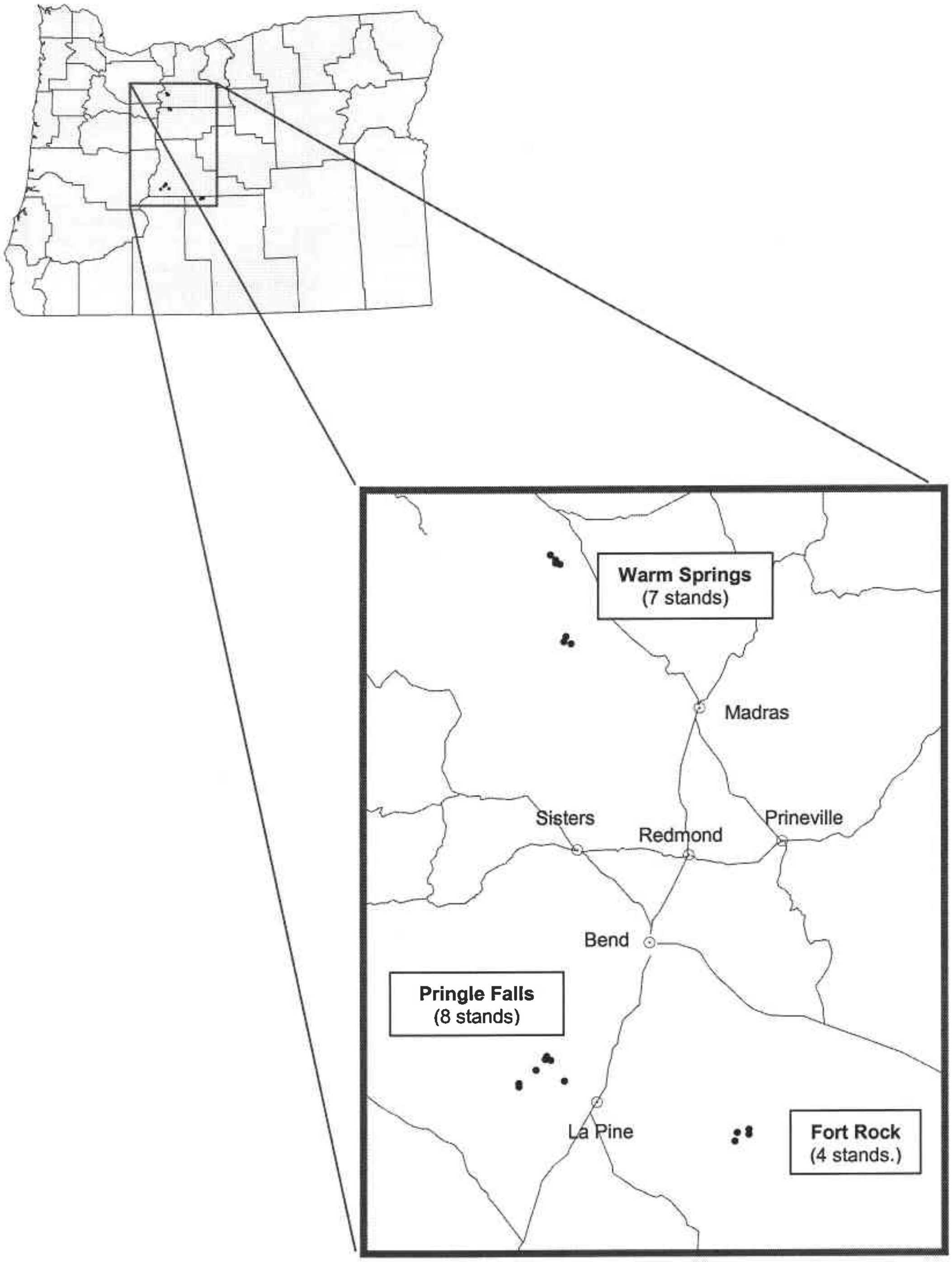

FIGURE 1.1. Location of the 3 areas and 19 stands used in the long-term project. The studies in this dissertation are located in stands at the Fort Rock and Pringle Falls sites.

on a 20-m grid within square 1-hectare treatment blocks. Where necessary, smaller blocks of 0.64 or 0.36 hectare were installed. The large plots were the sampling unit for seedlings larger than 10 cm in height, whereas the small plots were the sampling unit for seedlings smaller than 10 cm in height and for new germinants. Seed traps were installed on similar grids in each of two stands at Pringle Falls and Fort Rock.

MEASURED VARIABLES AND ANALYSIS METHODS

Response variables measured in this project were those of primary interest to ecologists and silviculturists. Response variables included seed counts and percent viability, germinant density, seedling density, and an index relating the spatial relationship between seedlings and shrubs (constructed specifically for this project).

Although some plots sampled in this project were from controlled experiments, the project itself drew largely from operational units. Hence, explanatory factors were chosen to describe the range of conditions at the stands selected for study. Other important variables were selected for measurement or characterization on the basis of previous research in ponderosa pine regeneration. Class variables describe forest floor substrates; plant associations (a proxy for site quality); shrub species composition; and rodent caching.

The studies in this project use a variety of statistical methods to quantify regeneration processes, and to test for differences between site factors influencing those processes. Generally, the statistical models were not intended to yield predictive tools, but were the vehicle for testing hypotheses about the effect of factors on regeneration. Seed production and seasonal weather fluctuate drastically, causing germination and survival to vary from year to year. Because the time of this project was restricted to one or two seasons, such variation cannot be incorporated into the statistical models. However, other site factors important in the regeneration process are probably consistently influential regardless of weather and seed production. Therefore, it should be possible in the short term to define the relevant factors shaping regeneration dynamics; this assumption has been basic to the various components of the project. For long-term dynamics, the study areas established for this study will be maintained and measured into the future so that predictive models representing the range of variation in seed production and seasonal weather can be developed.

OVERVIEW OF THE CHAPTER ANALYSES

This project comprises one literature review chapter (Chapter 2), an initial pre-project regeneration analysis located in a separate study area (Chapter 3), and three chapters specific to study areas at the Fort Rock and Pringle Falls sites (Chapters 4-6). Chapters 4-6, the project's core studies, address a partial chronosequence of ponderosa pine regeneration processes from seedfall to seedling establishment. The relationships among the core analysis chapters are illustrated in Figure 1.2.

Chapter 2 is a review of processes that drive natural regeneration in ponderosa pine forests, and of the factors that contribute to successful

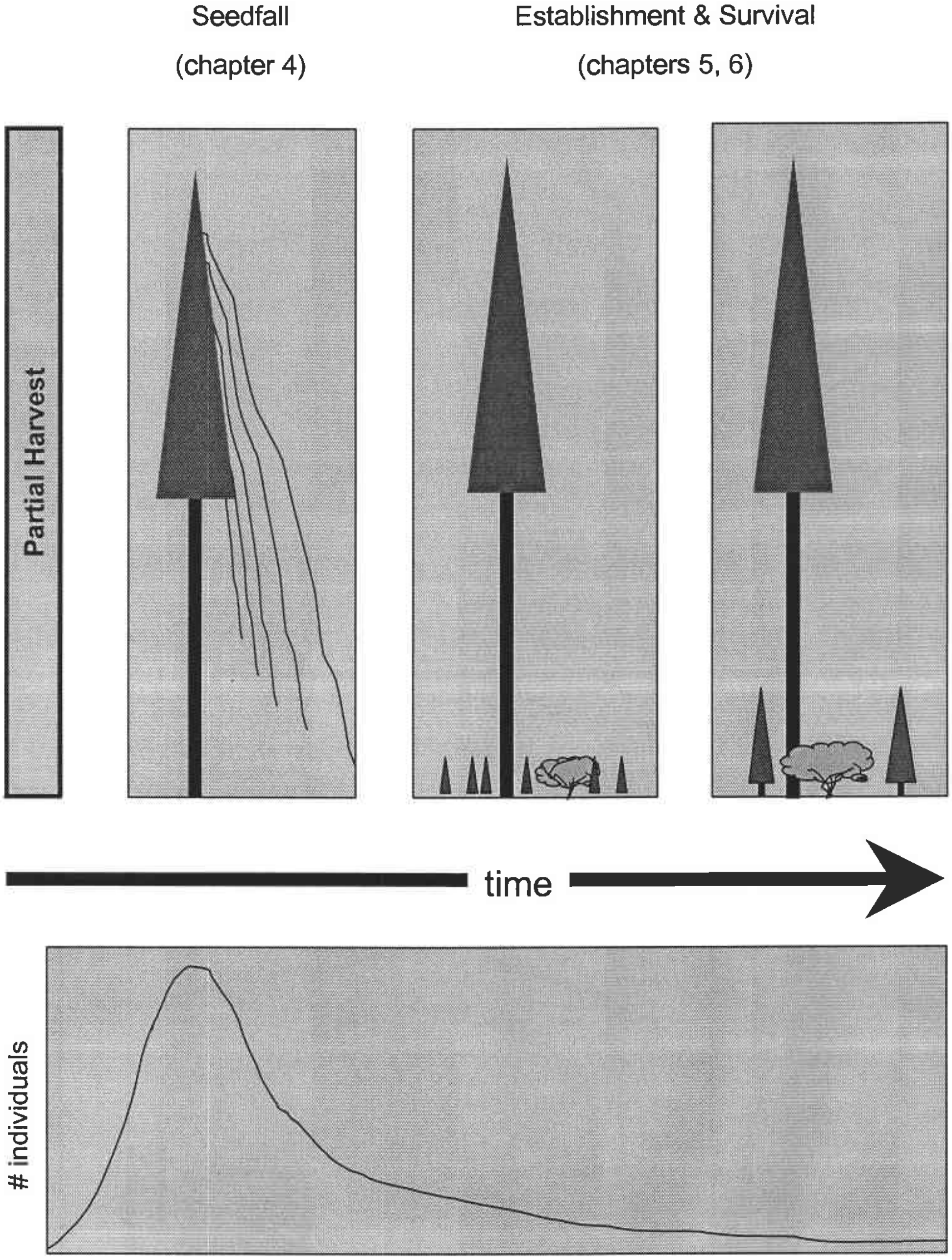

FIGURE 1.2. Schematic diagram of the chronosequence of natural regeneration represented by the core studies in this project.

recruitment. The intent was to summarize the literature relevant to ponderosa pine seedling recruitment, particularly with respect to the pumice region of central Oregon. It does not address the influences bearing on growth or survival after the seedling establishment stage (approximately 5-10 years of age).

Chapter 3 is an analysis of the spatial relationships between ponderosa pine seedlings, saplings, overstory trees, and shrubs. The analysis was conducted to guide design of the studies carried out in Chapters 4-6. The study subject was a multi-cohort old-growth stand containing a range in tree sizes (including 4 or more trees in each 10-cm dbh class from 0-100 cm) and virtually pure ponderosa pine. The stand was located in the Metolius Research Natural Area near Sisters, Oregon, approximately 45 miles northwest of the Pringle Falls and Fort Rock sites.

Chapter 4 focuses on the spatial and temporal patterns of seed rain. The analysis was based on seed collected over one year in two stands each at the Fort Rock and Pringle Falls sites. Results indicated the relationship between overstory trees and seed availability in stands with partial overstories.

Chapter 5, an observational study, addresses the temporal patterns of seedling emergence and survival over two seasons (one winter). The analyses are based on observational data collected at the four Fort Rock stands. New germinants were identified in late spring and were tracked over 1 or 2 summers to identify mortality trends. Germination and survival rates were compared over three primary conditions: forest floor substrate (bare soil vs. litter), shrub cover (shaded vs. unshaded), and degree of clustering (single vs. grouped seedlings, with at least the latter inferred to result from rodent caching).

Chapter 6, an experimental study, was designed to test and further expand upon the findings in Chapter 5. A seed-sowing experiment was conducted at two stands each at Pringle Falls and Fort Rock. Seed was sown under controlled conditions to test for differences in germination and survival rates among sites, forest floor substrates, light conditions (shaded vs. unshaded by shrubs), and depth of burial (0 vs. 1 cm, the latter to represent rodent caching). To assess the mechanisms driving the germination and survival patterns observed in this experiment, the specified conditions were also measured for microenvironmental differences, including light intensity, relative humidity, and air and soil temperature.

RELATIONSHIP TO THE DEMO PROJECT

It is expected that the studies in this project will provide a useful comparison to regeneration studies on variable retention harvests in Douglas-fir forests being conducted within the Demonstration of Ecosystem Management Options (DEMO) project (Halpern et al. 1999). Variable retention harvests are silvicultural treatments that retain some of the stand's initial structural elements after timber harvest, including living or dead components that are widely dispersed or aggregated (Helms 1998, Franklin et al. 1997). The DEMO project focuses on Douglas-fir forests west of the Cascade Crest across a gradient in site productivity. This project extends the range of that gradient by focusing on dry ponderosa pine forests located on Oregon forests on the east slope of the Cascade Mountains.

We hypothesized that the regeneration dynamics and stand growth patterns of ponderosa pine under partial overstories would differ from those stands in the DEMO project due to silvical differences of the species, and to the different environmental forces controlling natural regeneration and stand dynamics. Different forms of variable retention harvests (for example, seed-tree and shelterwood regeneration harvests) have been practiced for a longer period of time in ponderosa pine types of central Oregon, allowing investigation of a longer chronosequence than is currently possible in Douglas-fir types.

Whereas DEMO is a large-scale and multidisciplinary project, this study was restricted to seedling recruitment after regeneration cuts implemented as part of seed tree or shelterwood systems. Sampling and analysis methods also differ. DEMO is a controlled experiment following a randomized block design, whereas this ponderosa pine project had a greater operational emphasis and incorporated both experimental and observational data. By utilizing sites where treatments had been applied at various times in the past, the sites in this project provided a chronosequence that enabled a retrospective view of recruitment patterns.

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CHAPTER 2

PONDEROSA PINE SEEDLING RECRUITMENT: A REVIEW OF THE PRIMARY INFLUENCES

INTRODUCTION

In the Pacific Northwest, silvicultural systems that involve partial retention of overstory trees are being used for the development of two-story stands under multi-objective forest management (Franklin et al. 1997, Helms 1998). Although this type of silvicultural system has been advocated as a new approach, it has many similarities to conventional systems such as seed-tree or shelterwood systems with reserves. The primary objective of the regeneration cut in all these systems is the establishment and growth of a new cohort of seedlings. In many cases, natural regeneration is expected to provide all or some of the seedlings comprising the new cohort.

The retention of live overstory trees, however, may have important impacts on natural regeneration processes. Differences in the size, amount, and spatial distribution of retained overstory trees may critically influence the recruitment of new seedlings and the subsequent growth of the stand. Studies are underway to investigate natural regeneration dynamics under variable-retention harvests in conifer forests west of the Cascade Range. These include the Montane Alternative Silvicultural Systems (MASS) project and Date Creek project in British Columbia, and the Demonstration of Ecosystem Management Options (DEMO) project in Oregon and Washington (e.g. Senyk 1997, Wright et al. 1998, LePage et al. 2000, Halpern et al. 1999).

Recently, a project was initiated in the pumice region of central Oregon to study early regeneration patterns of ponderosa pine (*Pinus ponderosa*) beneath partial overstories (Keyes and Maguire 2000; Chapters 1, 4-6). A range of post-harvest structures were selected, resembling heavy thinning, shelterwood regeneration cut, or seed tree regeneration cut, with overstory trees retained in dispersed patterns throughout the stands (that is, not aggregated in clumps). As part of that project, a review of the existing research literature was conducted that revealed a rich base of information about the process of natural regeneration in ponderosa pine forests. The objectives behind partial overstory retention regeneration cuts may be relatively new, but investigations into ponderosa pine regeneration during the past century have been numerous. The results of those studies are directly relevant to questions faced by forest managers desiring natural regeneration beneath partial overstories.

This paper summarizes the primary influences on ponderosa pine regeneration, and presents a synthesis of those influences in a qualitative, conceptual model of ponderosa pine seedling recruitment. In the absence of quantitative models of natural regeneration under variable-retention systems, it is intended that this review and framework will assist managers of ponderosa pine forests in making better-informed decisions about the manipulation of stand elements to secure natural regeneration.

NATURAL REGENERATION PROCESS

The overall process of recruitment leading to an established seedling cohort may be divided into several relatively discrete stages: 1) seed production and seedfall, 2) post-flight seed losses and redistribution 3) germination and seedling establishment. The factors that contribute to patterns of natural regeneration are complex and interactive, but the most relevant factors act at specific stages.

At each of these stages, seeds or seedlings are exposed to a stage-specific host of influential factors that determines the probability of successful recruitment. Any single factor's importance (relative to other factors) usually depends on the specific regeneration stage. Moreover, in what Schupp (1995) referred to as the "seed-seedling conflict", a factor may have a positive influence on recruitment at one stage and a negative effect at another stage. For example, Keyes et al. (2001) found that large seedlings in an old-growth ponderosa pine stand in central Oregon had a negative spatial association with shrub cover, but very small seedlings had a positive spatial association with shrub cover. The mechanisms driving those patterns were not identified, but it was suggested that a facilitative effect of shrub presence on the microenvironment of small seedlings shifted to a competitive relationship once seedlings became established and larger.

The primary factors driving regeneration processes also differ depending on site. Site-related characteristics important to the natural regeneration process include climate, soil properties, tree species silvics (shade and drought tolerance, growth rates), seed size and palatability, small mammal species and population size, communities of fungal pathogens and invertebrate cone and seedling predators, debris decomposition rates and litter accumulation rates. Our regional emphasis in this paper is on ponderosa pine forests in central Oregon, located on pumice soils on the east slope of the Cascade Range. The climate in this region is relatively harsh, with cold winter temperatures (average minimum January temperature of -5.6° C), warm summer temperatures (average maximum July temperature of 27.5° C), low annual precipitation (less than 30 cm), and scant precipitation during the growing season (less than 4 cm total during July, August, and September) (based on data from NOAA climate station in Bend, Oregon).

Farmer (1997) produced a general model describing the ecophysiology of coniferous tree sexual reproduction, up to the stage of seed germination (Figure 2.1). In this review we illustrate components of that model and expand on it with a conceptual model specific to ponderosa pine seedling recruitment (Figure 2.2). The following review explains the elements comprising this model. Regeneration processes are discussed in temporal sequence, starting with seed production and ending with established seedlings.

Seed Production and Seedfall

The initial factor controlling regeneration success is seed production. Ponderosa pine seed production typically begins in trees as young as 16-20 years (Minore and Laacke 1992). Summer temperatures during the stage wherein strobilus initials are formed may be critical for optimum seed production

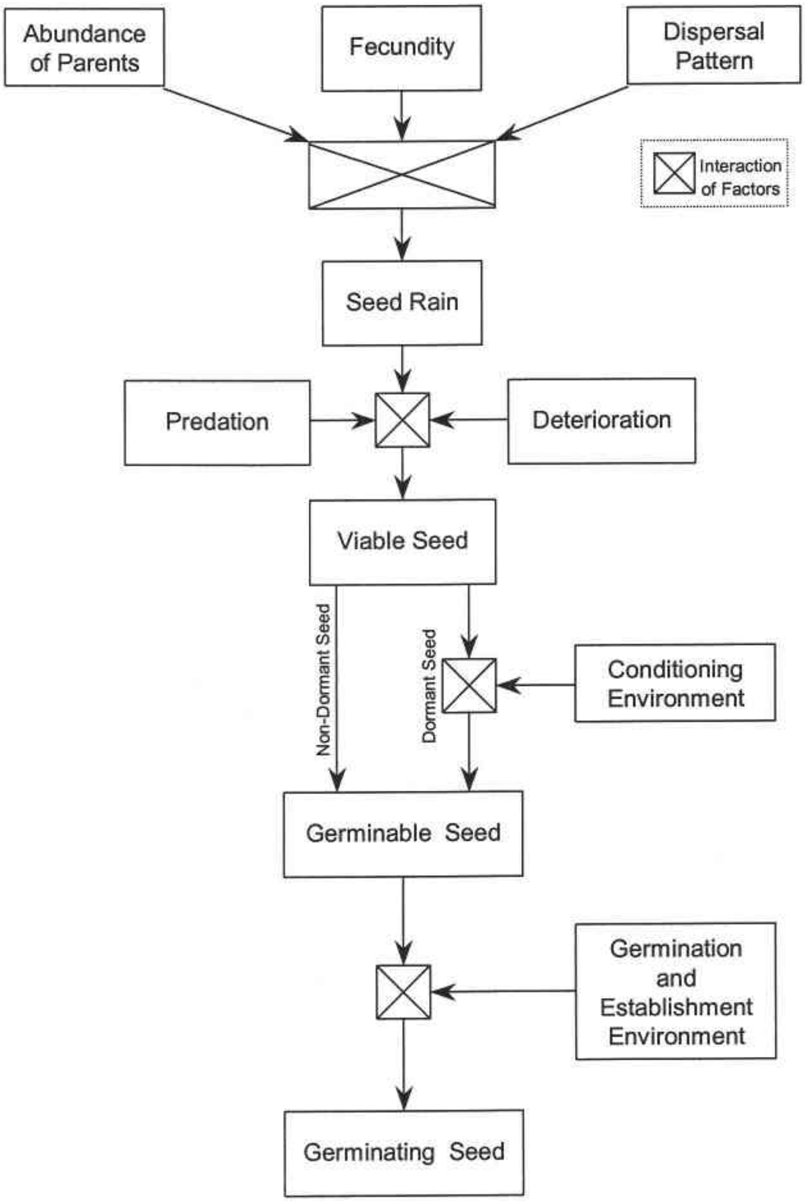

FIGURE 2.1. Farmer's (1997) model of seed ecophysiology.

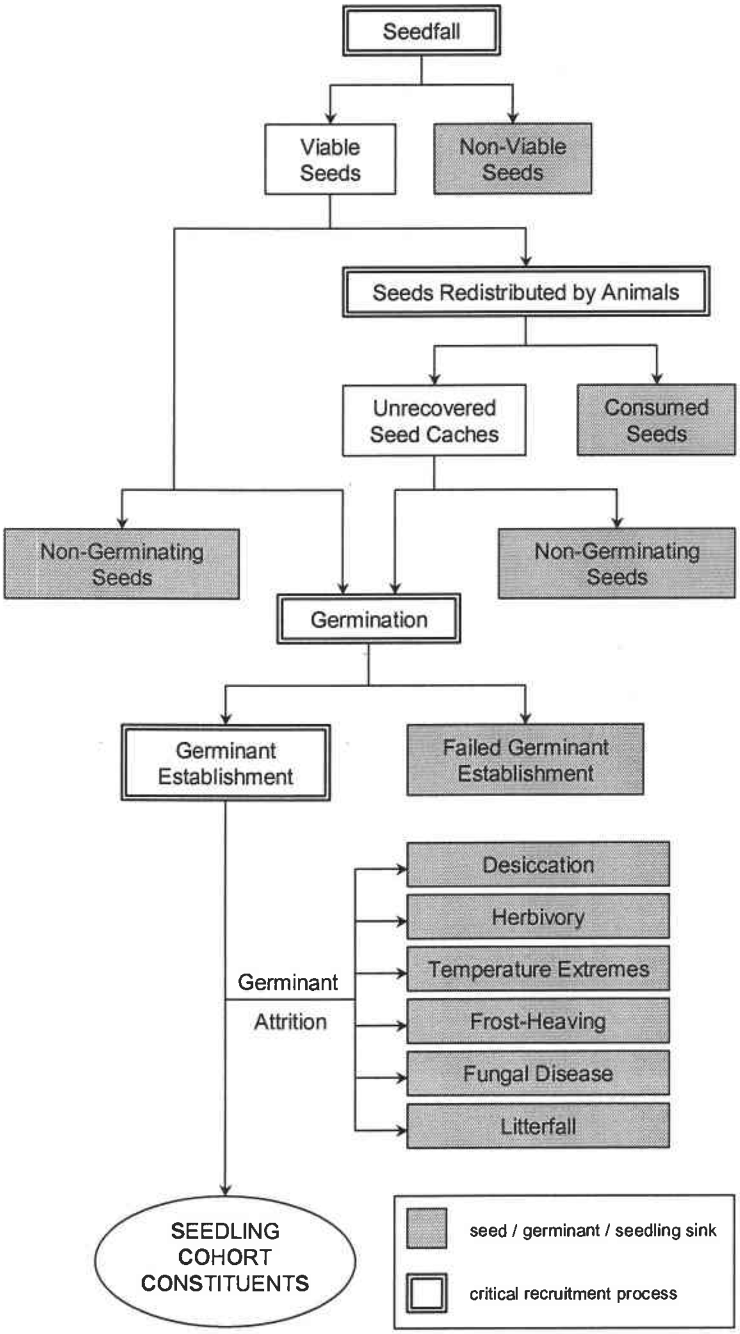

FIGURE 2.2. Conceptual model of the processes and primary factors influencing ponderosa pine seedling establishment and early survival.

(Daubenmire 1960). Cones mature over a two-year period, with mature cones beginning to drop seed in September (Oliver and Ryker 1990). Numerous studies document that larger and more vigorous trees tend to produce a greater quantity of seed. For example, in his study of 1909 and 1913 seed production in Southwestern ponderosa pine stands, Pearson (1923) found that smaller and less vigorous seed trees yielded less seed than large, vigorous seed trees. In Idaho, Foiles and Curtis (1973) reported that mature trees produced more seed than immature trees. In northern California, Fowells and Schubert (1956) found that 97 percent of the production of ponderosa pine cones was attributed to dominant trees. However, not all dominants proved to be seed producers. During years of poor seed crops, seed production may be virtually eliminated for all trees, regardless of their size or vigor.

Seed production in ponderosa pine is annually variable, and fluctuations can be drastic. Crops of up to a million or more per hectare are possible, but near-zero seed crops are not uncommon (Oliver and Ryker 1990). For ponderosa pine, good seed years usually occur every 4-5 years, but the cycle is not reliably periodic and good seed years cannot be dependably predicted in advance (Barrett 1979). McDonald (1992) used binoculars to identify seed production patterns of conifer species over a 24-year period in a stand of mostly ponderosa pine in northern California. Over that period, he found 10 years of no seed crop, 7 years of very light to light seed crop, and 7 years of medium to heavy seed crop (amounting to 0 to 760,000 sound seeds per hectare). In central Idaho, Curtis and Foiles (1961) reported seedfall exceeding 375,000 per hectare for only two of the five crops from 1936 to 1940. During intervening years, production ranged only from 10,000 to 37,500 per hectare. In western Montana, Shearer and Schmidt (1970) observed that over an 11-year period, the best crop was about 55,000 per hectare. In that study, less than approximately 200 seeds per hectare were caught during five of those years. Because of seasonal and site-to-site variability in factors that contribute to seed loss, seed germination, germinant emergence, and germinant survival, it is impossible to identify a specific number of seeds that are necessary for adequate ponderosa pine regeneration (Pearson 1923). To accommodate lack of viability, seed losses, and seedling mortality, production of approximately 500,000 seeds per hectare has been used as an estimated minimum necessary for adequate seedling regeneration after harvest (Heidmann 1992).

A varying percentage of the seed crop is not viable and hence incapable of germination. McDonald (1992) found that sound seed constituted 43 percent (range 31-59 percent) of the crop for seven above-average ponderosa pine seed crops in uncut ponderosa pine stands in central northern California. In central Idaho, Curtis and Foiles (1961) observed 83 percent soundness of ponderosa pine seeds from a heavy crop falling in small clearcuts in 1958. In central Oregon, Dahms and Barrett (1975) found the proportions of sound ponderosa pine seeds in a clearcut, an uncut old-growth stand, and an uncut immature stand to be 79.3, 80.0, and 86.6 percent, respectively. The proportion of the seed crop that is viable varies from year to year. There is a positive correlation between the amount of seed produced and the percent viability, as the favorable growing conditions that promote seed-crop quantity also increase seed quality (Barrett et al. 1983). McDonald's (1992) analysis, for example, found a strong relationship between cone counts and the percentage of seed that was sound.

The bulk of the seed crop falls between September and November (Oliver and Ryker 1990). In northern California, for example, Fowells and Schubert (1956) reported that 84 percent of ponderosa pine seed had fallen by November. In a central Oregon study, Dahms and Barrett (1975) found that 82-83 percent of the seed crop fell by early November. Curtis and Foiles (1961) reported that the majority of the 1958 seed crop in central Idaho fell between September 10 and 30. Studies have shown that viable seeds fall earlier than non-viable seeds (Fowells and Schubert 1956, Shearer and Schmidt 1970, and Dahms and Barrett 1975). In the study by Shearer and Schmidt (1970), the first month of seedfall produced most of the seed crop actually available for germination.

Like other western coniferous species, ponderosa pine seed dispersal occurs in an elliptical pattern originating with the tree (Minore and Laacke 1992). The actual shape and orientation of the ellipse depends on tree heights, prevailing wind direction and speed, and topography (e.g., Dahms and Barrett 1975). Although the patterns of seed density around trees differs by species, they are similar in that seed density declines monotonically with distance from the tree (Green 1983). Models of theoretical seed flight distance have been based on seed tree height and windspeed (e.g. Siggins 1933). Isaac (1930) observed that the density of wind-dispersed ponderosa pine seed was greatest at a distance of 91 m from the source when dropped at a height of 45 m above ground into a wind of approximately 5.6 km/hr. Because of the difference in weight between viable and non-viable seeds, the proportion of non-viable seeds increases with distance from the parent tree (Minore and Laacke 1992). Barrett's (1966) study of ponderosa pine seed flight patterns in central Oregon found that little seed carried beyond about 30 m from a parent tree. In that study, the viability rate at eight chains from a clearcut edge was 67 percent, versus a viability rate of 86 percent among seeds falling within two chains from the edge.

Seed Losses and Redistribution

Seed predation, both before and after dispersal, can be an important factor in reducing the number of seeds available for germination. Ponderosa pine seed predators include invertebrates, birds, and small mammals. During the cone stage, damage is mostly attributed to invertebrates, and may be incurred by seeds within cones, or by the immature cones themselves. Four insects are responsible for the majority of these losses: ponderosa pine coneworm (*Dioryctria auranticella*), ponderosa pine cone beetle (*Conophthorous ponderosae*), ponderosa pine seedworm (*Cydia piperana*), and ponderosa pine seed chalcid (*Megastigmus albifrons*) (Blake et al. 1986). In five second-growth stands in Arizona, Blake et al. (1989) reported average cone losses of 39.3 to 91.5 percent by insects during one season. In western Montana, squirrels (*Tamiasciurus* spp.), rather than insects, were identified as the primary cause of cone and pre-dispersal seed losses (14 percent) (Shearer and Schmidt 1971). In the latter study, measures taken to prevent squirrels from climbing trees resulted in an increase in seedfall of more than threefold. In both studies, a substantial amount of cones was aborted due to unknown causes.

Most conifer seeds that do not germinate within about two years after dispersal succumb to pathogenic or saprophytic microorganisms (Farmer 1997). Fungi are the primary agents (Fisher 1941), but bacteria and viruses may also cause seed deterioration. The infection may occur after dispersal or during the flowering and fertilization stages (Farmer 1997). Although most research on seed- and germinant-deteriorating fungi has been conducted in nurseries (e.g. Timonen 1964), seed molds and damping-off fungi are common in forest soils (Farmer 1997). Ponderosa pine does not appear to be affected by either viruses or bacteria, but seed losses to molds are common (Roth 1970). In direct-seeding studies, molds were found to be problematic on ponderosa pine seeds in central Oregon (Stein 1955), southwest Oregon (Wagg 1958), and California (Fowells and Schubert 1951).

Post-dispersal predation of seeds by animals can be great (Janzen 1971). Although predation by birds has been observed (Eastman 1960), the primary agents of seed predation are small mammals. In the ponderosa pine range, these include deer mice (*Peromyscus* spp.), golden-mantled ground squirrels (*Citellus lateralis*), chipmunks (*Tamias* spp.), and shrews (*Sorex* spp.) (Cochran 1970, Lawrence et al. 1961). Hooven's (1966) study in central Oregon identified deer mice as the most important predator of ponderosa pine seed. Vander Wall's (e.g. 1992b) work with Jeffrey pine (*Pinus jeffreyi*) in Nevada identifies yellow pine chipmunk (*Tamias amoenus*) as the species of most significance. In addition to seeds, shrews and voles (*Microtus* spp.) also destroy new germinants.

Although they are present during all stages of stand development, seed predator populations are at their highest levels during early seral stages (West 1992). In general, seed predation rates are highest when animal populations are high. Predation is usually not a problem during good seed years, as production exceeds predation rates even at high animal populations. Small mammal populations are characterized by seasonal patterns of high fall densities and low spring densities (West 1992). At its height between September and November, seedfall happens to occur during the season of highest small mammal population density (West 1992, Gashwiler 1967).

Small mammals have long been regarded as an impediment to natural regeneration of western conifers, and are usually targeted in animal control efforts (e.g. Hooven 1966). Working in western Alberta, Radvanyi (1971) observed that small mammals ate 21-33 percent of lodgepole pine (*Pinus contorta*) seeds during the summer months, and 5-10 percent during the winter months. In his study of Douglas-fir (*Pseudotsuga menziesii*) seedfall, Isaac (1937) reported that birds and rodents consumed essentially all seeds during years of low to medium crops. In Arizona, Pearson's (1913) assessment of seed predation and ponderosa pine regeneration failures led him to conclude that the silvicultural practice of "direct seeding is almost hopeless unless the rodent evil can be eliminated."

Integrated pest management strategies for seed predators include reducing per-capita seed consumption, avoiding large populations of seed predators, and reducing seed predator populations (Keyes 2000). Per-capita seed consumption may be reduced by silviculturally favoring tree species of less-desirable seed, such as larch (*Larix* spp.) or true firs (*Abies* spp.), or by providing an alternate food source. By providing sunflower seeds as an alternate food source, for example, Sullivan and Sullivan (1982) were able to increase lodgepole pine seed survival by 30-60 percent. Silvicultural systems that minimize the area of early seral vegetation, such as uneven-age systems, may maintain lower seed predator population densities by reducing habitat quality and enhancing the effectiveness of natural predators (West 1992). Direct control measures, such as poisons, shooting, and diseases, have been tested but proven to be expensive, sometimes dangerous, and only moderately and temporarily effective (Black and Lawrence 1992, Smith and Aldous 1947). Heidmann (1992) proposed that site preparation be conducted prior to harvest to initiate a crop of advance regeneration. West (1992) suggested that best results might be achieved by scheduling harvests during years of high seed production, when seed production oversaturates seed predation pressure. Isaac (1943) reported that Douglas-fir seedfall exceeds predation pressure during years of heavy crops.

Ironically, the unrecovered seed caches of these animals may play an important role in establishing new seedlings. In Jeffrey pine stands, for example, the majority of new seedlings are believed to originate from unrecovered caches (Vander Wall 1992a). Rodents in ponderosa pine forests rely heavily on ponderosa pine and bitterbrush (*Purshia tridentata*) seeds as part of their diet. During the course of the year, bitterbrush seeds are cached, partially eaten, removed and re-cached several times (Vander Wall 1995); the same may be true for ponderosa pine seeds. For most of the year, rodents probably rely most heavily on spatial memory and the presence of landmarks in relocating seed caches. Vander Wall (1991) discovered that yellow pine chipmunks found Jeffrey pine seeds using their olfactory sense when the seeds were wet, but could seldom find dry seeds by this method. In that study, chipmunks significantly found their own caches more often than the caches of other chipmunks, and they were unsuccessful at relocating their caches when landmarks near their caches were moved.

Rodents can play a role in increasing the actual dispersal distance of seeds from parent trees. In western Nevada, Vander Wall's (1992b) study reported that rodents removed 95-99 percent of Jeffrey pine seeds in a two-day period; seeds were then cached at average distances of 13.0 and 24.7 meters from their original location. In another analysis of the same experiment, the author observed that most seed was moved from closed forest to open bitterbrush shrubland (Vander Wall 1993). West (1968) noticed that most germinant clusters were found in the openings between established plants, but it is not known whether that spatial distribution was due to preference during caching, differences in cache recovery, or conditions more amenable to successful establishment at those locations.

For various reasons including overwinter mortality of small mammals, only a portion of the seeds cached by vertebrates is recovered, with the remainder available to germinate. Former caches are visually evidenced by seedlings growing in clusters. At two sites in central Oregon, West's (1968) one-time survey of small ponderosa pine seedlings (up to six inches tall) revealed that clusters of seedlings (assumed to have originated from seed caches) were responsible for 16-18 percent of ponderosa pine emergence sites. At another central Oregon site, Saigo (1968) reported that half of ponderosa pine regeneration could be attributed to rodent caches. The fact that individual seeds may also be cached makes it likely that this influence is underestimated.

Because unrecovered caches are essentially scattered installations of well-sown seeds, seed-caching vertebrates play a potentially influential role on the ponderosa pine recruitment process. The long-term effect of these caches is uncertain, however, and no studies have observed seedling clusters arising from caches long enough to determine whether they constitute an important portion of trees in a cohort. The number of seedlings within a cluster diminishes rapidly after emergence, with many clusters reduced to individual seedlings that are indistinguishable as cached seeds (Chapter 5). To further address this subject, long-term observational studies are needed to track the fate of seed caches over time.

Germination and Seedling Establishment

Viable seed that survives over-winter predation does not automatically germinate the following spring. Like many conifer species, ponderosa pine requires a period of environmental conditioning in order to break dormancy and develop a capacity for germination (Farmer 1997). This mechanism, referred to as conditional dormancy, is believed to have evolved to match germination with conditions for successful establishment. Little work has been conducted to clearly define the set of requisite conditions for ponderosa pine. Allen (1941) showed that germination of unchilled ponderosa pine seed will occur at high temperatures, but that chilling accelerates germination by reducing the temperature required for germination. Haig et al.'s (1941) summary of work with tree species in the western white pine (*Pinus monticola*) forest type indicated that when the germinating substrate is sufficiently moist, temperature appears to be the factor limiting germination.

Among those viable ponderosa pine seeds that do not germinate, few survive to germinate the following year. Shrub species in ponderosa pine forests, such as *Ceanothus* spp., are capable of long-term storage of seed in the forest floor, or seed banking. Seeds of western coniferous species, however, have been shown to rarely survive beyond one year. Isaac (1935), for example, showed that Douglas-fir seeds either germinate or decay in the first year. Pratt et al. (1984) showed that ponderosa pine seeds posses relatively short residence times in the forest floor. Many non-germinating seeds succumb to *Caloscypha fulgens*, a fungus that is responsible for seed mold in many conifers (Epners 1964). For seeds that survive to germinate, the new seedling's hypocotyl and radicle tissues may be rotted by damping-off and root rot fungi (*Pythium, Rhizoctonia, Fusarium, Corticum,* and *Cylindrocladium* spp.) (Farmer 1997). In ponderosa pine forests, *Pythium* and *Rhizoctonia* are particularly important (Roth 1970). Serious losses of ponderosa pine seedlings to damping-off and root rot fungi were reported by (Stein 1957) in central Oregon and by Wagg (1962) in southwest Oregon.

For those seeds that germinate, the seedling establishment stage, which generally lasts between 1 and 5 years, is the most critical stage of survival in an individual seedling's life history (Barnes et al. 1998). Within this context, the spatial patterns of establishment are largely regulated by forest floor substrates, understory and ground vegetation, microsites that ameliorate temperatures and water stress, and the spatial distribution of seed-bearing overstory trees. In large part, the survival of germinants requires conditions that enable their immature root systems to quickly establish and become functional prior to their desiccation. The relatively few seedlings that survive these conditions and grow vigorously are considered established (Barnes et al. 1998).

Natural regeneration in ponderosa pine forests commonly occurs in environments where below-ground resources are the growth-limiting factors (Oliver and Ryker 1990). In northeast Oregon, for example, Riegel et al. (1992) used combinations of trenching and thinning in an experiment designed to separate overstory and understory effects on understory biomass production. Those authors concluded that below-ground resources (water and plant nutrients), rather than sunlight, were the limiting factors. In a related study, Riegel et al. (1991) increased understory biomass production by 15 and 17 percent by adding water and nitrogen, respectively, during the growing season. When water and nitrogen were added in a single treatment, production was 36 percent more than the control, yet no relationship was found between understory biomass production and quantity of photosynthetically active radiation (PAR).

For new seedlings, soil moisture has a major impact on establishment. Moisture stress severely reduces germination and radicle elongation. In a laboratory study, Larson and Schubert (1969) found that moisture potential below -7 bars severely reduced germination rates. Similar findings were reported by Djavanshir and Reid (1974), who observed that ponderosa pine germination rates declined precipitously beyond -4 bars, and that germination was prevented at -8 bars. In their study, they also found that radicle elongation after germination is severely reduced at -4 bars or less. At field sites in central Oregon, Hermann (1968) showed that watering and shading of germinants substantially improved their survival.

In a typical year, most germinating seeds succumb to lethal levels of moisture stress during their first several summers. Hermann (1968) found that the positive benefits of watering during one summer does not carry over to improved survival during the next summer. Therefore, successful recruitment usually occurs in those locations where germinants are assisted by stand conditions that enable them to survive the long summers of moisture stress. A seedling's moisture stress is a function of its transpiration rate and the soil moisture stress at the root surface. In addition to internal factors like stomatal control, contributors to seedling moisture stress include air vapor pressure, wind speed, leaf temperature, soil temperature, and physical properties of the soil (Cleary 1970). Elements of the stand that influence these external factors can indirectly contribute to the potential for seedling establishment.

Occasionally, seed production and abnormal weather conditions combine to enable many seedlings to establish throughout the stand, irrespective of other stand factors. Such a scenario was reported by Pearson (1923), who studied the relation of weather patterns and seed crops to ponderosa pine seedling establishment in Arizona. Pearson found that when higher-than-normal early summer (May-June) precipitation followed an autumn of high seed production, new germinants were widespread. Conversely, years of low seed crops or dry early summers resulted in little establishment. The evidence of combined high seed production and early summer precipitation appears to persist beyond the first few years of seedling establishment studied by Pearson. Savage et al. (1996) used precise stem aging techniques to determine that the majority of all trees in the Pearson Natural Area had established in 1919, a summer of exceptionally high May-June rainfall that followed an autumn of abnormally high seedfall.

In addition to moisture stress, temperature extremes can restrict seedling recruitment. Excessively high temperatures can directly cause mortality in young seedlings. Hartley (1918) was the first American researcher to identify heat lesions at the base of conifer germinants as an agent of mortality in nurseries. Baker (1929) identified 54° Celsius as a temperature threshold above which germinants (1-3 months) of western conifers experience protoplasmic injury and rapid death. Root growth, which is most critical for successful seedling establishment, is primarily affected by soil temperature, but is affected by air temperature as well. Larson (1967) measured initial root growth of ponderosa pine seedlings under air and soil temperatures of 7, 15, 23, and 31° Celsuis. He found that optimum growth occurred at a soil temperature of 23° and air temperature of 15°. In that study, growth was facilitated by a constant temperature, rather than a thermal flux. Small ponderosa pine seedlings are also indirectly vulnerable to temperature and temperature fluxes via frost heaving (Heidmann 1976).

Like most western conifer seedlings, mineral soil is the preferred substrate for ponderosa pine germinant establishment (Morris 1970). In California, Dunning (1923) reported that duff clearly favored Douglas-fir and incense-cedar (*Libocedrus decurrens*) regeneration over ponderosa pine regeneration. In northern Idaho, Haig et al. (1941) reported that germination of species in the western white pine forest type was never satisfactory on duff. Also in northern Idaho, Larsen (1924) found that germination on burned and mineral soil substrates was 2-12 times better than on duff substrates. In central Idaho, Foiles and Curtis (1965) found that scarification increased both emergence and survival of ponderosa pine seedlings. Duff loses moisture to evaporation more rapidly than mineral soil (Roe and Squillace 1950). In addition, the thickness of a heavy litter layer can exceed the distance that can be bridged by the seed's radicle. Heavy litter also harbors communities of insects, fungi, and other pathogens that can cause germinant mortality (Farmer 1997). Also, dry needle litter has a large volume of pore space which contributes to low conductivity and high temperatures. Thus temperatures in needle litter usually exceed those in bare mineral soil and can reach a level where the seedling perishes by heat girdling or excessive transpiration (Farmer 1997).

Rotten logs have been shown to be important substrates for some tree species in wetter locations. Studies by Harmon and Franklin (1989), for example, have shown that logs are the primary seedbed for germinants in coastal Pacific Northwest forests. In their studies, they determined that the logs provided an environment where competition with forest floor mosses and herbs was relatively less than at forest floor sites. Cornett et al. (1997) similarly found that *Thuja occidentalis* in Minnesota predominantly regenerated on decayed stumps and logs. Such a relationship has not been shown for ponderosa pine forests, perhaps because the lower moisture content of woody debris at such sites disfavors seedling establishment.

Germinant establishment is improved by the presence of shrubs, which provide shaded microsites that reduce the intensity of solar radiation and ameliorate microenvironmental conditions. Shrubs in ponderosa pine forests, such as *Purshia tridentata, Arctostaphylos patula,* and *Ceanothus velutinus*, have been shown to be strong competitors for soil moisture (Barrett and Youngberg 1965, Tarrant 1957). Other workers, however, while acknowledging the competitive impact of shrub species, argued that their facilitative influence outweighs their competitive influence, at least during the first years following germination when ponderosa pine seedlings are particularly vulnerable to their environment (Conard et al. 1985, Zavitkovski and Woodard 1970). Dyrness and Youngberg (1966) noted a high proportion of ponderosa pine seedlings occurring directly beneath shrubs in central Oregon. In California, Show (1924) determined that brush cover increased ponderosa pine seedling survival, and that seedlings increasingly benefited from cover at increasingly poorer sites.

Holmgren et al. (1997) produced a conceptual model illustrating the co-occurrence of facilitative and competitive influences by live vegetation on individual plants in xeric ecosystems. In their model, facilitation is the dominant force when the costs associated with reduced light levels are more than offset by improved water relations. The dominant force probably also depends on the life stage of the seedling. Callaway and Walker (1997) presented evidence from past studies supporting the argument that the net effect of this co-occurrence is facilitative when seedlings are small, but becomes competitive once seedlings become established and increase their demands for site resources. This concept is consistent with the ”seed-seedling” conflict discussed by Schupp (1995). Spatial patterns supporting this theory were observed by Keyes et al. (2001) in an old-growth ponderosa pine stand in central Oregon, where small seedlings were positively associated with shrub cover and larger ponderosa pine seedlings were negatively associated with shrub cover (some of the negative association could have been induced by shading out of the shrubs by larger seedlings).

Exactly what mechanisms are responsible for this facilitative role are not clear, but microenvironmental buffering is likely a key. Shade from shrubs can reduce the evaporative demands on the juvenile tissues of germinants and small seedlings during summer drought. While examining the soil conditions beneath shrubs in the ponderosa pine forest type in central Oregon, Youngberg (1966) found that brush exerted a beneficial effect on temperature and soil moisture. In his study, soil moisture depletion occurred at a slower rate beneath shrubs (*Ceanothus velutinus*, *Purshia tridentata*, *Arctostaphylos patula*, and *Artemisia tridentata*) than beneath grasses or in the open. At some sites, the permanent wilting point under brush was never reached. Youngberg (1966) also found that soil temperatures in the open were 20-30 °F warmer than beneath brush. In Montana, Wahlenberg (1930) found that sites beneath *Ceanothus* brush had lower soil temperature, greater relative humidity, less evaporation, and greater soil moisture than open sites. Frost-heaving, which has been identified as a source of mortality to young ponderosa pine seedlings (Heidmann 1976), might be reduced by the presence of shrubs.

This microenvironmental effect of shrubs on regeneration spatial patterns has also been reported in other forest types occurring on xeric sites. Callaway et al. (1996) described a facilitative effect of *Artemisia tridentata* on *Pinus monophylla* regeneration in Nevada. In central coastal California, Dunne and Parker (1999) found that higher levels of soil moisture beneath *Arctostaphylos glandulosa* led to lower drought mortality of *Pseudotsuga menziesii* in those shaded environments. Working with natural regeneration of white fir (*Abies concolor*) and Douglas-fir on harsh sites in the Sierra Nevada, Tappeiner and Helms (1971) found that soil moisture and potential evaporation varied significantly under different combinations of shrub composition and overstory cover, and found that those microsites were associated with different germination, survival, and growth rates. Similar examples of facilitation via microenvironmental amelioration have been described for other environments in which moisture stress is an important factor, including savannas, deserts, grasslands, salt marshes, and sand dunes (see Holmgren et al. 1997, Callaway and Walker 1997).

In addition to reducing soil evaporation and seedling transpiration, shrubs may improve water relations by increasing the amount of soil water available in the upper horizons occupied by the roots of young seedlings. Since the coining of the term “hydraulic lift” by Richards and Caldwell (1987), evidence has been growing to support the theory that during nocturnal hours, water moves passively from plant roots to upper soil horizons of lower water potential (Caldwell et al. 1998). Mooney et al. (1980) advanced the theory to explain the dense root mats and unexpected soil moisture present in upper soil horizons beneath *Prosopis tamarugo* in the Atacama Desert. Richards and Caldwell (1987) provided strong evidence that hydraulic lift occurs with *Artemisia tridentata* through a comprehensive series of experimental tests. Dawson’s (1993) study of sugar maple (*Acer saccharum*) trees during drought conditions produced comparable findings. In that study, 3-60 percent of the hydraulically lifted water was usurped by neighboring plants. This phenomenon has not yet been reported for shrub species common to ponderosa pine forests, but it remains an intriguing possibility as a mechanism for enhancing germinant survival.

These beneficial effects of shrubs may be undermined to some degree by their negative effects. For example, a minimum light intensity is required for seedling survival, although ponderosa pine seedlings can survive shading down to 20-30 percent of full sunlight (Atzet and Waring 1970). At sites where annual leaf turnover of shrubs is heavy, germinants may be buried by litterfall. Christy and Mack (1984), for example, theorized that most germinants in Douglas-fir—western hemlock (*Tsuga heterophylla*) forests were found on logs rather than soil because logs had sloughed off litter. With their relatively low foliar densities, shrubs in dry ponderosa pine forests are unlikely to have this severe burial effect on seedlings. The presence of shrubs improves the habitat for many rodents known to be predators of seeds and germinants, including ground squirrels and deer mice (West 1992). It is reasonable to expect, however, that heavy brush cover discourages larger seedling-browsing mammals from browsing those germinants that escape seed predation and rodent clipping.

Like shrubs, graminoids can provide shade for germinants, but the high below-ground competition that they exert disfavors germinant survival and growth. In a study of the competitive impacts of herbaceous vegetation on ponderosa pine seedling survival and growth, Pearson (1942) found Arizona fescue (*Festuca arizonica*) to be a potent competitor for soil moisture. Arizona fescue that had been clipped was less aggressive than unclipped, but best seedling survival and growth occurred in plots that had been cleared of all live grasses. Pearson attributed these findings to the seasonal growth habit of Arizona fescue, which grows during May and June when precipitation is most restricted. He noted that other grass species in the region, including *Muhlenbergia montana* (mountain muhly), *Bouteloua gracilis* (blue grama), and *Blepharoneuron tricholepis* (beardless bunch), compete less aggressively with seedlings than Arizona fescue because they remain dormant during the dry early summer months. In central

Oregon, Youngberg (1966) reported lower soil temperatures under cover of *Sytanion hystrix* (squirreltail), but soil moisture depletion occurred more rapidly than in the open or beneath shrub species.

In managed stands, the retention of a partial live-tree overstory after harvest can be expected to improve germinant survival by partly shading the understory, moderating understory temperatures, and reducing solar radiation at the forest floor. In Arizona, for example, Barton (1993) found that water stress determined the lower elevational limits of three *Pinus* species. Below these limiting elevations, emerging *Pinus discolor* germinants survived only in those microsites shaded by “nurse trees.” Silviculturists have applied this concept for decades, particularly in harsh environments, in the use of shelterwood harvests (e.g. Smith et al. 1997). For enhancing recruitment in ponderosa pine stands, Barrett (1979) suggested retaining 25-37 trees per hectare in order to reduce heat and frost damage to seedlings.

The retention of overstory trees may have negative effects as well. Excessively dense overstory retention levels may exclude ponderosa pine regeneration. Pearson (1936) determined that shading that reduces light intensities below 50 percent of full light results in slender seedlings that are susceptible to bending under normal snow loads. He estimated that light intensities at 10 percent of full light results in outright seedling mortality. Atzet and Waring (1970) concluded more conservatively that ponderosa pine cannot persist at light intensities below 20-30 percent of full sunlight.

Another potentially negative effect of overstory retention includes burial by annual needle turnover. In California, Tappeiner and Helms (1971) found that for new Douglas-fir germinants under a sparse canopy, more than half of all mortality (over approximately 1.5 years) was attributed to burial beneath overstory litterfall during the first autumn after germination. Kelsey and Harrington (1979) found no phytotoxins in the litter of mature ponderosa pine trees, discounting allelopathy as a possible limit to germinant survival.

A third disadvantage of overstory retention is the maintenance of tree-based rodent populations. Tree squirrels (*Sciurus* spp.), for example, usually do not stray far from trees; in clearcuts they are problematic seed predators only along cutting unit perimeters (Smith and Aldous 1947). Retention of overstory trees improves the habitat for these species within cutting units, and therefore may increase the area of the unit that is exposed to seed predation.

After seedlings have become established for several years, the effects of overstory retention on understory seedlings are expressed in growth reduction rather than mortality. The long-term effect of overstory trees on ponderosa pine seedling growth is a substantial topic that cannot be fully addressed here. It can be generally reported, however, that higher levels of overstory density (or shading) result in increasingly reduced seedling growth (e.g. Pearson 1940, McDonald 1976, Oliver and Dolph 1992, McDonald and Abbott 1994, McDonald et al. 1997).

CONCLUSION

This paper has in a qualitative sense attempted to present the factors of primary relevance to ponderosa pine regeneration. A complex mix of climate, overstory stand structure, understory plant communities, forest floor substrates, and seed-caching and seed-predating animals constitutes the environment in which the natural regeneration of tree seedlings must become established. The spatial patterns of ponderosa pine seedling regeneration are the product of all of these elements as they influence the fate of regeneration from seed to established seedling. Reviewing past findings from a broad range of disciplines and geographic locations offers an efficient method for modeling, at least conceptually, the dynamics of natural regeneration.

It is also important to relate the primary factors to their relevant stage of natural regeneration. George and Bazzaz (1999) referred to these factors as species-specific "ecological filters" that differentially influence seedling establishment and survival. In their study of a hardwood stand in New England, those authors identified ferns as important filters; tree seedlings must penetrate the fern stratum in order to survive. The literature reviewed in this paper indicates that given an adequate supply of viable seed, stand characteristics that do not ameliorate the summer drought for seedlings may be collectively considered the primary filter limiting establishment of seedlings in ponderosa pine forests. Under this condition, it is the availability of shading structures (notably, shrubs) that enables germinants and young seedlings to avoid desiccation that predominantly determines the likelihood of natural regeneration success.

This review represents one method of integrating the factors influencing natural regeneration of ponderosa pine in a single model. An alternative approach is to conduct a research project that incorporates many factors and their influences at various scales and stages of regeneration across a range of conditions. Clark et al.'s (1999) review of forest tree seedling recruitment research indicates that many past studies were geographically limited, short in duration, and restricted to a single stage of regeneration. We have attempted to address these concerns with the establishment of a long-term project designed to track the fate of ponderosa pine regeneration in central Oregon over a longer time span than has been possible in many past studies (Keyes and Maguire 2000). Results from the initial set of analyses from that project are presented in this dissertation, which focuses on the spatial and temporal patterns of ponderosa pine seedfall, emergence, and early seedling survival at dry ponderosa pine sites (*Pinus ponderosa* / *Purshia tridentata* plant association (Volland 1985)) in central Oregon.

The conceptual model in this paper was constructed specifically for ponderosa pine, and many of the papers included in the review are from Pacific Northwest forests, many from central Oregon in particular. Although the regeneration factors identified in this paper are important in other regions, their relative importance and the stages of their primary impacts may be different. Differing precipitation and temperature regimes, soil attributes, and species' silvics might indicate different site- and species-specific natural regeneration filters. The structure of this paper's conceptual model, however, is transportable to other species and regions.

This review reveals the importance of overstory trees, shrubs, forest floor substrates, and small mammals as stand characteristics that directly or indirectly influence the process of ponderosa pine natural regeneration process at various stages. The review also highlights the need for additional work to elaborate on the fine scale of the ponderosa pine seedling establishment process in central Oregon, particularly in stands with partial overstories. The focus of this dissertation will be on the spatial and temporal patterns of seedfall, and on the near-term effects of effect of shrub cover, substrate, and seed caches on ponderosa pine emergence and establishment. This will be accomplished by a set of studies that are characterized by intensive temporal and spatial data collection during those periods when those regeneration processes are most active. An observational study of autumn seedfall will provide more details on the temporal and spatial distribution of seedfall as they are affected by the presence of overstory trees (Chapter 4). An observational study of tree regeneration immediately after spring emergence will provide an assessment of the relative importance of shrubs, substrate, and seed caches on regeneration (Chapter 5). An experimental study of those factors will enable more control of external variables, as well as an indication of the processes that drive shrub-seedling relationships (Chapter 6). The time frame encompassed by these studies represents the period when natural regeneration is most strongly influenced by these stand elements.

Although the data collected for these studies will be spatially and temporally intensive, their duration of measurement is limited by time constraints.

To partially compensate for this shortcoming, an analysis of seedling – shrub spatial associations will be conducted (Chapter 3), the causes for which may be hypothesized from this review and results from the observational and experimental studies proposed above. An analysis of permanent-plot data is necessary to properly determine the long-term influences of shrubs and seed caches on tree recruitment, but such an analysis is not possible in this particular project. However, the baseline documentation, tagged seedlings, and permanently-monumented study sites established for this dissertation project provide the prospect for such a follow-up analysis at a later opportunity.

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CHAPTER 3

SEEDLING SPATIAL PATTERNS AND THEIR RELATION TO SHRUBS AND OVERSTORY TREES IN AN OLD-GROWTH PONDEROSA PINE STAND

INTRODUCTION

Seedlings of ponderosa pine (*Pinus ponderosa*) often face a harsh environment and can experience competition for scarce resources. This environment includes summers of high daytime temperatures, great diurnal thermal flux, and drought. In ponderosa pine forests, it is likely that tree recruitment is influenced by the spatial patterns of existing vegetation, especially as they modify microclimate, site conditions, and resource availability. In extreme environments, seedlings are especially influenced by competitive and facilitative forces imposed by adjacent vegetation (Callaway and Walker 1997). Shrubs and overstory trees may inhibit a seedling's survival and growth by competing for limiting resources such as soil moisture. Conversely, the shade cast by shrubs and trees may ameliorate the seedling's physical environment by reducing air temperatures, soil temperatures, and evaporative demand (Tappeiner and Helms 1971, George and Bazazz 1999). These influences may simultaneously affect individual seedlings (Holmgren et al. 1997), with their net effect determining seedling survival probabilities and growth rates. Because competitive forces are repulsive and facilitative forces are attractive, the cumulative effect of competition and facilitation at the stand level should be reflected in the spatial patterns of regeneration density.

In this study we analyzed the spatial patterns of recruitment in an undisturbed old-growth ponderosa pine stand in central Oregon. The first objective of the study was to determine the relationship of neighboring trees and shrubs to regeneration. We hypothesized that the density of regeneration would be associated with the density of nearby overstory trees, shrubs, and regeneration in larger size classes. Information from these tests would indicate whether the net relationships between tree regeneration and the components of stand structure were competitive or facilitative. The second objective of the study was to characterize the spatial distribution of regeneration and to identify possible differences in those patterns across different size classes of regeneration. We hypothesized that if overstory trees and shrubs influenced seedling recruitment and survival, then these influences would be evidenced by aggregated spatial patterns of recruitment as a result of net facilitative attraction or net competitive repulsion, as opposed to regular or random patterns under absence of interactions.

METHODS

Study Area

The study area is located 22 km northwest of Sisters, Oregon, in the Metolius Research Natural Area (RNA) on the east slope of the Cascade Range. The Metolius RNA covers parts of sections 25, 26, 35, and 36 of T12S/R9E, Willamette meridian (roughly 44.5° N latitude, 121.6° W longitude). Elevation is approximately 920 meters. The area's continental climate is typical of central Oregon, with cold winters (-0.5° C mean January temperature; weather data from Sisters, Oregon) and warm summers (17.4° C mean July temperature). Mean annual precipitation at Sisters is 408 mm, occurring mostly as snow. Only 36 mm of rain falls during the summer months (June through August), resulting in an annual period of drought.

The study was conducted at a forested site on flat terrain not dissected by streams. The soils are derived of basaltic pumice parent material erupted from volcanoes of the High Cascades, and are deep, coarse-textured, and poorly developed (Hall 1972). The open-canopy, multi-cohort old-growth stand consists of ponderosa pine with trace amounts of grand fir (*Abies grandis*). Overstory trees were moderately clumped rather than randomly or regularly dispersed. The understory vegetation is composed primarily of the deciduous antelope bitterbrush (*Purshia tridentata*), with some western needlegrass (*Stipa occidentalis*).

Data Collection and Analysis

A 4.5-hectare inventory unit was established at the study area in 1981 by Sarah Greene (USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331). Within the unit, all trees ≥10-cm diameter at breast height (140 cm; dbh) were inventoried and mapped. In 1986, dbh was recorded for all live trees in the unit. During the same year, a grid of 28 2-m radius, circular regeneration plots was established in the unit. Regeneration plot centers were located at 25-m intervals along the grid. Measurements at these plots included tallies of three size-classes of regeneration: stems 0.1-9.9 cm tall, stems 10.0-139.9 cm tall, and stems 0.1 cm dbh (breast height; 140 cm tall) to 9.9 cm dbh. For simplification in this study, these classes are referred to as germinants, seedlings, and saplings, respectively. In addition, diagrams of bitterbrush cover within each 2-m radius regeneration plot were sketched in the field and were later used to visually estimate shrub cover as absent, trace (1 percent), or in increments of 5 percent. Data from one of the regeneration plots were lost, so the number of plots used in the analysis was 27.

Overstory density conditions over the plots were calculated at two different scales by summing overstory tree basal areas in circular areas of 5 and 15 m radii centered on the regeneration plot centers. Regeneration plot data were used to calculate density (stems per plot) of germinants, seedlings, and saplings.

A preliminary assessment of spatial autocorrelation was performed for each of the three regeneration classes to assess whether the assumptions of linear regression were violated. Tests were based on calculations of Moran's I statistic, a coefficient that measures the dependence among variable values between spatial points (Upton and Fingleton 1985). Moran's I was calculated at six regular distance classes (0-36m, 36-71m, 71-107m, 107-142m, 142-177m, 177-213m). The number of pairs in each class ranged between 28 and 92. The Bonferroni approximation procedure (Rawlings et al. 1998) was used to determine overall significance (α=0.05).

Simple and multiple Poisson regressions were conducted to quantify the explanatory value of stand structure variables that were hypothesized to influence regeneration density (n=27). There were three response variables: number of stems per plot for each of the three regeneration size classes. Because these data were counts expected to follow the Poisson distribution, Poisson regression models (with log link function) were used for the tests (Neter et al. 1996). The primary explanatory variable tested was overstory tree basal area per hectare, which was calculated for each regeneration plot. This measure was used as a plot-specific estimate of overstory density, and was assumed independent of the sizes of constituent trees. Two variants of overstory basal area were used in order to test whether the effects of overstory trees on regeneration were manifested at different spatial scales for the different sizes of regeneration. The two overstory density variants were calculated by summing the basal area of trees within radii of 5 and 15 meters from the center of each regeneration plot, then using the appropriate expansion factor to express basal area on a per-hectare basis. Because the sapling class included relatively large stems with potentially substantial competitive impact, the number of saplings per 2-m radius regeneration plot was also tested as an explanatory factor for germinant and seedling densities. The effect of shrubs, using percent shrub cover measured within each regeneration plot, was tested for significance alone and with adjustments for overstory density. All tests of significance were conducted at the $\alpha=0.05$ level.

Quadrat-based spatial analysis tools were used to characterize the spatial distribution of regeneration density. Variance/mean ratio, Index of Dispersion (a statistical test to determine the significance of the variance/mean ratio), and standardized Morisita's Index were calculated for each regeneration size class to determine whether they occurred in clumped, random, or regular patterns (Greig-Smith 1983, Krebs 1989).

RESULTS & DISCUSSION

Stand Structure

Stand density in 1986 was 350 trees (>10 cm dbh) per hectare, with 24.1 m^2/ha of basal area (SDI=477 metric). Nearly all of the overstory was ponderosa pine (> 99% of basal area). The range of local basal areas calculated within 5-m radius around the regeneration plots was great at 0.00-1.68 m^2, or 0.0-32.2 m^2 per hectare. The densities at the high end of the range of 5-m plot densities are extremely high for ponderosa pine stands in this region, which more typically support basal areas of 15-25 m^2 per hectare, or 0.19-0.32 m^2 per plot. These local densities are partly an artifact of the clumpiness of the overstory and the small area sampled using a 5-m radius. Such high overstory tree densities can be expected to have a substantial competitive effect on understory vegetation, including regeneration.

Average bitterbrush cover per 2-m radius regeneration plot was 27.4% (standard deviation = 18.1%). Quadratic mean dbh was 29.6 cm, but the largest tree was 121.3 cm dbh. The frequency distribution of dbh (Figure 3.1) illustrates the broad range of tree sizes in the stand. More than 84% of stems (295 of 349 trees per hectare) were less than 30 cm dbh, with more than 76% of stems (267 of

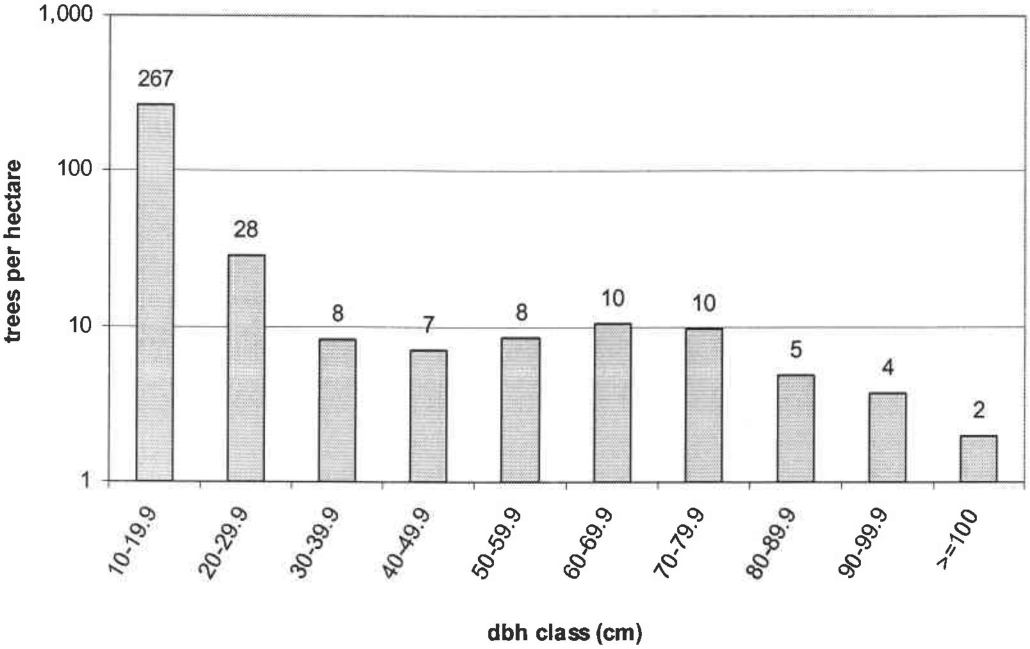

FIGURE 3.1. Frequency distribution of overstory trees by diameter class (note logarithmic scale of y-axis).

349 trees per hectare) in the smallest (10.0-19.9 cm) diameter class. This structure indicates a substantial increase in tree density in recent decades that is likely attributed to the exclusion of fire from the stand.

Regeneration stocking was also very high. The total density of regeneration in all classes in 1986 was 11.8 per 2-m radius regeneration plot, or 9,402 stems per hectare. Most of these stems (64.6 percent) were in the <10 cm height class, however. In addition, 60.7 percent of stems in the <10 cm class were in clusters of up to 17 stems, probably due to rodent caching, that are likely to winnow over time to fewer stems per cluster (Chapter 5). When each cluster is regarded as a single emergence site, the total regeneration density remains very high at 6,219 stems per hectare. Lacking fire, silvicultural thinning, or another stand disturbance that reduces stand density, stems in the current regeneration stages will lead to a stand density that far exceeds the density comprised by the overstory trees.

Influence of Stand Structure on Regeneration

For each of the three regeneration classes, the Moran's I tests indicated no spatial autocorrelation. Table 3.1 shows the distance classes tested and the significance of Moran's I for each class. Using Bonferroni approximation, spatial autocorrelation was not significant for germinants (P=0.792), seedlings (P=0.317), and saplings (P=0.212).

For the two smaller regeneration classes (< 140cm height), the influence of the overstory was most apparent when basal area was calculated for the trees

TABLE 3.1. Results of the Moran's I tests for spatial autocorrelation of regeneration density by regeneration classes. Moran's I statistic was almost uniformly non-significant (α=0.05) at each distance class. The overall correlogram was non-significant for each regeneration class.

	Moran's I (*P*-value)		
Distance Class (m)	**Germinants**	**Seedlings**	**Saplings**
0 – 36	-0.199 (0.132)	0.041 (0.277)	0.088 (0.207)
36 – 71	-0.108 (0.237)	0.000 (0.336)	-0.226 (0.035)
71 – 107	-0.009 (0.354)	0.035 (0.159)	0.001 (0.320)
107 – 142	0.049 (0.165)	-0.095 (0.252)	0.059 (0.157)
142 – 177	0.020 (0.295)	-0.205 (0.053)	-0.95 (0.315)
177 – 213	-0.130 (0.272)	0.008 (0.375)	-0.038 (0.498)
Overall Significance	(0.792)	(0.317)	(0.212)

closest to the regeneration plot (Table 3.2). Total overstory basal within a 5-m radius was the most significant factor (negative) on density of germinants (P=0.0007) and seedlings (P=0.0043). Sapling density was not significantly related to overstory basal area within a 5-m radius, but there appears to be an upper limit on regeneration density in scatterplots of saplings and the other two regeneration classes, conditional on overstory basal area (Figure 3.2). Despite scale differences on the Y-axis, the response patterns are consistent across the three regeneration classes. The very high densities around some regeneration plots likely precludes the possibility of regeneration surviving at those fully-occupied sites.

Germinants and seedlings were also negatively related to sapling density (P=0.0029 and P=0.0269, respectively). The effect of sapling density was significant even when overstory basal area within a 5-m radius was included in the model. Scatterplots and tests of overstory basal area within the 15-m radius did not reveal any relationships with germinants or seedlings. These results indicate that although the presence of overstory trees does adversely affect density of small regeneration, that influence is exerted only by those trees in close proximity.

Germinant density was positively associated with percent bitterbrush cover (P=0.0141), a relationship that was also significant when 5-m overstory basal area per hectare was included in the model. For seedling density, bitterbrush cover was not a significant factor when tested alone, but did have a significantly positive effect when 5-m overstory basal area was included in the model.

TABLE 3.2. Response variables (Y), explanatory variables (X), and regression coefficients ($ß_x$) of single-factor and two-factor Poisson regression models with log link function (n=27; significant factors at $\alpha=0.05$ in bold).

Y	X	$ß_x$	*P*-value
Germinants (0.1 – 9.9 cm tall)	*One-factor models*		
	5-m Overstory Basal Area	**-0.0089**	**0.0007**
	15-m Overstory Basal Area	0.0007	0.9559
	Number of Saplings	**-0.1120**	**0.0029**
	Percent Shrub Cover	**0.0094**	**0.0141**
	Two-factor models		
	5-m Overstory Basal Area	**-0.0091**	**0.0003**
	Number of Saplings	**-0.1174**	**0.0014**
	5-m Overstory Basal Area	**-0.0119**	**< 0.0001**
	Percent Shrub Cover	**0.0154**	**0.0005**
Seedlings (10.0 – 139.9 cm tall)	*One-factor models*		
	5-m Overstory Basal Area	**-0.0143**	**0.0043**
	15-m Overstory Basal Area	-0.180	0.4094
	Number of Saplings	**-0.1568**	**0.0269**
	Percent Shrub Cover	0.0112	0.0888
	Two-factor models		
	5-m Overstory Basal Area	**-0.0140**	**0.0031**
	Number of Saplings	**-0.1582**	**0.0205**
	5-m Overstory Basal Area	**-0.0194**	**0.0006**
	Percent Shrub Cover	**0.0221**	**0.0070**
Saplings (0.1 – 9.9 cm dbh)	*One-factor models*		
	5-m Overstory Basal Area	-0.0062	0.2467
	15-m Overstory Basal Area	**0.0565**	**0.0341**
	Percent Shrub Cover	**-0.0354**	**0.0003**
	Two-factor model		
	15-m Overstory Basal Area	0.0348	0.1847
	Percent Shrub Cover	**-0.0340**	**0.0008**

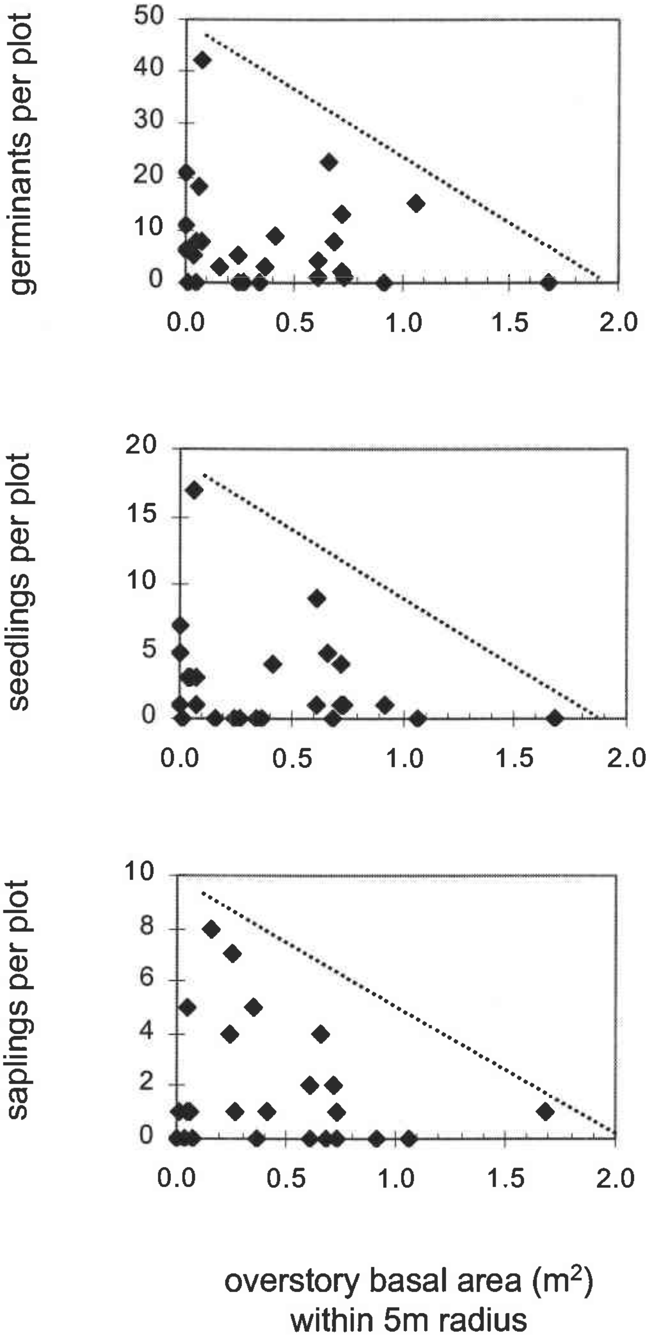

FIGURE 3.2. Regeneration stems per 2m radius plot versus total overstory basal area within a 5m radius. Dashed line illustrates a possible upper density limit for each of the three regeneration size classes (germinants are 0.1-9.9 cm tall, seedlings are 10.0-139.9 cm tall, saplings are 0.1-9.9 cm dbh).

In contrast to germinants, sapling density was most significantly related to bitterbrush cover (P=0.0003), not overstory density. The regression coefficient for bitterbrush cover was negative, indicating a net competitive relationship between saplings and bitterbrush. The relationship of saplings to overstory basal area within a 5-m radius was not significant (P=0.2467). In contrast, the effect of 15-m overstory basal area was significantly positive (P=0.0341).

Since stems in the germinant class are probably too small to exert any influence on shrubs, the positive association between germinant density and shrub cover may represent a facilitative effect of shrubs on germination and/or small seedling survival. Shrubs in the ponderosa pine zone, such as *Purshia tridentata*, *Arctostaphylos parryana*, and *Ceanothus velutina*, have been shown to be strong competitors for soil moisture (Barrett and Youngberg 1965, Tarrant 1957). However, others have argued that the facilitative influence of shrubs outweighs their competitive influence, at least during the first years following germination when seedlings are particularly vulnerable (Conard et al. 1985, Zavitkovski and Woodard 1970). Shade from shrubs may reduce the evaporative demands on germinants and small seedlings, whose developing root systems may be overtaxed during periods of drought. Tappeiner and Helms (1971) reported such an influence on natural regeneration of *Abies concolor* and *Pseudotsuga menziesii* on harsh sites in the Sierra Nevada. They observed that soil moisture and potential evaporation varied significantly under different combinations of shrub composition and overstory cover, and found that those microsites were associated with different germination, survival, and growth rates. In central Oregon, Dyrness and Youngberg (1966) noted a high proportion of ponderosa pine seedlings occurring directly under shrubs.

Our findings may indicate that the net effect of shrubs is facilitative when seedlings are small. We theorize that whereas both the shrubs and overstory trees compete with the small seedlings for scarce resources, only the shrubs buffer extremes of the physical environment sufficiently to offset the competitive influence, resulting in a net facilitation effect. The relationship appears to become competitive once seedlings become fully established, perhaps because seedlings outgrow the zone of environmental buffering and increase their demands for site resources. Had overstory trees also provided this beneficial shading effect, positive associations between regeneration density and overstory density would have been expected, rather than the negative associations and non-significant associations found here for germinants and saplings.

However, the observation of patterns limits inferences into the processes driving those patterns. An alternative explanation to the facilitation hypothesis is that ponderosa pines seedlings and bitterbrush seedlings are adapted to similar microenvironments, and the recruitment patterns of both species were controlled by the distribution of beneficial microsites. Rather than indicating that survival of regeneration was better for those saplings away from the influence of shrubs, the negative association between sapling density and shrub cover may indicate that competition has caused shrubs around saplings to diminish in size.

It is possible that the positive association between saplings and overstory basal area is due to the fact that stems in the sapling class are from the same cohort as smaller overstory trees constituting the 15-m radius basal area estimates. More than three quarters of all overstory trees were in the 10.0-19.9 cm dbh class. The basal areas calculated from trees within a 15-m radius may have consisted of a relatively large proportion of trees from this smallest overstory tree size class. The 15-m overstory basal area was not significant with percent shrub cover in the model.

Although causal relationships are hypothesized in this paper, causality cannot be directly inferred from the observational data we analyzed. Additional measurements are necessary to confirm the theorized ameliorating effect of shrub cover on early seedling establishment and/or survival. Inferences into regeneration dynamics in this study of spatial patterns are limited by the one-time collection of data that lacks information on the temporal patterns of ponderosa pine and bitterbrush establishment and growth. Repeat measurements to document seedling emergence and mortality trends can be used to relate those important processes to the presence of shrubs and overstory trees. Such an approach was used in the analysis presented in Chapter 5. To further explain the processes driving regeneration dynamics, controlled experiments can be conducted that measure microenvironmental variables affected by shrubs and overstory trees, and relate these to seedling emergence and survival. That approach was used in the study presented in Chapter 6.

Other factors and processes that were not accounted for in this analysis may also have been responsible for the regeneration patterns observed here. For example, we assumed uniform soil resources among the plots, and heterogeneity of soil profiles was not addressed as an explanatory factor. Another potentially important factor may have been the local populations of small mammals such as yellow pine chipmunk (*Tamias amoenus*), which have been shown to be important cachers of western tree and shrub seeds. Vander Wall's (1992) studies in Nevada indicated that the majority of newly-established Jeffrey pine (*Pinus jeffreyi*) seedlings may originate from unrecovered caches. The patterns observed in this study, rather than reflecting competitive-facilitative relationships between vegetation elements, could reflect the locations where the intensity of seed caching or the frequency of unrecovered caches is greater (Vander Wall 1993). Alternatively, shrubs may have helped protect small seedlings from clipping or grazing.

Spatial Patterns

The quadrat-based spatial pattern analyses consistently indicated that all three size classes of regeneration were aggregated at the 2-m radius scale (Table 3.3). Variance/mean ratios were greater than 1, and the Index of Dispersion showed that these were highly significant ($P<0.005$) when compared to the Chi-square distribution (Greig-Smith 1983). This result was corroborated by significant values for standardized Morisita's Index. Because the stand lacks any obvious topographic heterogeneity, the spatial distribution may have been influenced by the spatial patterns of overstory trees and shrubs. For this 2-m radius spatial scale, the magnitude of the variance/mean ratio was inversely related to size

TABLE 3.3. Results of quadrat-based spatial pattern analysis indicating aggregation among all three regeneration size classes. Values for Index of Dispersion all have P-values < 0.005. Values for Standardized Morisita's Index are statistically significant at α=0.05.

	Variance / Mean	Index of Dispersion	Standardized Morisita's Index
Germinants	12.10	314.6	.526
Seedlings	5.52	143.5	.529
Saplings	3.26	84.9	.519

class, showing that aggregation was stronger among seedlings than saplings, and strongest among germinants.

The trend from germinants to saplings offers evidence that the spatial patterns of ponderosa pine stems develop toward regularity at a fine scale, most likely as a result of spatially-influenced, competition-induced mortality patterns. The transformation of spatial distributions of larger trees from a clumped pattern to a more regular pattern was observed by Kenkel (1988) in a juvenile, even-aged boreal stand of jack pine, and by Moeur (1993) in old-growth mixed-conifer stands in the Rocky Mountains. For the 2-m scale that was used in this study, results suggest that ponderosa pine stands may experience density-dependent mortality – and the associated trend toward a more regular spatial pattern – at a very early stage. Unlike point-pattern spatial analysis methods (such as Ripley's *K* (Diggle 1983)), quadrat-based methods such as that employed here (Morisita's Index) are subject to problems related to quadrat scale (e.g. Maguire 1985). Point-pattern methods, however, require mapping all individuals within the study area, a procedure that can practical for larger stems such as overstory trees but impractical for very small stems such as seedlings. This study's findings are presented with the understanding that they may be partly a function of the small scale of study, and with the recognition that different quadrat sizes might have yielded different results.

CONCLUSION

This study found distinctive spatial patterns between ponderosa pine regeneration and adjacent vegetation. Overstory tree density had a negative relationship with the density of small regeneration stems (<140 cm tall). The overstory effect operated at a small spatial scale (5-m radius), but not at a larger scale (15-m). Like overstory trees, saplings (0.1-9.9 cm dbh) were negatively associated with germinants (0.1-9.9 cm) and seedlings (10.0-139.9 cm). Shrub cover was negatively related to saplings, but was positively related to germinants and seedlings. For the single, fine scale addressed by this study, quadrat-based spatial analyses revealed that regeneration in each size class was aggregated, and that aggregation was greatest at smaller regeneration sizes.

Starting from hundreds of thousands of seeds per hectare, mortality typically winnows a regeneration cohort as it passes through the critical stages of germination, emergence, and establishment (Chapter 2). During the first several summers after seedfall when this filtering effect is especially important, fine-scale microsites that enhance survival probabilities operate most strongly and contribute to a clumpy spatial distribution. Once established, stand disturbances or competition within clumps drives seedlings toward to more spatially regular pattern. In ponderosa pine stands, surface fires were historically the disturbance type with the most profound effect on tree densities and spatial patterns (Agee 1993). In the absence of fire, tree densities are denser and probably more clumpy than was previously typical. These stand structures are more susceptible to high-intensity crown fires conditions (Van Wagner 1977), and support trees that are less vigorous and more susceptible to bark beetle outbreaks (Furniss and Carolin 1977). To increase stand and tree resistance to such stand-replacing disturbances, silvicultural thinning to reduce density and clumpiness is necessary in many stands similar to the one studied here.

The specific mechanisms that produced the spatial patterns in this study were not identified and cannot be inferred from the data available. We propose that the spatial patterns are manifestations of important relationships between ponderosa pine regeneration and adjacent vegetation, namely: that regeneration is particularly sensitive to the influences of adjacent vegetation; that the relationships between regeneration and adjacent vegetation change as stems become larger; and that these relationships are borne out in regeneration spatial patterns that begin as highly aggregated and gradually transform during stand development to a more random distribution. Amelioration of microenvironmental conditions, such as soil and air temperature and solar radiation, and competition for belowground resources, especially soil moisture, are hypothesized as the primary agents driving the observed spatial patterns (Youngberg 1966, Holmgren et al. 1997). However, these hypotheses cannot be supported by the limited set of data collected for this study, which does not permit inferences of causality. Other potential factors affecting regeneration spatial patterns include, for example, elements of microsite (such as forest floor litter, soil nutrients), seed-caching animals (Vander Wall 1992), or seedling-clipping and seedling-browsing animals (Lawrence et al. 1961). Analyses of repeat measurements of seedling establishment and growth, preferably including the remeasurement of labeled seedlings in permanent plots, would provide a better assessment of the role of shrubs and overstory trees on ponderosa pine regeneration dynamics.

A data-intensive project has been conducted in central Oregon to better address the relationships of overstory trees and shrubs to seedling emergence and survival (Chapters 4-6). Studies in that project relate the spatial relationship of stand vegetation to the emergence, survival, and growth of individual seedlings, and also address the effects of forest floor substrate and the effects of seed caching by animals. The project also includes a comparison of the air and soil temperatures, light intensity, and relative humidity for seedlings emerging beneath shrubs versus those in the open. Although those studies are based in disturbed stands, they should help clarify the mechanisms influencing the regeneration spatial patterns that were observed in this study.

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CHAPTER 4

SPATIAL AND TEMPORAL PATTERNS OF PONDEROSA PINE SEED RAIN BENEATH PARTIAL OVERSTORIES

INTRODUCTION

Among the most important influences on natural seedling regeneration is the availability of viable seed. Successful recruitment of a new seedling cohort depends on an adequate supply of seed to compensate for the attritional impacts of harsh environments, poor substrates, seed-predating animals, herbivorous animals, and competitive vegetation. Forest managers who depend on natural regeneration must have a good understanding of the magnitude and spatial patterns of seed rain under different stand and site conditions.

On federally managed forests of ponderosa pine (*Pinus ponderosa*) on the east slope of the Cascade Range, traditional harvests are increasingly being replaced by silvicultural treatments that resemble variable-retention harvests. Variable-retention harvests are characterized by the retention of some live overstory trees during and after harvest to ameliorate aesthetic impacts and maintain ecological functions (Franklin et al. 1997). With the exception of several studies in seed-tree, shelterwood, and group-selection harvests (e.g. Curtis and Foiles 1961), forest managers in this region have a limited basis for predicting the spatial patterns of seed rain beneath partial overstories and for prescribing adequate numbers and spatial distribution of leave trees.

This paper presents an analysis that was conducted as part of a larger study designed to address stand and site influences on the recruitment and growth of ponderosa pine seedlings under conditions resembling variable-retention harvests (Keyes and Maguire 2000). For this analysis, the primary objective was to determine whether the distribution of seeds under these conditions could potentially limit the seedling recruitment process and the availability of seedlings, or conversely, whether seed availability could be manipulated to lower recruitment where it could otherwise become a problem, particularly in absence of fire. The results of this analysis, in which the relationship between ponderosa pine seedfall and the spatial distribution and size of overstory trees is quantified, are relevant to ponderosa pine forests in the volcanic pumice zone of central Oregon.

METHODS

Study Areas

The study was based on data collected on the Deschutes National Forest, at sites located approximately 50 kilometers south of Bend, Oregon (Figure 4.1). Soils in this region are poorly developed, sandy-textured and very porous. The parent material is air-lain pumice erupted from Cascade volcanoes. In most stands, the primary site factor limiting growth is soil moisture. According to data from a NOAA climate station in Bend, the area typically receives less than 30 cm of precipitation annually, most of which falls during the winter months. Less than 4 cm of rain falls between June and October.

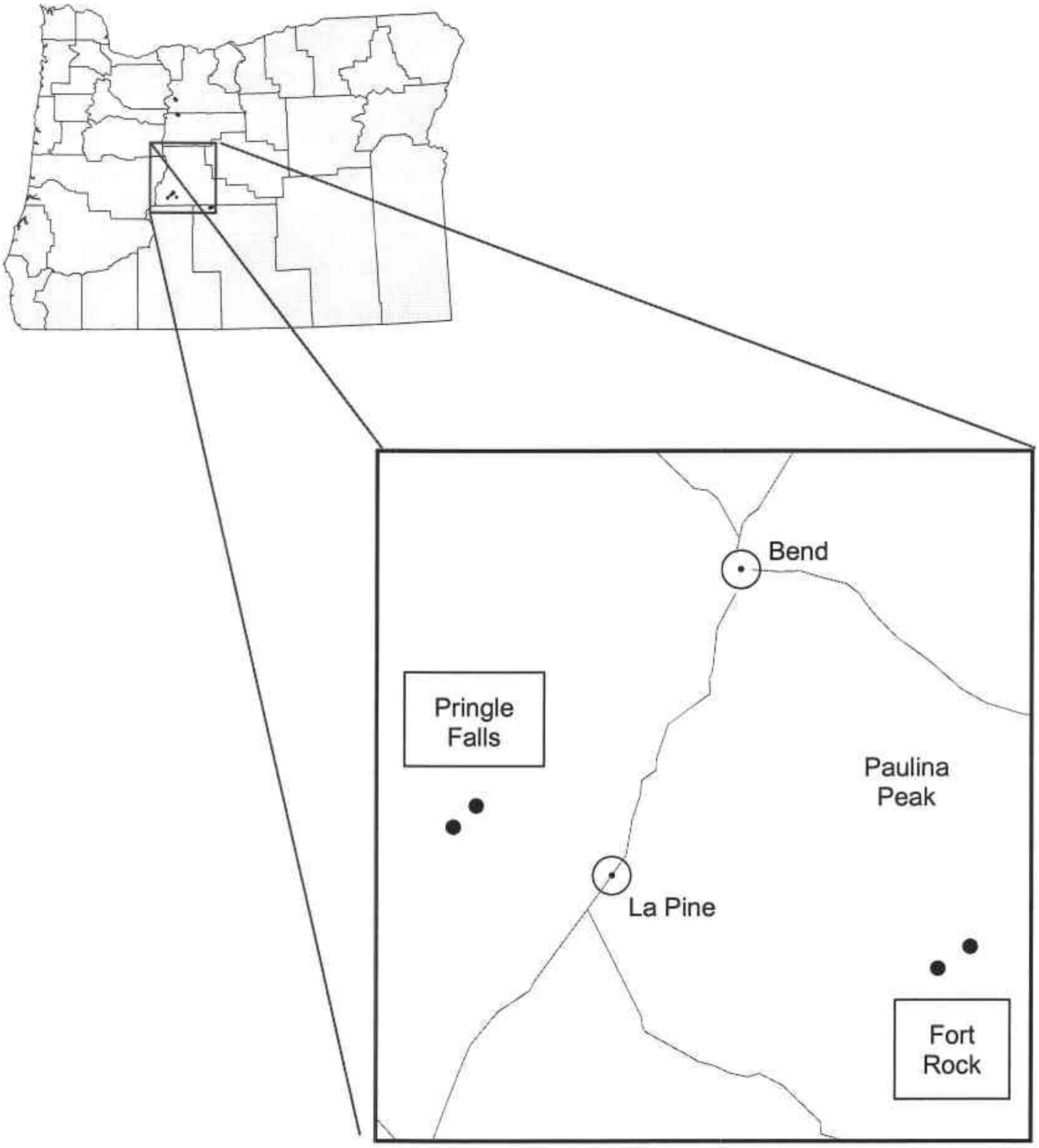

FIGURE 4.1. Location of the four stands used in the study.

The four stands used in the study represent a gradient of overstory density. Structural characteristics of the study's four stands are presented in Table 4.1. Overstory density ranged from 4.2 to 18.1 m^2/hectare, and from 18 to 80 trees/hectare. Although density varied, individual tree dimensions were similar in all four stands. All overstory trees were ponderosa pines. Most were large and appeared vigorous with large, full crowns. Quadratic mean diameters at breast height were between 50 and 60 cm, and live crown ratios averaged 44 to 62 percent. The stands had been harvested at least 10 years ago and showed no signs of recent disturbance.

Two stands were located on the more mesic western half of the Deschutes National Forest close to the Cascade foothills ("Pringle Falls"), where stands are often mixtures of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and lodgepole pine (*Pinus contorta*). In disturbed stands in this area, snowbrush (*Ceanothus velutinus*) and greenleaf manzanita (*Arctostaphylos patula*) form dense shrub canopies in the understory, and antelope bitterbrush (*Purshia tridentata*) occurs in minor amounts. At Pringle Falls, shrub cover (mostly snowbrush and greenleaf manzanita) averaged 66 percent of the forest floor.

Two stands were located at a second site on the more xeric eastern half of the Deschutes National Forest, near the transition from dry forest to high desert ("Fort Rock"). In that area, ponderosa pine occurs in pure stands. Antelope bitterbrush is the dominant shrub, and Idaho fescue (*Festuca idahoensis*) is an important and widespread graminoid. At Fort Rock, shrub cover (mostly

TABLE 4.1. Attributes of stand structure for the four stands used in the study. Qmd is quadratic mean diameter at breast height. LCR is live crown ratio. Shrub cover is percent of forest floor surface area covered by shrub foliage. Understory Veg. codes: ARPA=*Arctostaphylos patula*, CEVE=*Ceanothus velutinus*, FEID=*Festuca idahoensis*, PUTR=*Purshia tridentata.*

Site	Stand	Trees / Ha	Basal Area (m^2/Ha)	Qmd (cm)	Ave. Ht. (m)	Ave. LCR (%)	Shrub Cover (%)	Understory Vegetation (Spp.)
Pringle Falls	Rapmaster	39	10.8	59.3	31.7	44	77	CEVE ARPA
	Round Mtn.	80	18.1	53.7	29.8	50	54	CEVE ARPA
Fort Rock	Pie	18	4.2	54.8	21.8	61	38	PUTR FEID
	Sunray	47	13.2	59.8	24.4	62	40	PUTR FEID

bitterbrush) averaged 39 percent and graminoid cover (mostly Idaho fescue) averaged 32 percent.

Data Collection and Analysis

The spatial and temporal patterns of seed rain were observed over one seedfall season, from early September 1999 to early June 2000. Seed traps were located at 20-m intervals on grids in each of four stands: two at the Pringle Falls site (16 traps at Rapmaster; 7 traps at Round Mountain) and two at the Fort Rock site (16 traps each at Pie and Sunray). Overstory trees >20-cm dbh were measured for dbh, height, and live crown ratio. Tree and seed map locations were mapped by x-y coordinates to the nearest 0.1 m using a laser rangefinder.

The seed traps were square wooden frames with 11.4-cm deep walls, and a 61.0- by 58.4-cm (0.356-m^2) open surface. Trap tops were covered with 12.7x12.7-mm hardware cloth to allow ponderosa pine seeds (typically 5-8 mm long) to enter the trap while excluding vertebrate seed predators. Trap bottoms were covered with nylon mosquito screening and a protective base of 6.4x6.4-mm hardware cloth to enable rain and melted snow to pass through. Traps were placed on the ground.

The Fort Rock traps (32) were installed on September 2, 1999 and the Pringle Falls traps (24) were installed on September 7, 1999. Seeds were collected on October 4-5 and October 30-31. Seeds were collected again at the Fort Rock stands on November 30; heavy snow prevented collection at the Pringle Falls site on that date. Over-winter seedfall was collected at both sites on June 6,

2000. During summer 2000, trees were classified by the number of fresh (1999 crop) cones found within each tree's crown projection area: 0-10 cones, 11-25 cones, or greater than 25 cones.

Seeds were sealed in plastic bags, transported to the lab, and stored at 4°C until March 2001. All whole seeds were dissected with razors to distinguish between viable and non-viable seed. Seeds with a female gametophyte were considered viable for germination. For the October 4-5 Fort Rock collection, non-viable seeds were recorded as unfilled (full-size but empty seed), aborted (seed wing with undeveloped seed) or excavated (seed eaten from within by invertebrate; seed coat now packed with frass). Analysis of variance was conducted to test for differences in the quantity of viable seed collected between sites, and between stands within sites. T-tests were conducted to test for differences between sites in cumulative seedfall rates (proportion of total) on October 4-5 and October 30-31.

For each stand, contour maps portraying the within-stand variability of seedfall were produced from seed trap data using the "loess" locally weighted smoothing method (Cleveland 1979). These maps were overlain with points representing overstory tree locations to qualitatively illustrate the relationship between seed density and tree density in each stand. To better describe the distribution of seeds around potential seed trees, negative binomial probability density functions described by Clark et al. (1998) were fitted to the seedfall data by the method of maximum likelihood. This model assumes that total seedfall at any location is the cumulative contribution of seeds from all trees within the sampling area, and describes seed density as a function of the distance from a parent tree as well as its size. The function is:

$$L(S \mid p,\theta) = \prod_{j=1}^{m} \frac{\Gamma(s_j+\theta)}{\Gamma(s_j+1)\Gamma(\theta)} \frac{\hat{s}^{s_j}(b,x_j;p)\theta^{\theta}}{\left(\hat{s}(b,x_j;p)+\theta\right)^{s_j+\theta}} \tag{1}$$

where $\Gamma(\cdot)$ is the gamma function, S is the data set containing m seed traps, s_j is the observed rate of seed arrival at trap j, and θ is a fitted, dimensionless parameter describing degree of clumping. The expected seed abundance at trap j is the function $\hat{s}(b,x_j;p)$:

$$\hat{s}(b,x;p) = \frac{\beta}{\pi\alpha^2} \sum_{i=1}^{ntrees} b_i \exp\left[-\left(\frac{x_{ij}}{\alpha}\right)^2\right] \tag{2}$$

where x_j is the distance from a tree, b is the tree's basal area, and p is a vector of fitted parameters (α, β) maximizing the Equation 1 likelihood.

RESULTS & DISCUSSION

Seed Quality & Amount

The seeds collected in the traps varied in quality. Analysis of the seed collected at the Pie and Sunray stands over one month showed that 76 and 62 percent, respectively, of total seedfall was in a condition sufficient for germination (Figure 4.2). Most of the remainder was either aborted or unfilled seed, with only a fraction of a percent of all collected seed excavated by insects. Among fully-formed seeds (aborted and excavated seeds excluded) that fell between September 2 and October 4-5 at Pie and Sunray, 88 percent and 72 percent were viable.

In small clearcuts (0.1 to 1.2 hectare) in central Idaho, Curtis and Foiles (1961) identified via germination tests that 83 percent of the heavy 1958 crop of ponderosa pine seeds was viable. In central Oregon, Barrett (1966) used a cutting test to determine that 86 percent of ponderosa pine seeds that fell within two chains from a clearcut edge were sound. At eight chains from the edge, the viability rate dropped to 67 percent. In studies of ponderosa pine seedfall in an uncut old-growth stand and an uncut immature stand near Pringle Falls, Oregon, Dahms and Barrett (1975) observed average viability rates of 80.0 and 86.6 percent, respectively. In the same study, seed viability in clearcuts at central Oregon's Winema National Forest averaged 79.3 percent. For 7 higher-than-average ponderosa pine seed crops in central northern California, McDonald (1992) reported a much lower average viability rate of 43 percent (range 31-59

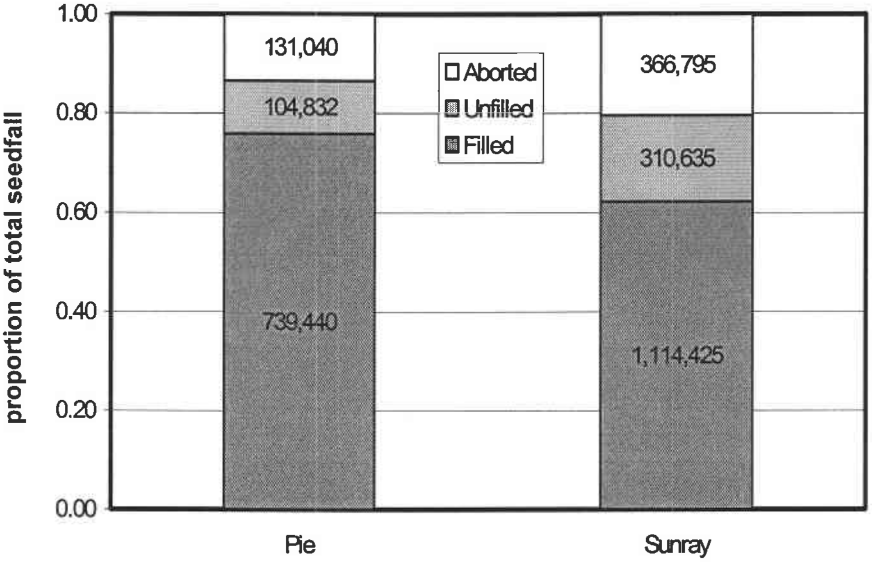

FIGURE 4.2. Seed quality distribution for seeds collected at the Fort Rock sites between September 2 and October 4, 1999. Values within columns are stand-average seed counts per hectare.

percent) in uncut stands. Fowells and Schubert (1956), Shearer and Schmidt (1970), and Dahms and Barrett (1975) all reported that sound ponderosa pine seeds tended to fall earlier in the season than unsound seeds. In this study, the proportion of seed that was viable was recorded only for the October 4-5 Fort Rock collection. The viability rates of the entire seed crop (including seed that fell after October 4-5) were probably somewhat less than the 72-88 percent reported above because only 50-72 percent of the total seedfall had occurred prior to October 4-5 (see below).

For the year of seedfall studied, seed production was not a limiting agent on regeneration at any of the four stands. A total 2,166 viable seeds were collected over the full sampling period. Across all four stands, this averaged more than one million viable seeds per hectare (Table 4.2). There was a substantial difference in viable seed collected among the two sites, however: the amount of viable seed at the Fort Rock stands was more than six times the amount collected at the Pringle Falls stands. This site effect was strongly significant (P<.0001). Within each site, the amount of viable seed increased with overstory density (P<.0001).

At both Fort Rock stands, the amounts of viable seed collected were well above the amount typically considered a large seed crop (about 500,000 per hectare; e.g. Barrett et al. 1983). Between 1958 and 1981, McDonald (1992) reported crops of 0 to 760,000 sound seeds per hectare in uncut stands. During an 11-year period in western Montana, Shearer and Schmidt (1970) observed that

TABLE 4.2. Total viable seeds (per hectare) collected at the four stands between September 1999 and June 2000.

Site	Stand	seed traps	Ave. viable seeds / trap (95% CI)	Ave. viable seeds / ha
Pringle Falls	Rapmaster	16	7.3 (0, 15.6)	205,355
	Round Mtn.	7	14.4 (7.6, 21.2)	405,154
Fort Rock	Pie	16	42.1 (16.7, 67.5)	1,182,870
	Sunray	16	79.6 (25.0, 134.2)	2,235,870
Mean				1,105,841

the best crop was about 55,000 per hectare, and that for five of those years less than approximately 200 seeds per hectare were caught.

Temporal Seedfall Patterns

The trends in seedfall over time are presented in Figure 4.3. Within the first 30 days, or by October 4-5, between 50 and 72 percent of the year's total viable seedfall had occurred. At the Fort Rock stands, where a late fall collection was possible, 89 to 93 percent of viable seed fell by November 30, which was 86-87 days after the start of trapping. These temporal seedfall patterns are similar to those identified in previous studies, which have shown that the majority of seedfall occurs in late summer and early fall, and that little seedfall occurs after the start of winter. For example, Curtis and Foiles (1961) found that most of the 1958 seed crop in central Idaho fell between September 10 and 30. At the Stanislaus National Forest in northern California, Fowells and Schubert (1956) found that 84 percent of seed had fallen by November. At sites in central Oregon not far from this study's sites, Dahms and Barrett (1975) found that just 38-39 percent of seed fell by early October, but that by early November, 82-83 percent of seedfall was complete.

Dahms and Barrett (1975) also found that Pringle Falls seed fell at a more rapid rate than Winema National Forest seed, and speculated that a difference in elevation between the sites might have been responsible (the Winema site elevation was about 225m higher than that study's Pringle Falls sites). Although in this study the Fort Rock stands are at a higher elevation than the Pringle Falls

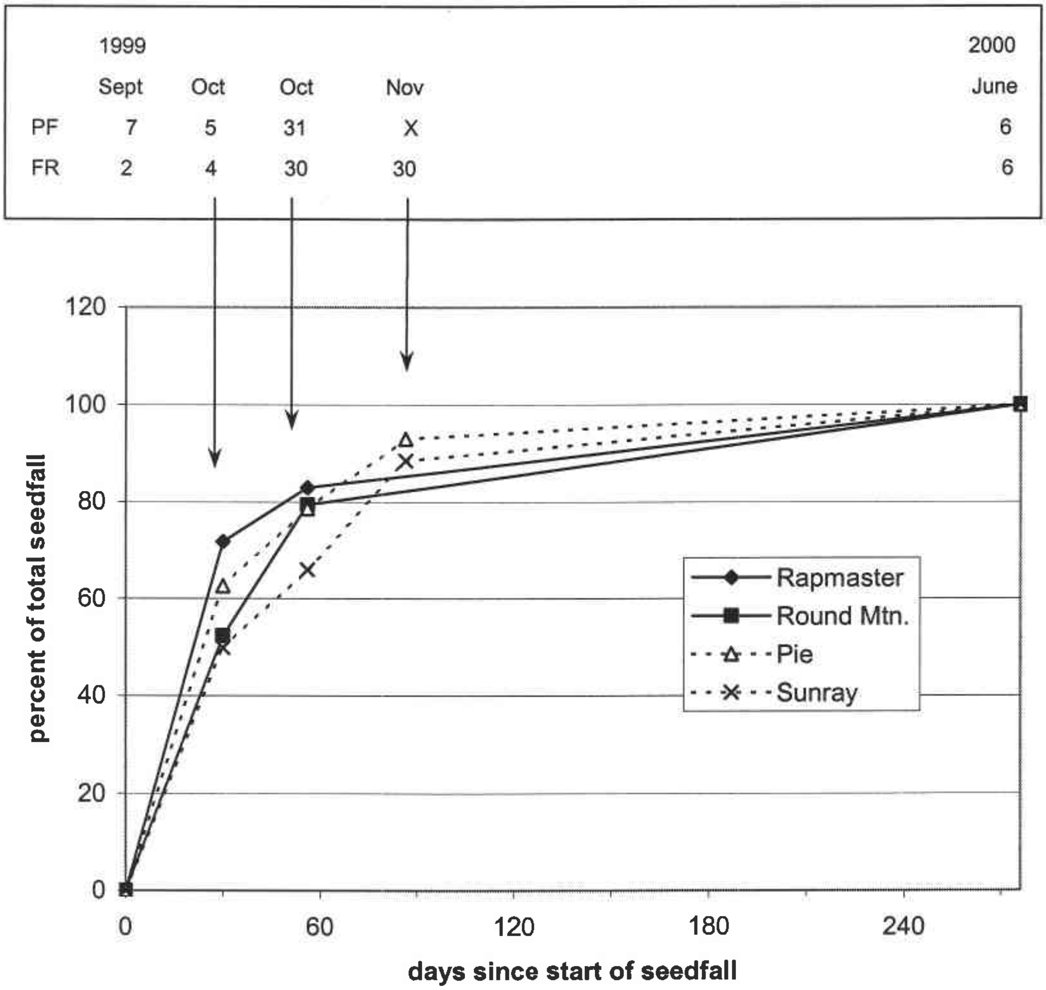

FIGURE 4.3. Temporal pattern of viable seedfall from early September, 1999 to June 6, 2000 at Pringle Falls (PF) and Fort Rock (FR). There was no significant difference in cumulative seedfall rates among sites for the October 4-5 or October 30-31 tallies (P=.4642 and P=.2231, respectively). Note that a late fall (November 30) collection was possible only at the Fort Rock stands.

stands, no significant difference was found in the cumulative seedfall rate between the two sites (P=.4642 for October 4-5 tally; P=.2231 for October 30-31 tally).

Spatial Seedfall Patterns

The spatial distribution of retained overstory trees did not result in conclusive spatial patterns of seed dispersal. To illustrate this, contour maps of the smoothed seed rain data and overstory tree points are presented in Figure 4.4. The maps illustrate that seedfall was not uniformly distributed throughout the study areas, although with the exception of Pie, seedfall variability was not great. When the contours are visually related to seed tree locations in each stand, however, there are no strong seed shadows around overstory trees that fit the classic model (seed density greatest near overstory trees, and least at distances from overstory trees).

The fitted seed rain profiles illustrated the variability in effects of seed trees on seed rain (Figure 4.5). All four models depicted a decline in seed proportion with distance from overstory trees. Steepest relationships (negative binomial) of seedfall proportion and distance from seed tree were revealed at Rapmaster and Sunray. At those stands, most seed was estimated to fall within close proximity to tree crowns. At Pie and Round Mountain, however, the profiles were nearly flat, indicating that locations of overstory trees were not strongly related to the seedfall spatial distributions. Lack of spatial heterogeneity in the seed distributions and overstory tree distributions, or variability in fecundity of trees, could have contributed to these weak shadows.

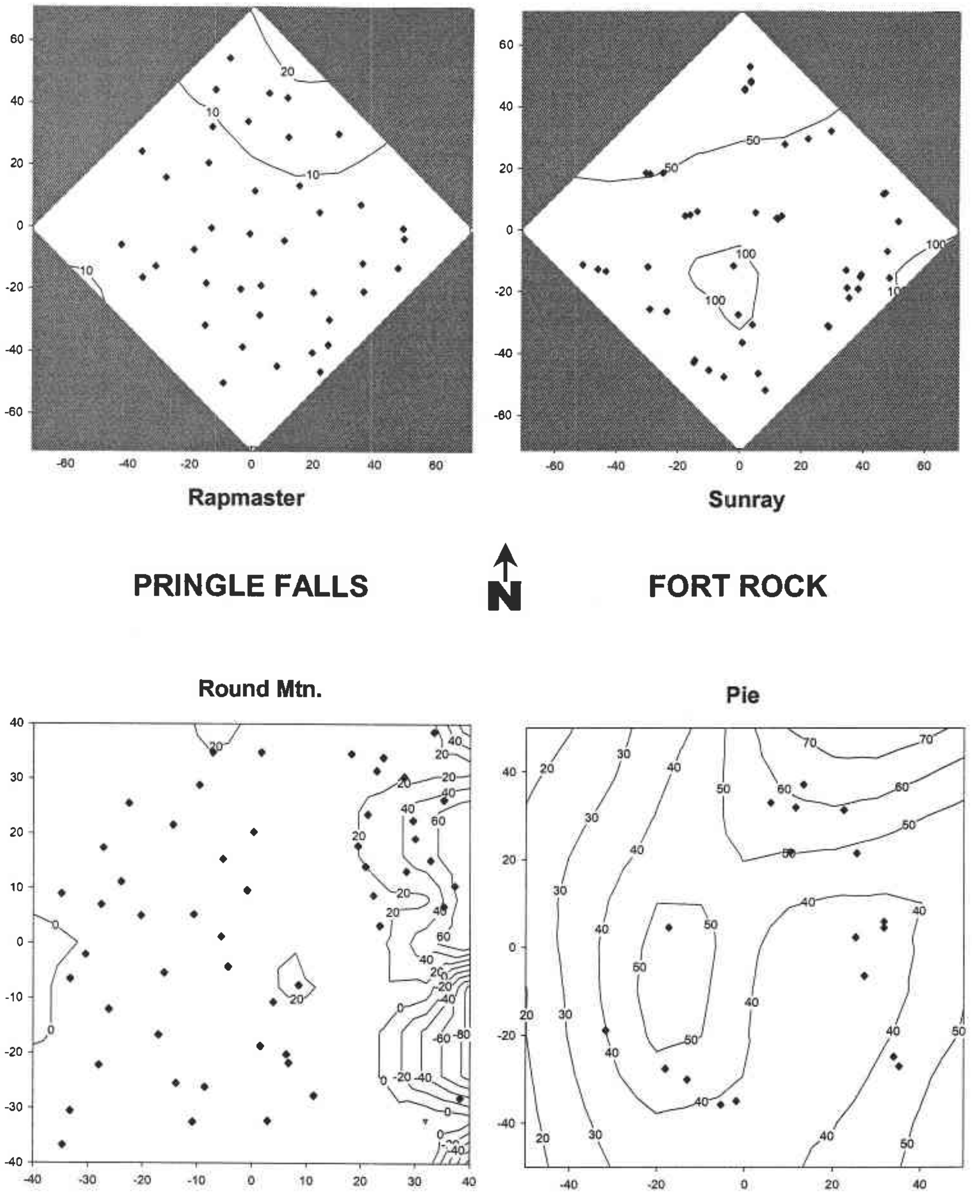

FIGURE 4.4. Contour maps of overstory tree and smoothed seedfall data. Points denote location of overstory trees. Isopleth values are seed counts. Axis values represent distance in meters.

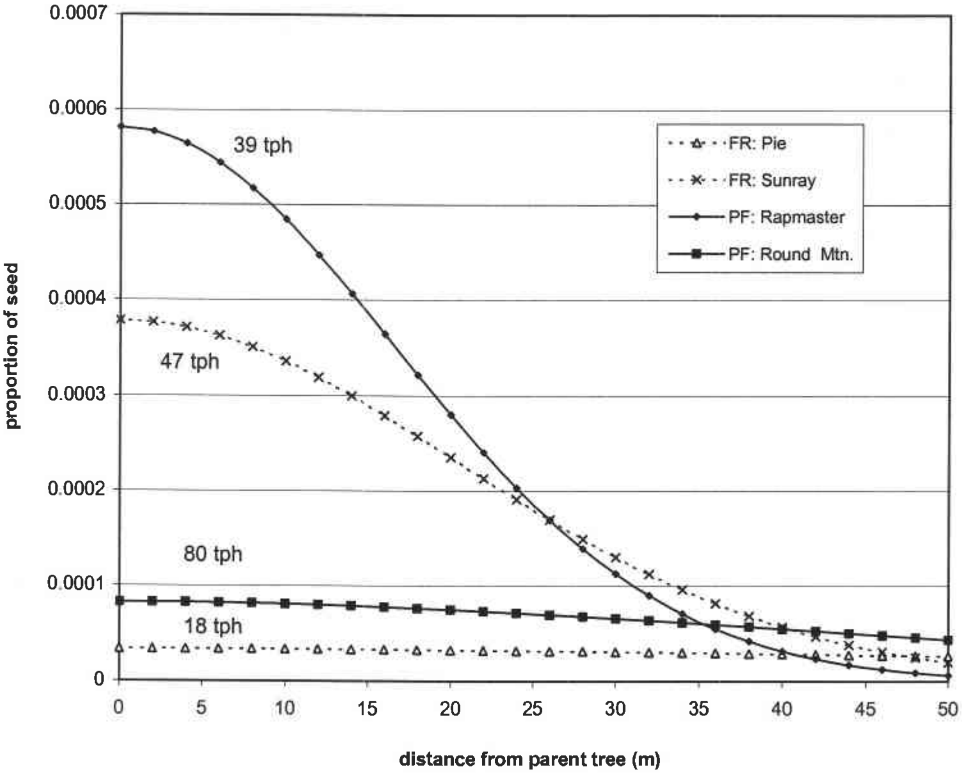

FIGURE 4.5. Seed shadows fitted to each of the four stands in the study. Tph is trees per hectare. PF is Pringle Falls; FR is Fort Rock.

The influences of speed and direction of wind, stand structure, and topography outside the study units may have contributed to the spatial distribution of seeds within the units, either enhancing or masking the spatial relationship between seed trees and seedfall. In their study of seedfall in two clearcuts in central Oregon, Dahms and Barrett (1975) believed differences in topography and surrounding tree heights contributed to differences in the amount of seed collected at different directions and distances from the clearcut boundaries. In this study, each of the four stands was relatively flat, but surrounding topography and stand structures differed among stands. The Round Mountain site is at the southern base of its namesake landform, and is surrounded by stands of similar or greater density. Rapmaster is bordered by a closed-canopy stand to the north and a more open stand to the west. The land surrounding Pie and Sunray is essentially flat, and adjacent stands are of similarly low density. These influences outside the study units may have played an important role in the spatial patterns of seed dispersal within the units, perhaps more so than within-stand characteristics such as spatial distribution of overstory trees that were the subject of this study.

It is of interest to note that of the four stands, the spatial distribution of overstory trees was most regular at Round Mountain and least regular at Pie. In addition, overstory density was greatest at Round Mountain (80 tph) and least at Pie (18 tph). In both cases, little trap-to-trap variability resulted in limited spatial heterogeneity in seed counts. One explanation for the lack of a steep relationship between seedfall proportion and distance from seed tree at these two stands may be the role of stand density and wind on seed dispersal. The relatively closed and regularly spaced canopy at Round Mountain, where density was 80 trees per hectare, may have contributed to greater uniformity in seedfall spatial patterns. In contrast, the openness of the canopy at Pie (18 trees per hectare) exposed the stand to greater wind exposure. At Pie, the influence of wind may have outweighed the influence of the stand's relatively clumpy tree distribution and produced a more uniform distribution of seed. Rapmaster (39 trees per hectare) and Sunray (47 trees per hectare), where seedfall was more related to the spatial distribution of overstory trees, may represent two canopy structures that are intermediate (moderate overstory density, more random overstory tree retention spatial pattern) between those at Round Mountain and Pie.

A second explanation concerns the actual fecundity of potential seed trees. Counts of cones at the base of overstory trees during the summer following seedfall provide a stand-level indication of the fecundity of trees in each stand (Table 4.3). In the Pringle Falls stands (Rapmaster and Round Mountain), most trees had 25 or fewer cones within the crown projection area (69.2 and 82.9 percent of trees, respectively), and trees with 10 or fewer cones constituted 33.3 and 56.8 percent, respectively, of all trees in the stand. In particular, cone counts at Round Mountain, where tree ages were younger than at the other three stands, indicate that most of those trees were not substantial contributors to the seed crop. In contrast, most trees at Fort Rock had more than 25 cones within the crown projection area (77.8 percent of trees at Pie; 70.3 percent of trees at Sunray). At Pie, no tree had fewer than 10 cones, and just 9 of 47 trees at Sunray had fewer than 10 cones.

TABLE 4.3. Counts of 1999 cones at the base of overstory trees (>20 cm dbh). Few trees at Pringle Falls produced heavy cone crops, but most trees (more than 70%) at Fort Rock produced at least 25 cones.

			Cones	
Site	**Stand**	**0-10**	**11-25**	**> 25**
Pringle Falls	Rapmaster	13	14	12
	Round Mtn.	29	15	7
Fort Rock	Pie	0	4	14
	Sunray	9	12	26

Essentially all trees in this study were mature, large, and vigorous, and were considered potential suppliers of seed. Typically, larger and more vigorous trees are believed to yield more seed than smaller and less vigorous trees. Foiles and Curtis (1973), for example, reported that mature trees produced more seed than immature trees in Idaho. In the study by Fowells and Schubert (1956), dominant trees were responsible for at least 97 percent of all ponderosa pine cones, but not all dominants were producers of seed. When data from all four stands in this study were combined, however, there was no apparent relationship between cone counts at tree bases and tree diameter, height, or crown ratio (Figure 4.6).

In contrast, when the relationship between cone production and tree diameter is viewed separately for each stand, it is apparent that the importance of the sizes of retained trees on seedfall varied among the four stands in this study (Figure 4.7). A positive relationship is visible at both Fort Rock stands, especially Pie, and is visible as well at Round Mountain. The seed shadow model does assume a non-linear relationship between fecundity and tree size (diameter). In all four stands, there was a positive relationship between fecundity and tree size (Figure 4.8). The two Fort Rock stands showed a steeper size:fecundity relationship than the Pringle Falls stands, with fecundity most strongly related to tree diameter at Pie. At Round Mountain and Rapmaster, tree size apparently had little bearing on productivity.

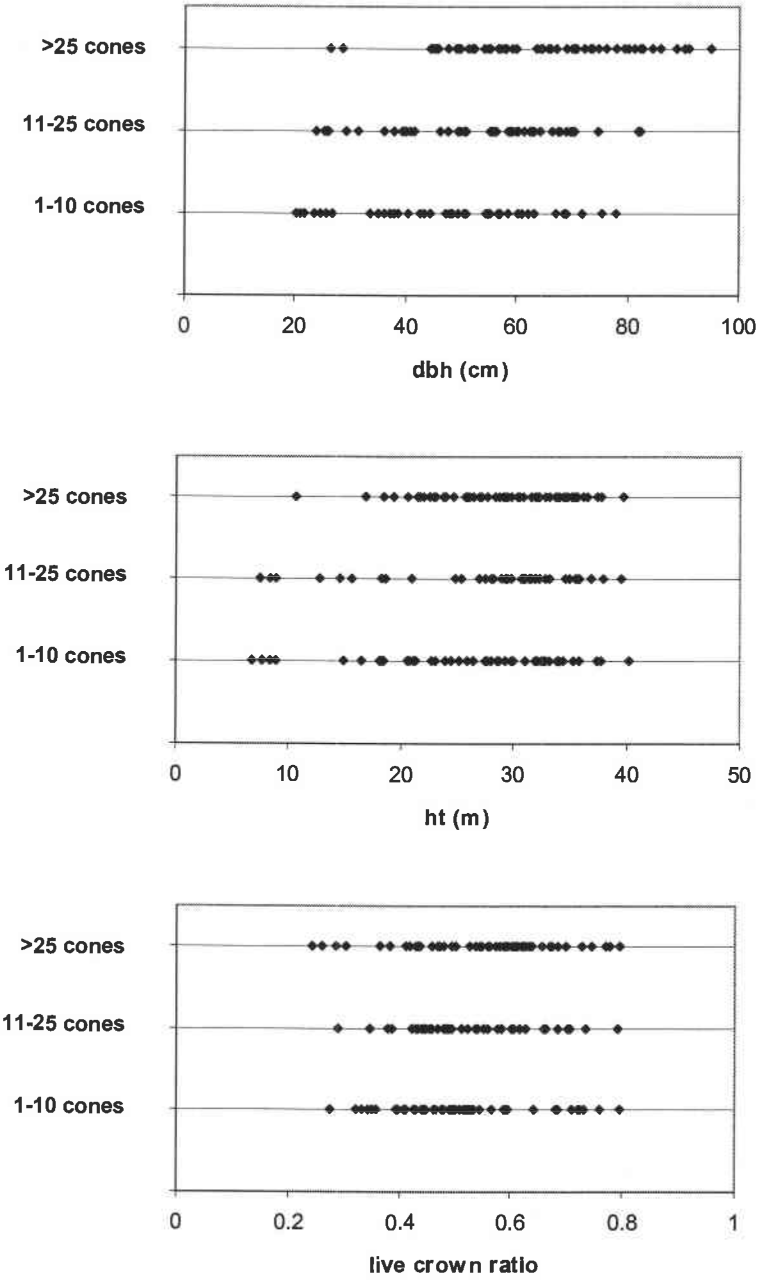

FIGURE 4.6. Relationship of tree characteristics to the number of cones found at tree base. Cone amount did not appear to be influenced by dbh, height, or live crown ratio.

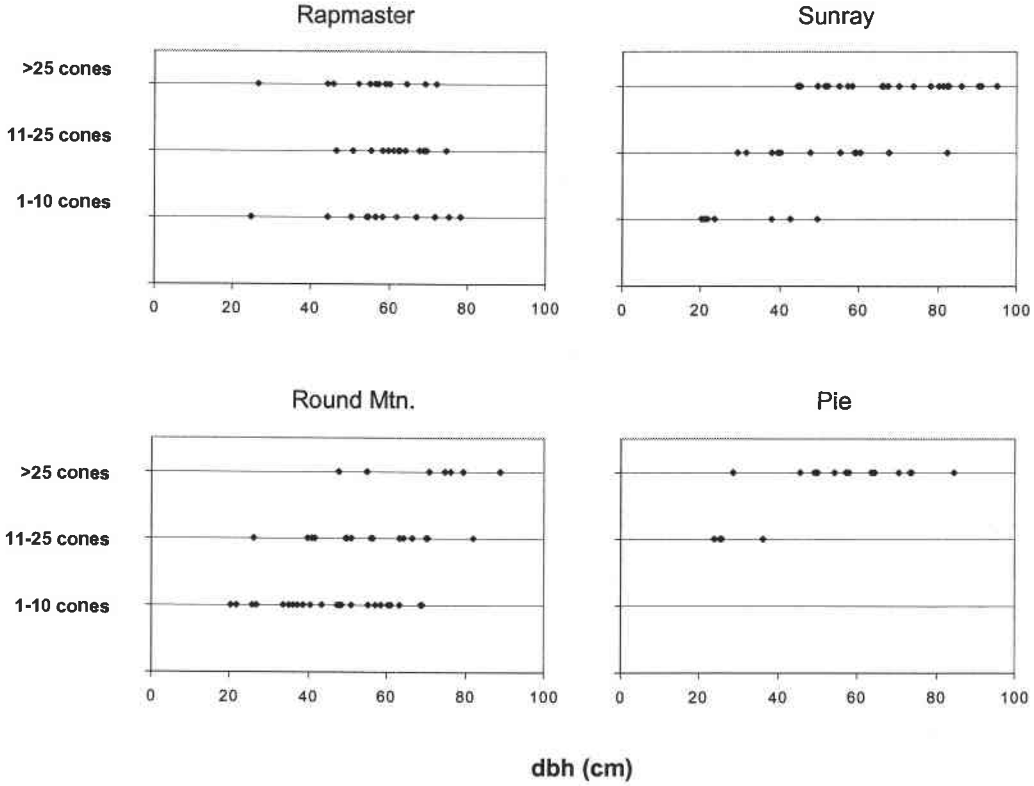

FIGURE 4.7. Relationship of dbh to number of cones found at tree base, separately by stand. With the exception of Sunray, a positive relationship is apparent.

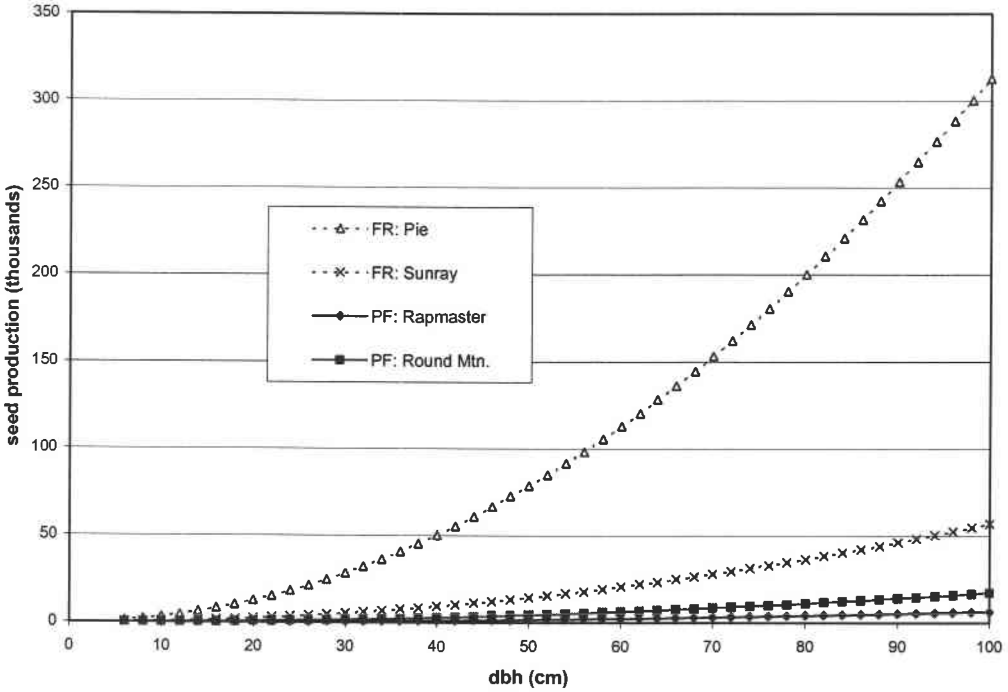

FIGURE 4.8. Tree fecundity as a function of tree size. Estimates of seed production fitted to each of the four stands in the study. PF is Pringle Falls; FR is Fort Rock.

CONCLUSIONS

This analysis of the 1999 ponderosa pine seed crop in stands of varying overstory tree density and spatial distributions suggested that seedfall was not a limiting factor on natural regeneration at any of the four stands in this study. Seedfall amounts varied more by site than by tree density and, for the year studied, the site of higher elevation and lesser productivity produced more seed. Within each of the two sites, however, the stand of higher density produced more viable seed. Of all seed that fell, 62-76 percent was viable; among whole seeds, 72-88 percent was viable. Most seedfall occurred within the first month after it started. There was no significant difference in the phenology among the two sites.

The number and spatial distribution of retained trees did not fully explain the spatial patterns of seedfall. For the trees retained after harvest in these stands, the cone crop of individual trees was positively related to tree size (dbh). This result was corroborated by positive relationships between seed production and dbh, although that relationship was strong only at one stand (Pie). The spatial analysis, which assumed equal fecundity for all trees of a given size, was complicated by variation in fecundity among trees (as measured by cone counts). For example, among trees at Rapmaster in the 50-60 cm dbh class, 5 produced more than 25 cones, 5 produced 11-25 cones, and 6 produced 10 or fewer cones. This variation was probably responsible for the apparent lack of well-defined seed shadows, and an analysis of seedfall patterns based only on fecund trees might have resulted in more pronounced seed shadows.

Other possible factors governing the spatial distribution of seed include characteristics of topography and stand structure outside of the study units. Spatial analysis of seedfall patterns at the four stands suggest that seed may be more evenly distributed and less strongly related to proximity of overstory trees when either overstory is relatively dense and trees are regularly distributed throughout the stand, or when overstory density is very low. For stands between these descriptions (i.e., moderately dense stands with a less-than-regular spatial distribution of trees), seedfall may have a negative binomial distribution, with seed density expected to be greatest around the bases of retained trees and less dense in the gaps between trees.

Beyond the quantity, quality, and spatial distribution of seed, successful recruitment of a sufficient crop of seedlings depends on many additional stand and site factors. In one study, Foiles and Curtis (1965) reported that on scarified soil in the northern Rockies, the establishment of a single seedling required 55 seeds (on average) due to seed losses and germinant mortality. Seeds and germinants are susceptible to a host of mortality-causing agents (Chapter 2), and for those germinants that successfully emerge, desiccation accounts for substantial losses (Chapters 5, 6). Factors that increase the emergence and early survival of germinants, such as mineral soil substrate and shrub cover, serve to decrease the number of seeds required per established seedling.

In the analysis presented in this paper, seed quantity during the year studied did not appear to be a factor that could limit regeneration density, especially at the Fort Rock sites, where the seed production was very high.

However, ponderosa pine produces seed crops that fluctuate annually in quantity (e.g. Dahms and Barrett 1975, McDonald 1992). Timing harvests to coincide with years of high seed production and low seed-predator populations provides an additional opportunity, beyond selecting the size and spatial pattern of residual trees, for enhancing the amount of seed actually available to produce seedlings.

Silvicultural studies in natural regeneration have traditionally approached the subject of natural regeneration from the perspective of securing regeneration in unstocked or understocked stands. In many stands, however, the absence of fire due to fire suppression during the past century has resulted in excess regeneration that is undesired and is associated with declining stand vigor and increased susceptibility to insect, diseases and fire disturbances. Hence in fire-susceptible stands, a more relevant perspective may be that of manipulating overstory density to minimize understory seedling recruitment and growth.

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CHAPTER 5

EFFECTS OF SEED CACHES, SUBSTRATE, AND SHRUBS ON PONDEROSA PINE SEEDLING RECRUITMENT

INTRODUCTION

In ponderosa pine forests, competition for belowground resources is intense and is the primary driver of understory growth (Riegel et al. 1991, Riegel et al. 1992). However, vegetation adjacent to seedlings exerts competitive and facilitative influences simultaneously (Callaway and Walker 1997), and facilitative influences are believed to be especially important for seedling recruitment in xeric ecosystems such as those where ponderosa pine commonly occurs. Vegetation adjacent to seedlings can ameliorate a harsh abiotic environment and improve the conditions for seedling emergence and early survival (Bertness and Callaway 1994, Holmgren et al. 1997). In ponderosa pine forests, shade from shrubs reduces light intensity and soil temperature, and increases the first-summer germinant recruitment rate (Chapter 6).

Additional factors that assist germinant emergence and early seedling survival, such as forest floor substrate and seed caches, can be important to ponderosa pine recruitment (Chapter 2). Mineral soil has been shown to be a better substrate than litter for the spring emergence of ponderosa pine germinants (Chapter 6). Duff evaporates more rapidly than mineral soil (Roe and Squillace 1950), and dry duff reaches high temperatures that can increase transpiration rates or even cause direct mortality (Farmer 1997). Many studies have shown that mineral soil is necessary for the establishment of ponderosa pine and most other western conifers (Dunning 1923, Haig et al. 1941, Foiles and Curtis 1965, Morris 1970). Similarly, seed caching improves the spring emergence rates of ponderosa pine germinants (Chapter 6). The seed-caching rodent community in ponderosa pine forests includes golden-mantled ground squirrels (*Citellus lateralis*), chipmunks (*Tamias* spp.), deer mice (*Peromyscus* spp.), and shrews (*Sorex* spp.) (Cochran 1970, Lawrence et al. 1961). In central Oregon, cached seeds that are not consumed by spring often germinate and emerge in clusters that are apparent during early summer.

Despite a prodigious body of research on ponderosa pine regeneration (Chapter 2), significant gaps in the understanding of early regeneration dynamics exist. For example, the specific temporal patterns of germinant mortality after emergence, and the microsite conditions affecting those patterns, have not been reported. Most researchers of ponderosa pine natural regeneration have restricted their focus to a single factor or seedling life stage, a situation common to many studies of seedling recruitment (Clark et al. 1999). Although they have been recognized as individually important factors at various stages of establishment (Chapter 6), the relative importance of shrub cover, substrate, and seed caches to the full natural regeneration process under field conditions is not clearly understood. Such information has direct relevance for the application of silvicultural practices in systems that depend in part or fully on natural regeneration. These practices include vegetation management for shrub control, scarification for site preparation, and the control of rodents (which have traditionally been regarded for their devastating seed predation impacts (e.g., Pearson 1913, Smith and Aldous 1947)).

This observational study of early seedling establishment (first 1-2 summers after emergence) was conducted in ponderosa pine stands that had been partially harvested recently in central Oregon. We characterized the temporal patterns of germinant emergence and survival, and quantified the influence of shrub cover, surface floor substrate, and seed caching on those patterns. Results of the study provide insight into the relative importance of these factors on the initial stages of ponderosa pine seedling recruitment in disturbed stands with partial overstories.

METHODS

Study Areas

The study was conducted in four stands at the eastern edge of the Deschutes National Forest, in the former Fort Rock Ranger District (43°30′ north latitude, 121°00′ longitude; Figure 5.1). The sites were approximately 75 km east of the Cascade crest, approaching the transition from ponderosa pine forest to western juniper (*Juniperus occidentalis*) high desert. The dry ponderosa pine forests in this region belong to the *Pinus ponderosa / Purshia tridentata* plant association described by Volland (1985).

Soils are derived from Cascades-erupted air-lain pumice, and are sandy-textured and very porous. Site quality was very similar among stands. The region annually receives less than 30 cm of precipitation, less than 4 cm of which falls

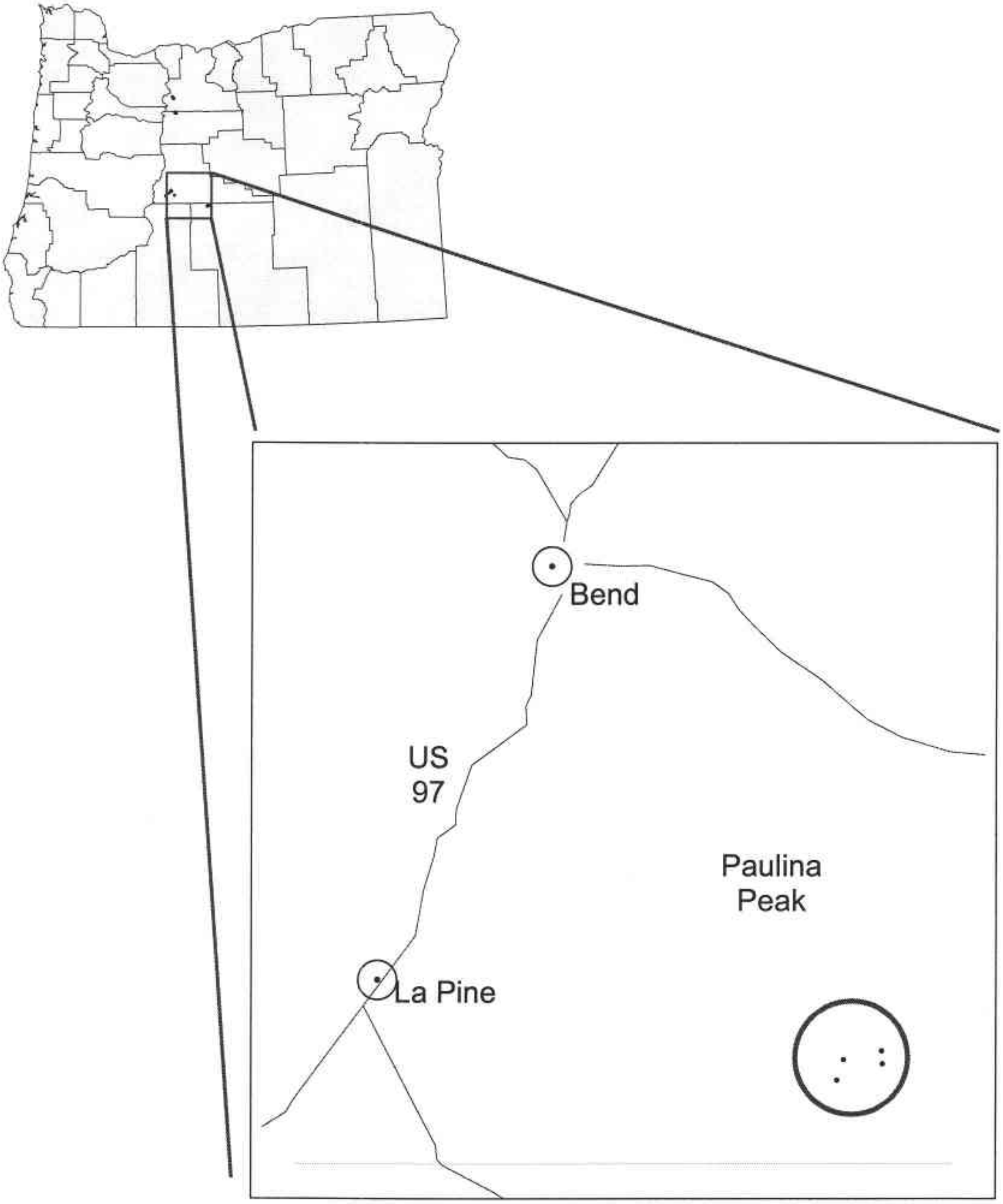

FIGURE 5.1. Location of the four stands used in the study.

during July, August, and September (NOAA climate station data from nearby Bend, Oregon). Mean air temperatures during July and August range from 7° to 27° Celsius. Extreme air temperatures during those months range from sub-zero to greater than 35°.

Overstory tree and understory shrub structure varied across the 4 stands in the study (Table 5.1). Overstory trees at the four stands were all ponderosa pines, mostly large trees with large, dense crowns. Quadratic mean diameters at breast height averaged 51.6 cm and ranged from 45.6 to 59.8 cm. The open-canopy stands had been partially-cut in the past (no less than 10 years prior) to varying densities of overstory retention (Figure 5.2). The logs were probably ground-skidded at all four stands. Basal areas averaged 7.8 m^2/ha, and ranged from 3.3 to 13.2 m^2/ha. Trees per hectare averaged 37, and ranged from 18 to 64. The understory plant community was similar at all four stands, and was dominated by *Purshia tridentata*, *Haplopappus bloomeri*, *Arctostaphlylos patula*, and *Festuca idahoensis*. Total shrub cover (based on crown projection area) averaged 35 percent and ranged between 25 and 40 percent. All four sites were flat or nearly so.

Data Collection & Analysis

The primary response variable in this study was germinant seedling density, expressed as total germinant counts per hectare. All newly emerged ponderosa pine germinants were tallied in 10-m^2 circular plots. In each of four stands, 16 plots were systematically located on grids with plot centers staggered

TABLE 5.1. Attributes of stand structure for the four stands used in the study. Qmd is quadratic mean diameter at breast height. LCR is live crown ratio. Shrub cover is percent of forest floor surface area covered by shrub foliage.

Stand	**Trees / Ha**	**Basal Area (m^2/Ha)**	**Qmd (cm)**	**Ave. Ht. (m)**	**Ave. LCR (%)**	**Shrub Cover (%)**
Pie	18	4.2	54.8	21.8	61	38
Metallurgy	20	3.3	46.1	15.6	72	25
Broken Wind	64	10.4	45.6	16.5	72	35
Sunray	47	13.2	59.8	24.4	62	40
Mean	37.3	7.8	51.6	19.6	66.8	34.5

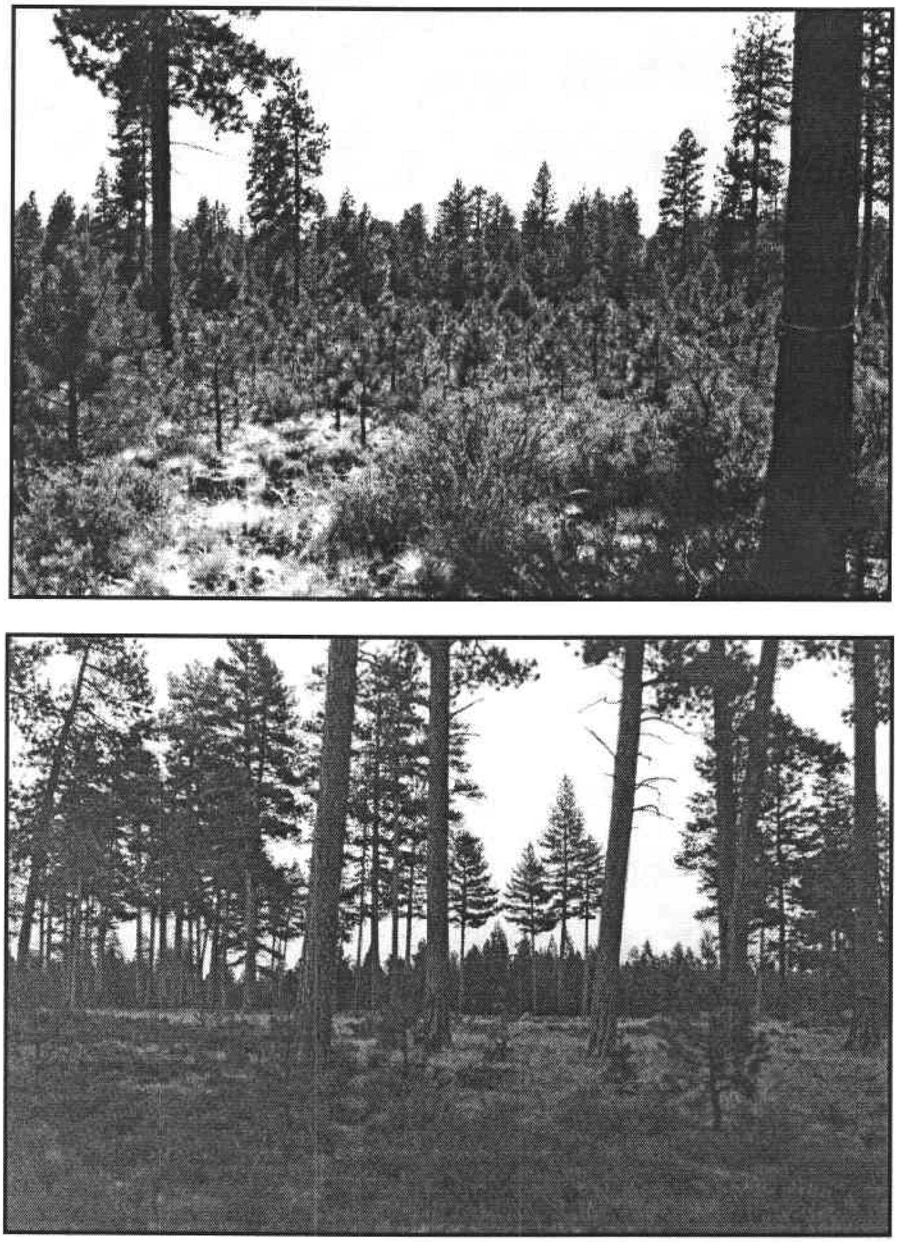

FIGURE 5.2. Two of the study's four stands: Pie (top, foreground) and Sunray (bottom, foreground).

at 20-m distances (n=64) (Figure 5.3). Germinants were recorded as occurring singly or in clusters of two or more (stems less than 2 cm apart at ground level), with the number of stems in each cluster also recorded. From the silvicultural perspective of potential crop seedlings, the total number of individual germinants and germinant clusters, or "emergence sites" (terminology borrowed from Vander Wall (1992)), can be a more important statistic than the total number of germinants. Therefore, the number of emergence sites per hectare was also calculated as a response variable. Surface substrate beneath each seedling was characterized as 1) mineral soil, 2) needle and shrub litter, 3) decayed log, or 4) decayed stump. To describe its relationship to understory shading, each seedling was recorded as occurring in the open, directly beneath live vegetation, or directly beneath dead vegetation or debris.

Germinant emergence and mortality data were collected for the 1999 regeneration cohort at Sunray, Pie, Metallurgy, and Broken Wind. At the start of summer 1999 (June 29-30), all new germinants were identified and labeled in all 16 plots at each stand. Survival checks were conducted throughout summer 1999 on 7 occasions until heavy snowfall in late November. The 1999-cohort germinants that survived over winter were inventoried again during the second summer (2000) on 3 occasions from June 6 up to November 6.

Germinant emergence and mortality data were collected for a second regeneration cohort (2000 cohort) at Sunray and Pie. The amount of viable seed available for the 2000 regeneration cohort was estimated with the use of seed traps, which collected seeds from September 2, 1999 to June 6, 2000. At both

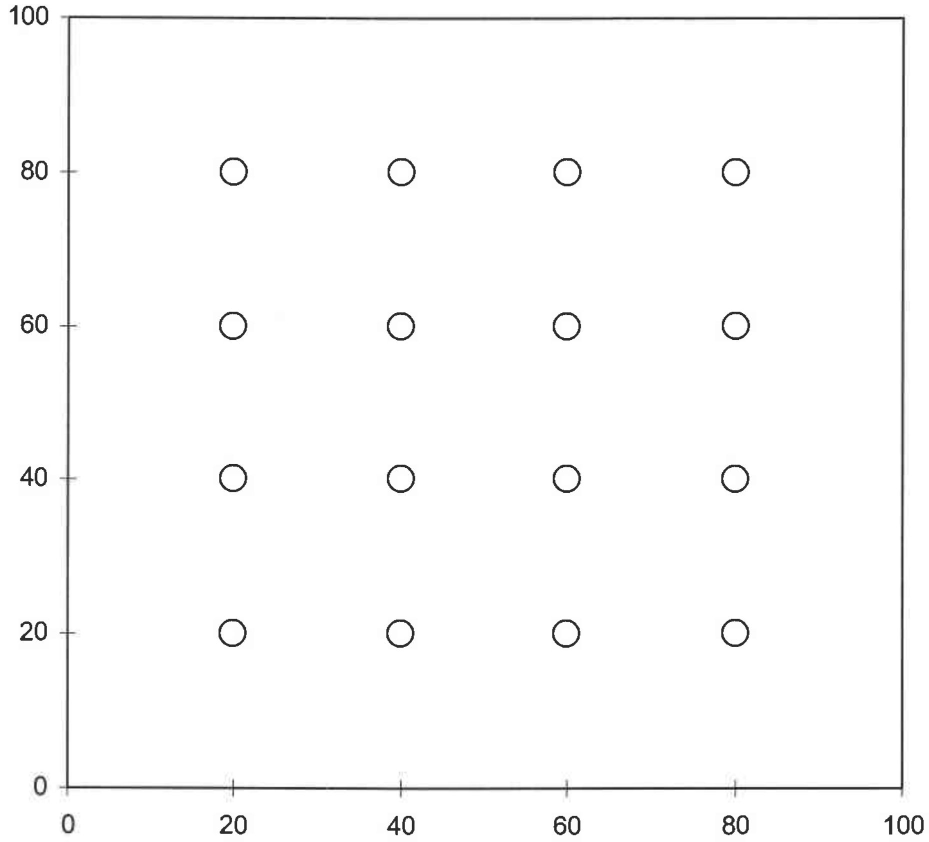

FIGURE 5.3. Layout of the 16 10-m^2 circular radius seedling plots within each stand (axes represent distances in meters).

stands, the crop of viable seeds was very large: more than 1 million seeds per hectare (complete seedfall results presented separately in Chapter 4). The 2000-cohort germinants at Sunray and Pie were identified and labeled on June 20, and were checked for survival during summer 2000 on 6 occasions until November 6.

Analysis of variance was used to test for differences in the densities of emerging germinants among mineral soil and litter-covered substrates; among live shade, dead shade, and no shade conditions; and between cached and uncached conditions. It was also used to test for differences in established germinants among those conditions. Fisher's Exact Test was used to determine whether the germinant emergence and establishment densities were significantly greater or less than expected from estimates of percent shrub cover.

RESULTS & DISCUSSION

The net germinant recruitment resulting from any given year's seed crop is the cumulative result of germinant emergence ('emergence'), and initial germinant survival ('establishment'). Failure during any one of these stages serves to winnow the regeneration cohort from the initial number of viable seeds to the eventual number of established germinants. In the following section a summary of the recruitment process at the four stands in this study is presented. Subsequent sections describe the germinant emergence and establishment rates under different conditions.

Temporal Patterns of Germinant Emergence and Establishment

In June 1999, 315 new germinants (1999 cohort) were identified in 64 plots at Sunray, Pie, Metallurgy, and Broken Wind. Germinant density averaged 4.9 per 10-m^2 plot (std. dev. 9.1; range 0-51). Because many germinants occurred in clusters of two or more, the number of actual emergence sites was less, at 1.91 per plot (std. dev. 3.4; range 0-19).

In June 2000, 1,570 new germinants (2000 cohort) were identified in 32 plots at Sunray and Pie. Germinant density was an order of magnitude greater than in 1999, averaging 49.1 per 10-m^2 plot (std. dev. 42.6; range 1-164). Again, many germinants were in clusters, with the total number of emergence sites averaging 21.3 per plot (std. dev. 16.2; range 0-58). In a separate study (Chapter 4), seed traps were used from September 2, 1999 to June 6, 2000 to estimate quantity of seed available for germination (viable seed) in spring 2000. The amount of viable seed produced was 2,235,870 per hectare at Sunray, and 1,182,870 per hectare at Pie. As a percent of available seed, the 2000 germinant emergence rates at the two stands were similar: 2.68 percent at Sunray, and 3.22 percent at Pie.

Since seedlings were first identified after emergence in June, reasons for the differences between the quantity of available seed and the quantity of germinants can only be hypothesized. The seeds collected in traps were protected from seed predation, but the seeds falling in the study plots (where emergents were identified) were not protected. In ponderosa pine forests, rodent species such as deer mice (*Peromyscus* spp.), golden-mantled ground squirrels

(*Citellus lateralis*), chipmunks (*Tamias* spp.), and shrews (*Sorex* spp.) consume large quantities of seed and are often responsible for regeneration failure (Cochran 1970, Hooven 1966, Lawrence et al. 1961). Birds in central Oregon are responsible for another (smaller) portion of ponderosa pine seed losses (Eastman 1960). Seeds that were not consumed by animals may have been rotted by fungi, bacteria, viruses, or molds (Fisher 1941, Farmer 1997, Roth 1970). After germination, losses may have been caused by damping-off fungi, especially *Pythium* and *Rhizoctonia* species (Roth 1970). Large losses of ponderosa pine seedlings to damping-off fungi and root rot fungi have been reported in central Oregon and southwest Oregon (Stein 1957, Wagg 1962).

Just 16 germinants (5.1 percent) of the 1999 regeneration cohort survived past one fall, and 10 germinants (3.2 percent) survived past two falls (Figure 5.4). The vast majority (88.9 percent) of all mortality during the full 495-day study period occurred by August 2, 1999, or within 34 days of the initial inventory. Observations indicated that most mortality occurred due to desiccation. Only 2 germinants in the 1999 regeneration cohort died during the winter and spring months (December 1, 1999 to June 6, 2000). That amounted to 0.6 percent of total mortality, indicating that the winter-spring period was minimally important to seedling recruitment. In the study area, frost-heaving was apparently not as important to ponderosa pine recruitment as was reported in other areas (e.g. Heidmann 1976). Similarly, burial by autumn litterfall, an important factor on Douglas-fir germinant mortality in California (Tappeiner and Helms 1971), was relatively unimportant here. Of the 303 1999-cohort germinants that died during

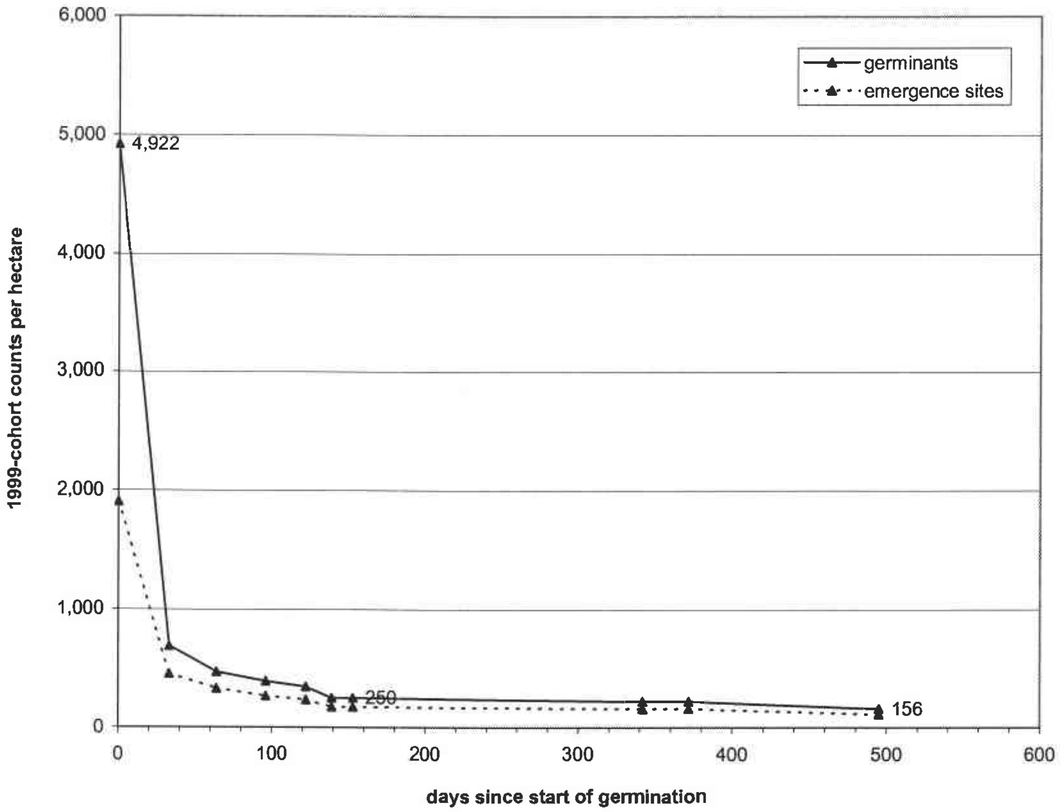

FIGURE 5.4. Temporal mortality pattern of 1999-cohort germinants and emergence sites (all four stands) from June 29-30, 1999 to November 6, 2000.

summer months, 299 (98.7 percent) died during the first summer (1999) and 4 (1.3 percent) died during the second summer (2000). These data indicate that that the probability of survival is high for ponderosa pine germinants that avoid desiccation and survive their first summer.

Just 121 germinants (7.7 percent) of the 2000 regeneration cohort survived past one fall (Figure 5.5). Nearly two-thirds (65.8 percent) of all mortality during the full 149-day study period occurred by July 18, or within 28 days of the initial inventory. Desiccation was responsible for most mortality.

The cumulative seedling recruitment patterns over two summers at Sunray and Pie are illustrated in Figure 5.6. Germinant densities were clearly different between years. Within years, however, germinant densities did not vary much between the two stands, despite a substantial difference in overstory basal area (other characteristics of site and stand structure were similar). These trends suggest that differences in overstory tree structure between stands were not as important as weather-related differences or other variables in determining the absolute levels of seedling recruitment.

Seed Caches

If germinant clusters can be assumed to have originated from animal seed caches, the effect of seed-caching animals on germinant emergence was strongly positive. Many more germinants occurred in clusters than occurred individually in the 1999 cohort (P=.0026) and the 2000 cohort (P=.0084). In the 1999 cohort, an average of 4.1 germinants per plot (83.2 percent of all new germinants) were in

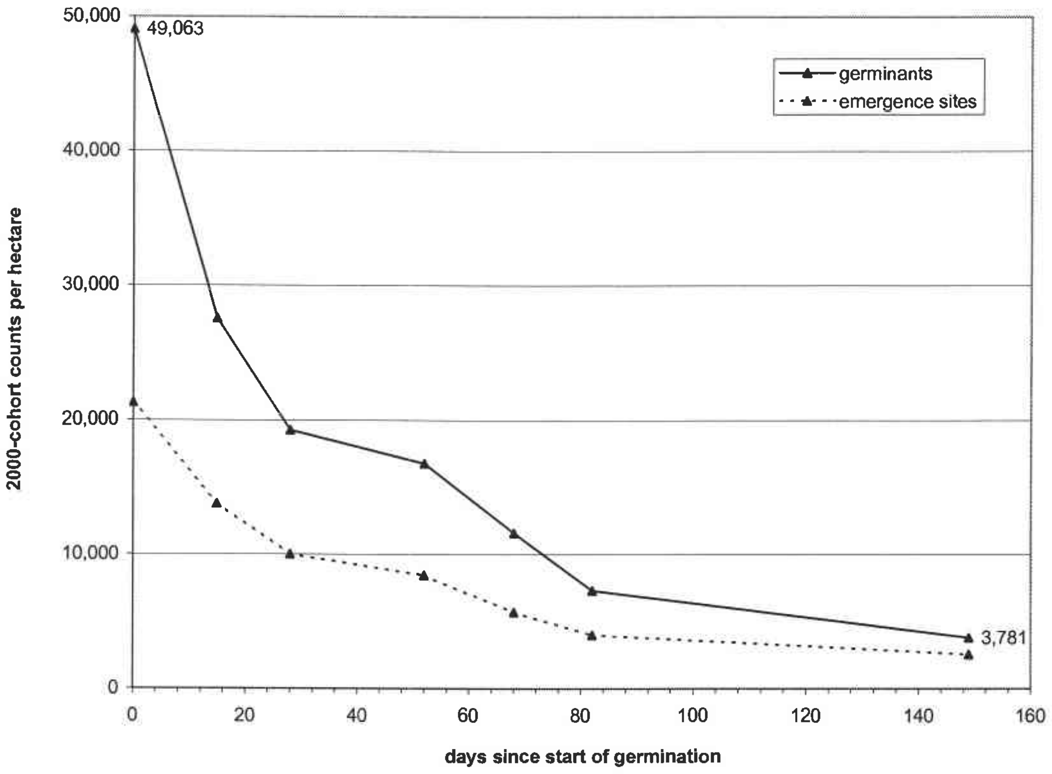

FIGURE 5.5. Temporal mortality pattern of 2000-cohort germinants and emergence sites at Sunray and Pie from June 20 to November 6, 2000.

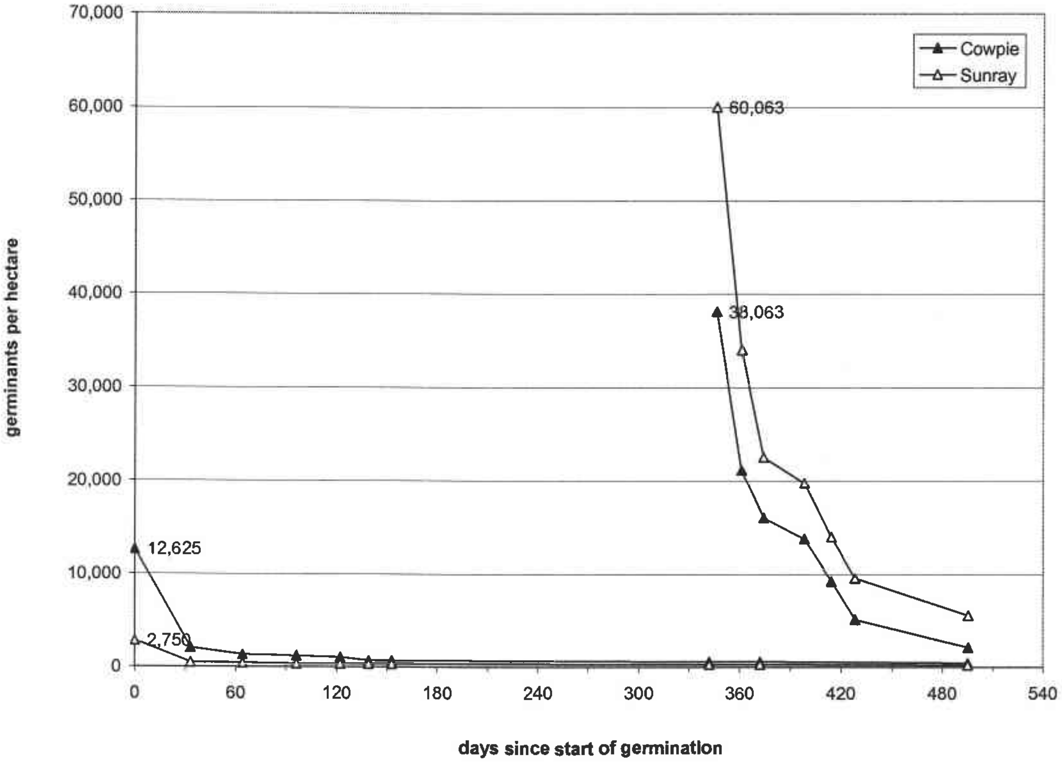

FIGURE 5.6. Cumulative seedling recruitment (germinants new in 1999 and 2000) at Sunray and Pie over two seasons (June 29-30, 1999 to November 6, 2000).

clusters of two or more, versus 0.8 individual germinants per plot (Figure 5.7, top). In the 2000 cohort, an average of 33.7 germinants per plot (68.7 percent of all new germinants) were in clusters of two or more, versus 15.3 individual germinants per plot (Figure 5.7, bottom). Because rodents also cache individual seeds, some single germinants in this study may have been from cached seeds, and the effect of seed caching on germinant emergence was probably underestimated.

The caching effect was present at all stands. In the 1999 cohort, germinants occurring in clusters at Sunray, Pie, Metallurgy, and Broken Wind comprised 66.7, 85.1, 81.4, and 84.6 percent, respectively, of all new germinants. Cluster sizes ranged from 2 to 14 germinants per cluster. In the 2000 cohort, germinants in clusters at Sunray and Pie comprised 71.9 and 63.7 percent, respectively, of all new germinants. Cluster sizes ranged from 2 to 46 germinants per cluster.

The caching effect was still substantial when clusters of germinants were regarded as single regeneration units, or emergence sites. Clusters in the 1999 cohort accounted for more than half of all emergence sites, with clusters averaging 1.1 per per plot (10-m^2) (std. dev. 2.4; range 0-14) and single germinants averaging 0.8 per plot (std. dev. 1.3; range 0-6). Clusters in the 2000 cohort comprised 28.2 percent of all emergence sites, with germinant clusters averaging 6.0 per 10-m^2 plot (std. dev. 4.7; range 0-17) and single germinants averaging 15.3 per plot (std. dev. 13.1; range 0-52).

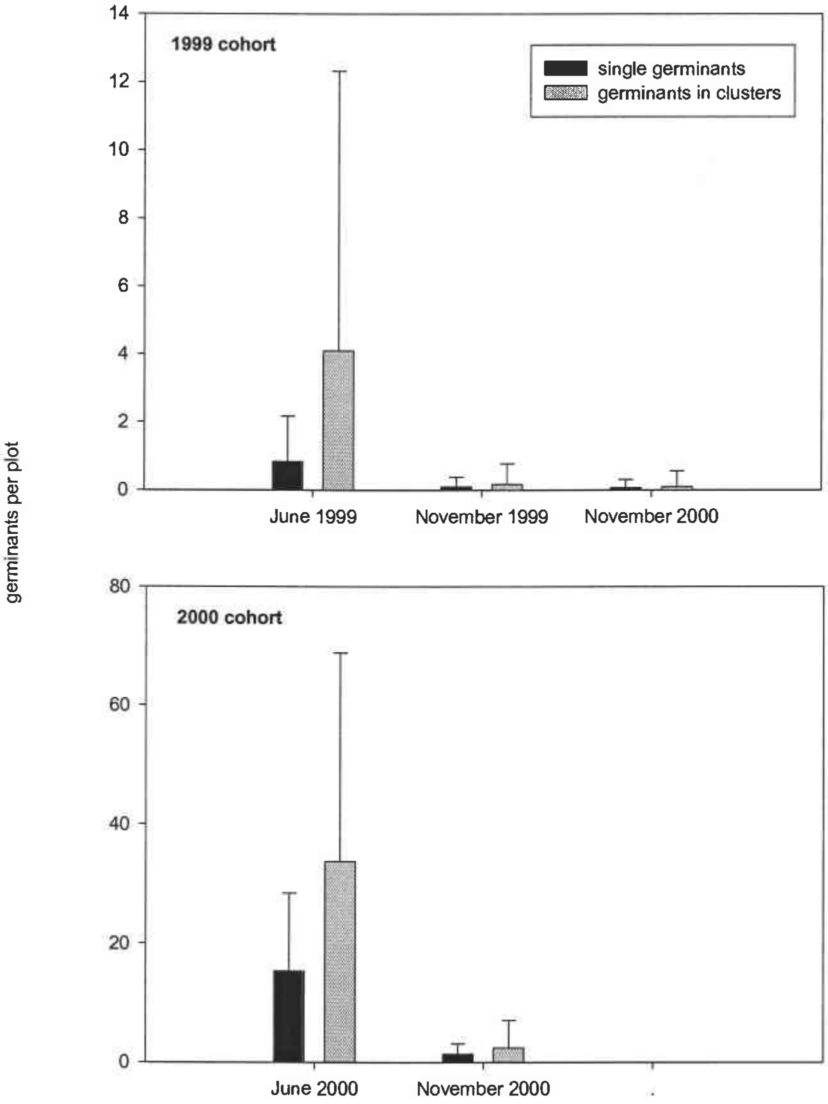

FIGURE 5.7. Relationship of caching to emergence (June) and end-of-fall establishment (November) for 1999-cohort germinants (top) and 2000-cohort germinants (bottom).

The mortality rate of germinants in clusters was not significantly greater than the mortality rate of individual germinants in the 1999 cohort (Figure 5.8; P=.31). As summer progressed, the frequency distribution of cluster sizes (number of germinants in a cluster) changed, with mortality reducing cluster sizes rapidly at first, and later more gradually (Figures 5.9, 5.10). For example, one of the largest clusters in the 1999 cohort began with 8 seedlings, was reduced to 4 seedlings by the next tally in August, and held 3 seedlings at the end of the study in November 2000. Overall, the largest cluster of the 1999 cohort held 14 germinants in June, whereas by November the cohort's largest cluster held three. The largest cluster of the 2000 cohort held 46 germinants in June, whereas by November the cohort's largest cluster held 11. This quick reduction in cluster sizes suggests that the effect of seed caching on regeneration can easily be underestimated, since older individual seedlings may have originated as cache-based germinant clusters.

Clusters continued to account for a large proportion of established seedlings after one and two summers (Figure 5.7). Of the 16 germinants in the 1999 cohort that survived to the end of the first summer (November 30), 10 were originally from clusters. By the end of the second summer (November 6), 6 of the 10 surviving germinants (60.0 percent) were originally from clusters. Among 2000-cohort germinants, 77 of the 121 one-season survivors (63.6 percent) were originally from clusters. Despite drastically different values for absolute germinant counts between years, the proportions of survivors originating from clusters were strikingly similar.

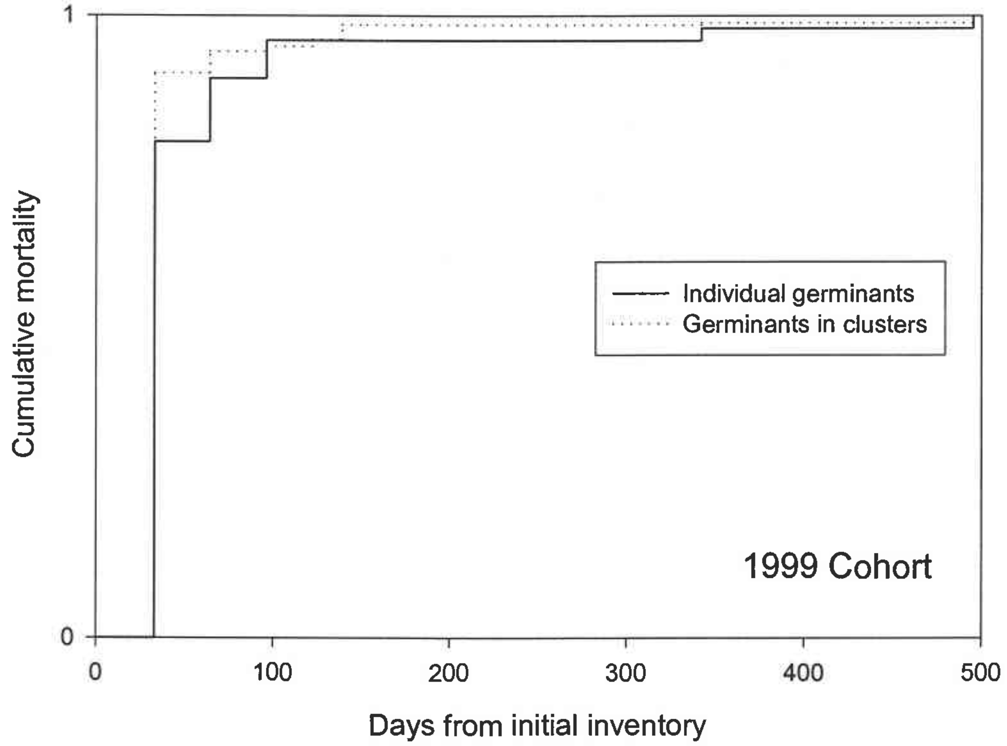

FIGURE 5.8. The cumulative mortality distribution of clustered germinants and individual germinants was not significantly different (P=.31). The x axis is days since emergence; the y axis is proportion of germinants dead.

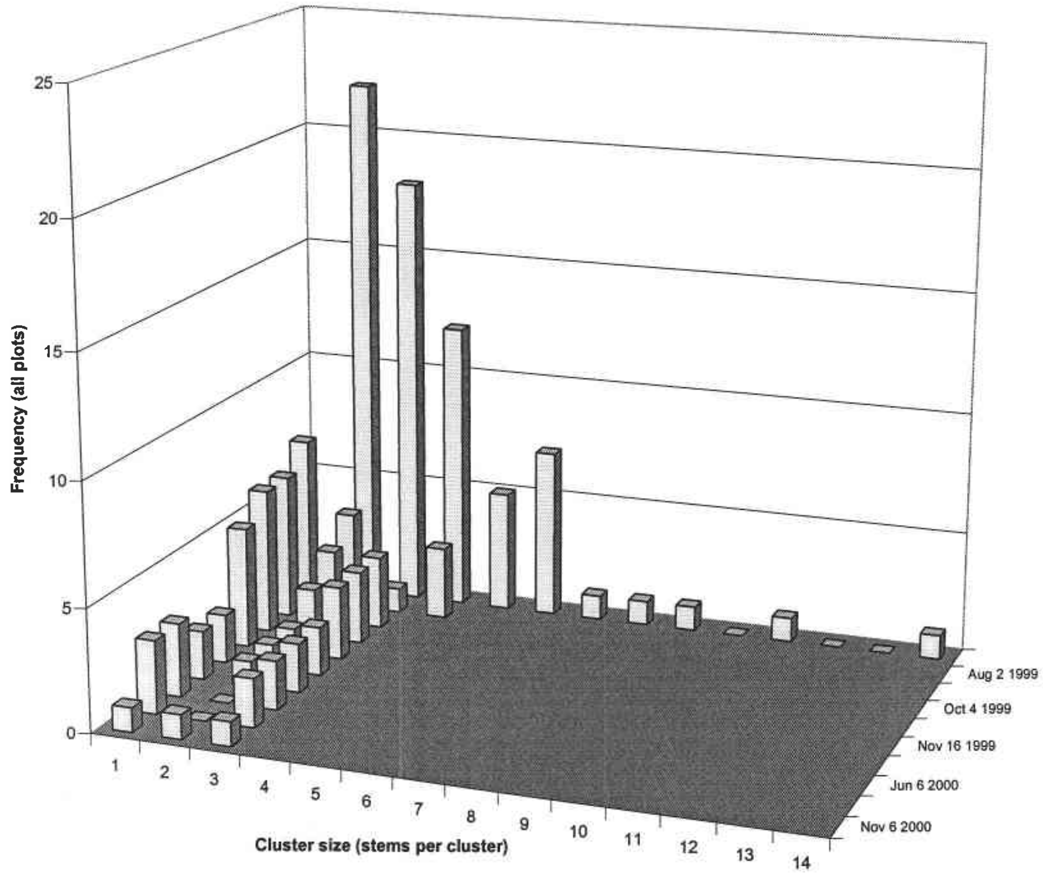

FIGURE 5.9. Frequency distributions of seedling clusters (two or more) in the 1999 germinant cohort over time. The distributions illustrate the temporal pattern of seedling attrition that reduced cluster sizes from June 29, 1999 to November 6, 2000.

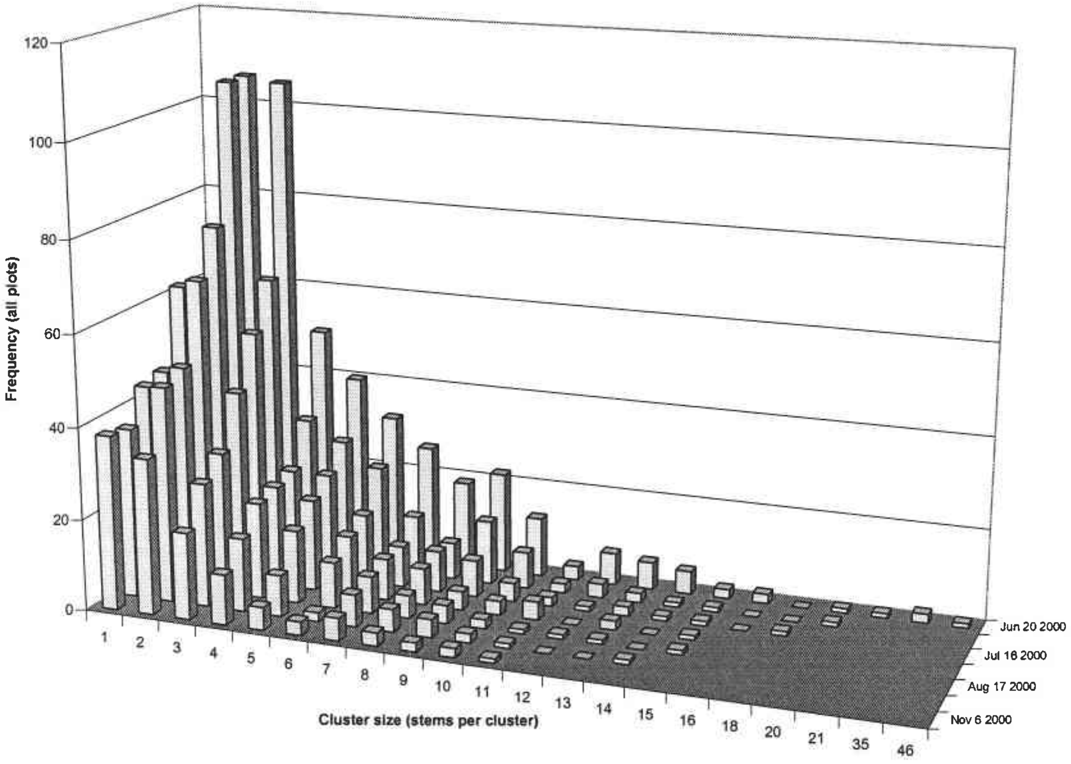

FIGURE 5.10. Frequency distributions of seedling clusters (two or more) in the 2000 germinant cohort over time. The distributions illustrate the temporal pattern of seedling attrition that reduced cluster sizes from June 20 to November 6, 2000.

Clusters also remained an important share of the surviving emergence sites, and the proportions of surviving emergence sites that originated as clusters were strikingly similar between cohorts at about 45 percent after one year. In the 1999 cohort, they comprised 5 of 11 surviving emergence sites (45.3 percent) by the end of one summer (November 1999), and comprised 3 of 7 surviving emergence sites (42.7 percent) after two summers (November 2000). In the 2000 cohort, clusters comprised 37 of 81 surviving emergence sites (45.7 percent) by the end of one summer (November 2000).

These data point out the possible importance of seed-caching rodents on ponderosa pine regeneration in this region. Seed-eating forest rodents are most widely regarded for their voracious appetites and negative impacts on the regeneration of western conifers (e.g. Isaac 1937, Pearson 1913, Radvanyi 1971). Although they consume many seeds, the seed caches created by seed-eating rodents have been shown to comprise the majority of Jeffrey pine (*Pinus jeffreyi*) emergence sites in Nevada (Vander Wall 1992). Studies in central Oregon have shown that seed caches may be important to ponderosa pine regeneration as well (Saigo 1968, West 1968). Saigo (1968), for example, estimated that half of new seedlings were from cached seeds. In this study, the large number of germinants emerging and establishing in clusters suggests that annual fluctuations in rodent population sizes and levels of seed predation and seed caching could have a substantial impact on annual seedling cohorts.

Substrate

Bare mineral soil substrate was shown not to be critical for germinant emergence. Within the 1999 germinant cohort, 3.3 germinants per plot (66.0 percent) emerged through litter, versus 1.7 germinants on mineral soil (34.0 percent) and 0 germinants on woody debris (Figure 5.11, top). Within the 2000 cohort, 35.0 germinants per plot (71.3 percent) emerged through litter, versus 12.8 germinants (26.2 percent) on mineral soil and 1.3 germinants (2.5 percent) on woody debris (mostly rotten logs) (Figure 5.11, bottom).

In addition to greater germinant emergence on litter substrates, germinant establishment was better on litter than mineral soil. In the 1999 cohort, mortality rates were significantly higher for germinants on mineral soil than germinants on litter substrate (P=.0002) (Figure 5.12). On litter substrate, 0.23 germinants per plot (7.2 percent) survived the first summer, and 0.16 (4.8 percent) survived two summers (Figure 5.11, top). In contrast, only .02 (1.2 percent) of the 1999-cohort germinants on mineral soil survived the first summer, and none were alive after two summers. First-summmer survivors of the 2000 cohort included 3.50 germinants per plot on litter, 0.25 germinants per plot on mineral soil, and 0.03 germinants on debris (survival rates of 10.0, 1.9, and 2.5 percent, respectively) (Figure 5.11, bottom).

The higher emergence rates on litter possibly reflected a greater availability of litter-covered microsites (percent litter cover was not measured). In any case, litter did not appear to discourage germinant emergence. The regeneration of western conifers is commonly disfavored by the presence of thick

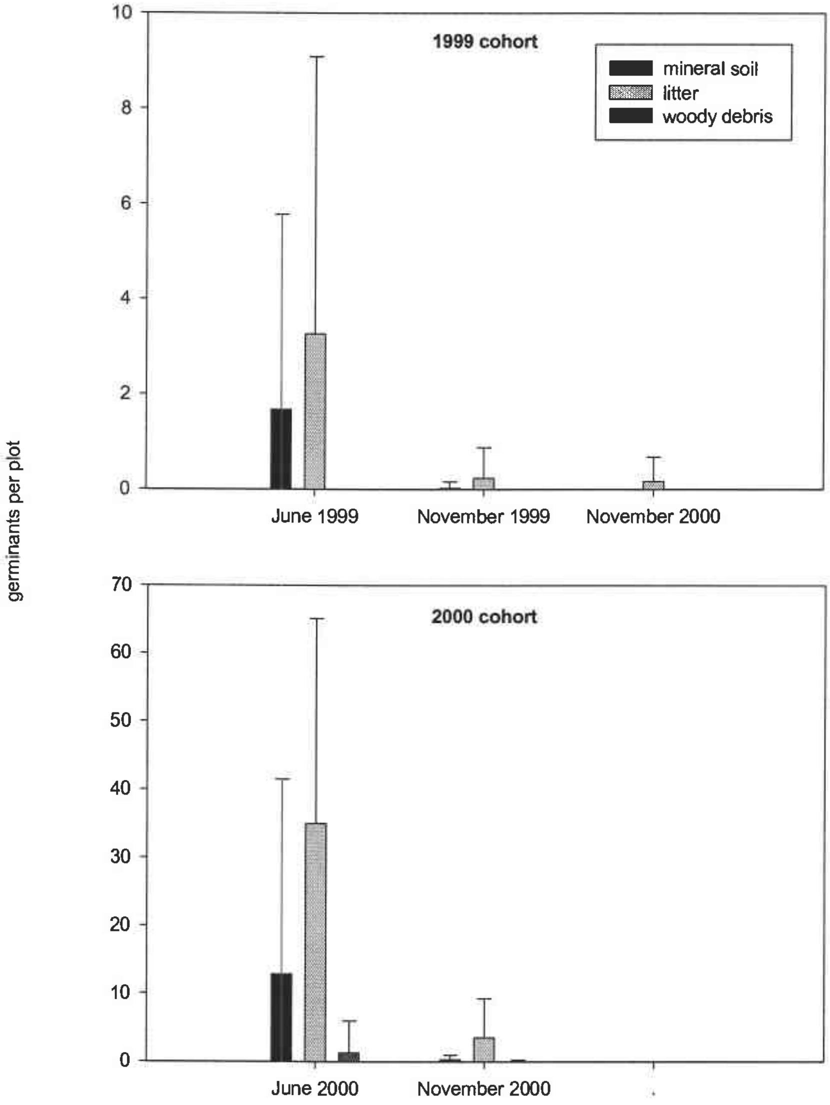

FIGURE 5.11. Relationship of substrate to emergence (June) and end-of-fall establishment (November) for 1999-cohort germinants (top) and 2000-cohort germinants (bottom).

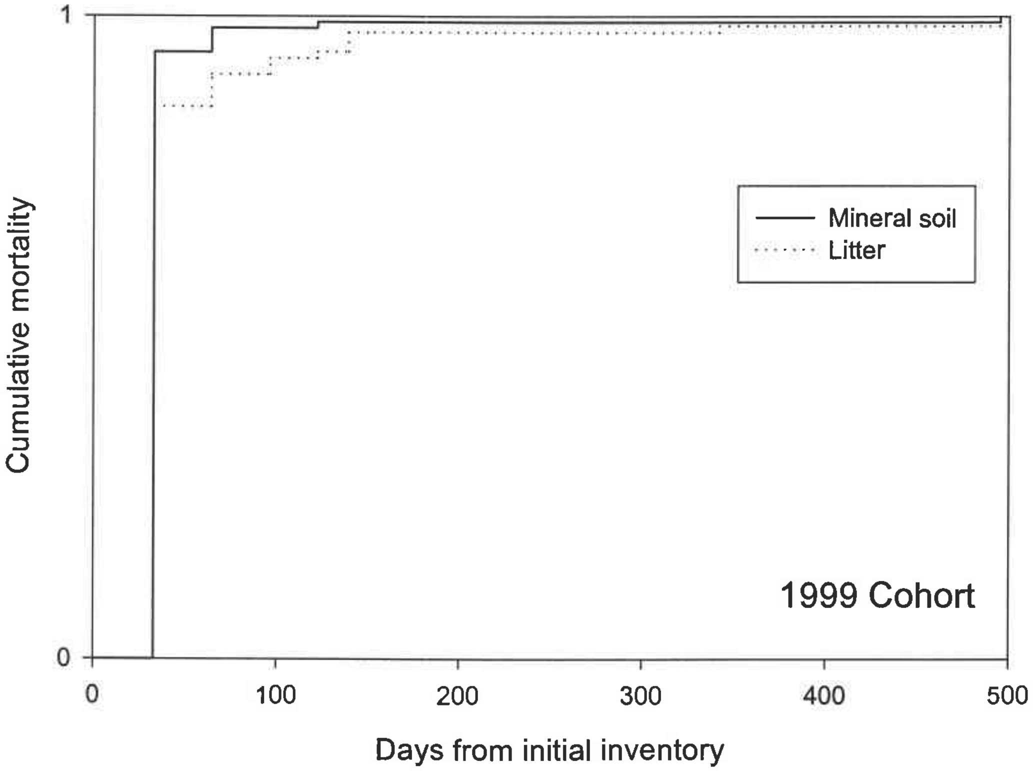

FIGURE 5.12. Cumulative mortality distributions among germinants on mineral soil and litter substrates in the 1999 cohort. Mortality occurred significantly more rapidly for seedlings on mineral soil substrates than for seedlings on a litter substrate (P=.0002). X axis is days since emergence; y axis is proportion of germinants dead.

litter, or a continuous duff layer in which litter fragments are bound by fungal mycelia and/or organic materials (Haig et al. 1941, Morris 1970, Foiles and Curtis 1965). Duff provides habitat for pathogenic fungi and insects, and when dry it possesses a low conductivity that results in higher surface temperatures (Farmer 1997). However, the litter layers at these sites were thin – usually less than a centimeter deep. Litter layers are typically thin in central Oregon, and litter layers in the study areas were probably reduced further by disturbance that occurred during logging. The relatively thin litter layers may have assisted germinant emergence by improving the microenvironment for seed germination or radicle growth. The higher survival rates of seedlings on litter suggest that the litter operated as thin mulch to improve microenvironmental conditions. Alternatively, the high rates of seed caching may have enabled many germinants to avoid the problems associated with germinating on litter. Woody debris, which has been identified as an important substrate for recruitment in more mesic ecosystems (Harmon and Franklin 1989, Cornett et al. 1997), was a poor substrate for seedling establishment here.

Shrub Cover

Shrub cover did not improve germinant emergence rates. More germinant emergence occurred at unshaded sites than at sites shaded by live and dead understory vegetation. Among the 1999 cohort, 3.6 germinants per plot (72.4 percent) were unshaded, versus 1.4 per plot (27.6 percent) shaded (Figure 5.13, top). Of the shaded germinants, 78.2 percent occurred under live shade (mostly

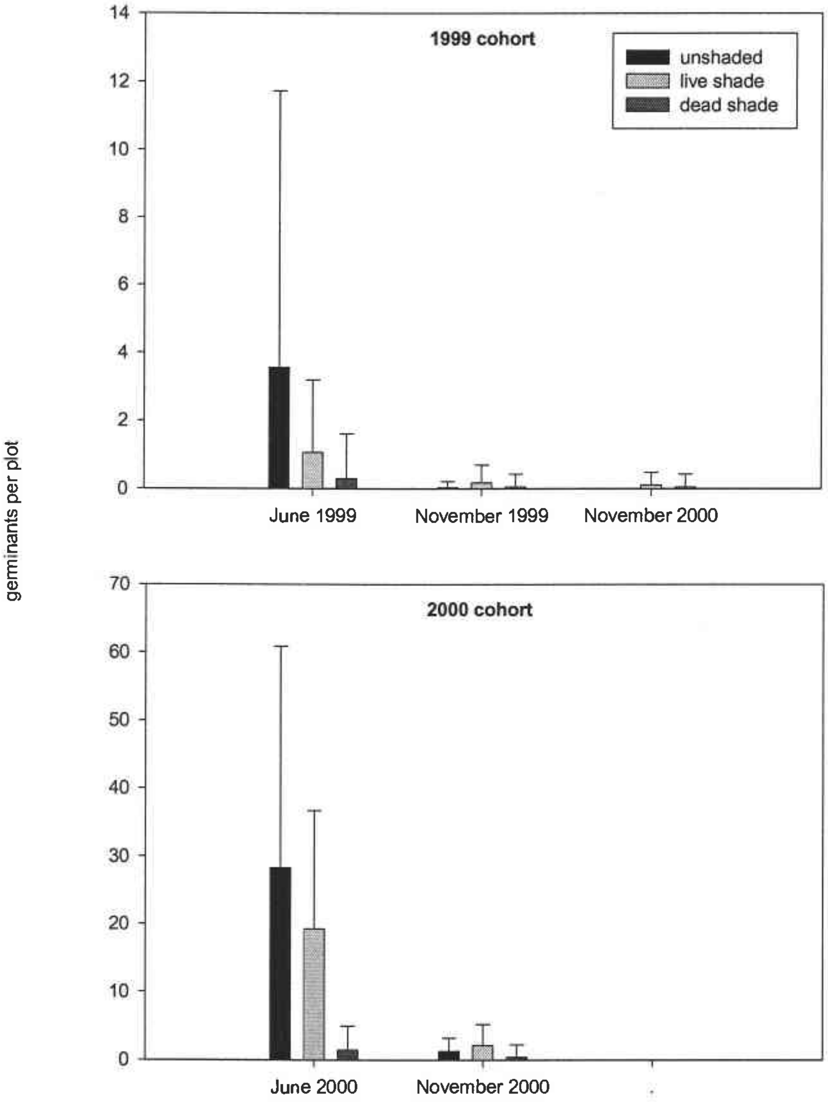

FIGURE 5.13. Relationship of understory shading to emergence (June) and end-of-fall establishment (November) for 1999-cohort germinants (top) and 2000-cohort germinants (bottom).

shrubs, some grasses), and 21.8 percent occurred under dead shade (mostly dead shrubs, some debris). The proportion of 1999-cohort germinants shaded by live shrub cover was significantly lower than expected from estimates of percent shrub cover (34.5 percent) (Fisher's Exact Test, P=.0138).

Among the 2000 cohort, 28.34 germinants per plot (57.8 percent) were unshaded, versus 20.72 germinants (42.2 percent) shaded (19.25 live-shaded, 1.47 dead-shaded) (Figure 5.13, bottom). For 2000, the observed proportion of live-shaded germinants did not significantly differ from the expected proportion (34.5 percent) (Fisher's Exact Test, P=.1524).

Although it did not enhance germinant emergence rates, understory vegetation was an important factor on germinant survival and establishment. The survival rate of shaded germinants was far greater than unshaded germinants (Figure 5.14; P<.0001). Unshaded germinants of the 1999 cohort diminished from 3.56 per plot to 0.03 per plot by the end of the first summer (November 1999), and all unshaded germinants were dead by the end of two summers (November 2000) (Figure 5.13, top). Germinants under live shade and dead shade, however, diminished from 1.36 per plot to 0.22 per plot after one summer and to 0.16 per plot after two summers. After two summers (November 6, 2000), therefore, all survivors were located under either live shade (69.9 percent) or dead shade (30.1 percent). The proportion of 1999-cohort germinants shaded by live shrub cover that survived to November 2000 was significantly greater than the expected proportion assuming random germination and survival and given the percent cover of shrubs (34.5 percent) (Fisher's Exact Test, P<.0001). The fact that emergence

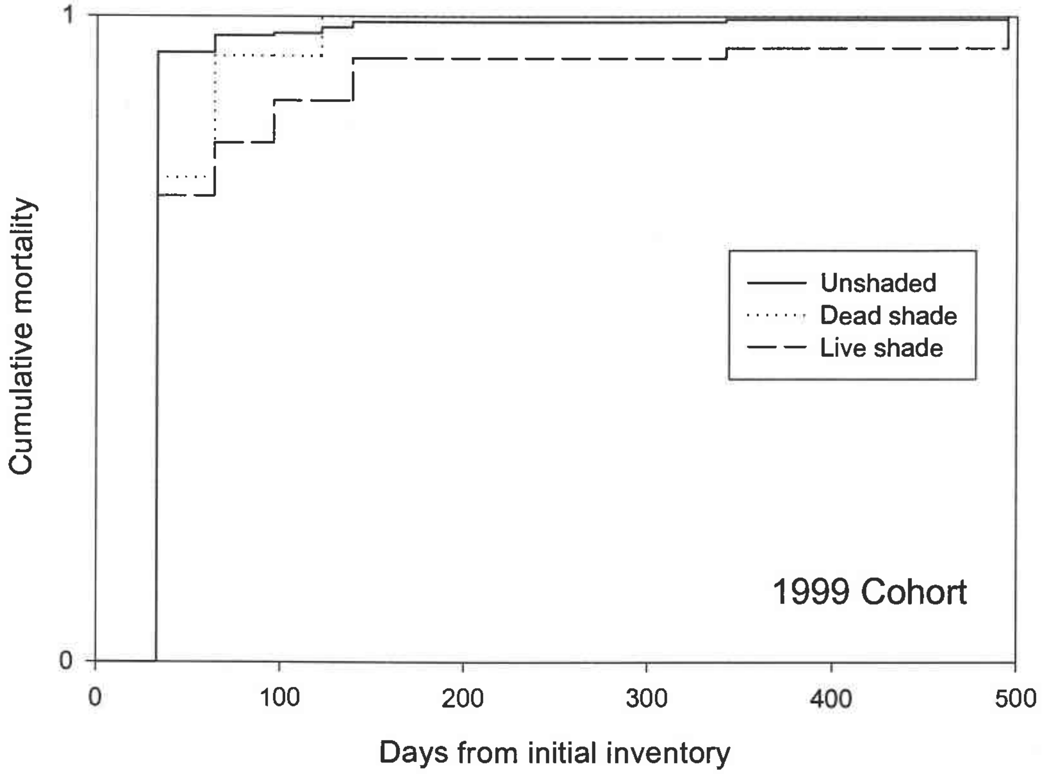

FIGURE 5.14. Cumulative mortality distributions of 1999-cohort germinants under live shade, dead shade, and no shade differed significantly (P<.0001). Mortality occurred most rapidly to unshaded germinants and least rapidly to germinants under live shade. X axis is days since emergence; y axis is proportion of germinants dead.

was higher at locations away from shrubs makes this greater density of survivors under shrub cover even more significant.

In the 2000 germinant cohort, unshaded germinants diminished from 28.39 per plot to 1.25 per plot by November, a survival rate of 4.4 percent (Figure 5.13, bottom). In contrast, shaded germinants diminished from 20.72 to 2.54 per plot, a survival rate of 12.3 percent. After one summer, therefore, the proportion of the 2000 regeneration cohort represented by shaded germinants went up from 42.2 percent to 66.9 percent. The proportion of 2000-cohort germinants shaded by live shrub cover that survived to November 2000 was significantly greater than the expected proportion assuming random germination and survival and given the percent cover of shrubs (34.5 percent) (Fisher's Exact Test, P=.0005). Like the 1999 cohort, higher numbers of survivors occurred beneath shrubs despite the fact that more emergence occurred away from shrubs.

The relationship of shade to emergence and establishment in this study is supported by the results of an experimental study conducted in the same area (Chapter 6). In that study, emergence rates of sowed seeds were unaffected by shrub cover, but establishment rates (based on new germinants inventoried after the fist summer) were significantly increased by shrub cover, which served to reduce light intensity and soil temperatures. It is not possible from this observational study to infer the specific role that live cover plays on germinant survival, but it is likely that the greater establishment rates under brush are due to an ameliorated microenvironment beneath shading structures.

CONCLUSIONS

This observational study led to several findings about the role of caching, substrate, and understory shade on the emergence and early survival of ponderosa pine germinants in central Oregon. For the year when seeds were collected, about 3 percent of the viable seed that was produced resulted in germinant emergents. Only a fraction of these survived their first summer, and most mortality occurred immediately after emergence.

Most emergents were in clusters, and germinants in clusters remained a substantial proportion of the cohort after two seasons. Clusters were not eliminated by the apparent within-cache competition, but rather declined in size, with large clusters reduced to small clusters (or individuals), shortly after emergence. This finding suggests many older ponderosa pine seedlings and saplings may have originated in caches, and that the effects of caching on recruitment can be easily undetected and underestimated.

Woody debris produced few germinants, and fewer yet survived on that substrate. More germinants emerged on a litter substrate than a mineral soil substrate, and most mortality occurred to germinants that emerged on a mineral soil substrate. In this study's pumice soil and bitterbrush system, the litter was thin, perhaps thin enough to permit germinants to establish while also serving to reduce evaporation at the soil surface (nearly all mortality was attributed to desiccation). However, this explanation is cautiously offered due to the substantial amount of seedlings in clusters from rodent caches. The many emergents from cached seeds were presumably not greatly affected by the litter during the critical phases of germination and radicle elongation.

Most germinants emerged without understory shading, but few of those exposed germinants survived. Most germinants alive after one year, and especially two years, had emerged beneath live cover. Ponderosa pine germinants likely benefited from shade by an improved microenvironment and decreased evaporative demand (see Chapter 6). Litterfall was light and did not pose a mortality issue for germinants (though only one winter was observed in this study), as may be the case in denser or more mesic ponderosa pine stands, where shrubs such as *Arctostaphlos patula* and *Ceanothus velutinus* dominate the understory.

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CHAPTER 6

MICROENVIRONMENTAL EFFECTS OF SHRUBS ON EMERGENCE AND SURVIVAL OF *PINUS PONDEROSA* GERMINANTS IN CENTRAL OREGON

INTRODUCTION

In stands of *Pinus ponderosa*, the processes and factors contributing to seedling recruitment are numerous and complexly related. In part, successful recruitment depends on the spatial relationship between a germinant or seedling and other vegetation growing at the microsite. Facilitative and competitive forces between those elements coexist simultaneously, with the balance between the forces determining their net relationship (Callaway and Walker 1997).

The conditions under which *Pinus ponderosa* most commonly occurs are xeric, and thus seedlings endure substantial stresses imposed by abiotic factors. In such environments, the importance of facilitation in plant communities increases as individuals benefit from an ameliorated microenvironment (Bertness and Callaway 1994, Holmgren et al. 1997). For forest managers, an improved understanding of these relationships can contribute directly to the silvicultural practices best applied to secure *Pinus ponderosa* natural regeneration.

Relatively little research on this topic has been conducted in the central Oregon pumice zone since direct-seeding was abandoned as a tool for reforestation in the Pacific Northwest. Most silvicultural research in the 1950s and 1960s on this subject concluded that the net influence of shrub species common in ponderosa pine forest types was competitive, and that shrub presence disfavored ponderosa pine recruitment. Shrubs such as *Ceanothus velutinus*, *Arctostaphlyos* *patula*, and *Purshia tridentata* were shown to be strong competitors for below-ground resources, especially soil moisture (Tarrant 1957, Barrett and Youngberg 1965). However, other studies found that soil moisture and nutrient contents were enhanced and seedling regeneration was either unaffected or improved by shrub cover (Dyrness 1960, Wollum and Youngberg 1964, Dahms 1950). To date, no comprehensive experiment has been conducted in central Oregon *Pinus ponderosa* stands to relate patterns of seedling emergence and survival to shrub cover, or to examine the specific processes behind those patterns.

In 1999 we initiated a research project to assess the dynamics of *Pinus ponderosa* seedling recruitment and growth in stands partially harvested under various silvicultural systems in central Oregon (Keyes and Maguire 2000). Although there was an apparent competitive relationship between seedling height growth and overstory trees and shrubs, our observations suggested that seedlings were associated spatially with shrub cover. We theorized that the positive spatial relationship observed between *Pinus ponderosa* seedlings and shrubs could be indicative of a facilitative influence of shrubs on seedlings at an early stage of their development. A supplemental study was designed to test this theory; this paper presents the results of that study's two experiments.

In the first part of the study, a seed-sowing experiment was designed to determine the relationship between shrub cover and ponderosa pine seedling recruitment. Its primary purpose was to test the hypothesis that seed germination and germinant survival are enhanced by the presence of shrub cover. It was also designed to evaluate the effects of seeding substrate and animal caching, and tested the hypotheses that 1) emergence and survival are greater for a bare-mineral substrate than a litter-covered substrate, and 2) that seed caching (shallow burying of seeds in clusters), as is typically performed throughout central Oregon ponderosa pine forests by small mammals such as *Eutamias amoenus* and *Citellus lateralis* (Saigo 1968), results in higher emergence and survival rates than wind-dispersed, non-cached seed.

In the second part of the study, an experiment was designed to explain the processes behind the shrub-related patterns of germinant recruitment. Specifically, we tested whether the summer microenvironment at the germinant scale was ameliorated by the presence of shrubs. If that were so, it would provide evidence of a facilitative shrub influence like that summarized by Holmgren et al. (1997) for other species in similarly extreme environments. We intended that this experiment would provide evidence for the mechanisms behind the associations identified in the sowing experiment.

METHODS

Study Area

The study was conducted in four stands at two sites in central Oregon on the lower eastern slope of the Cascade Range (Figure 6.1). In this region, plant growth is restricted by scarce soil water and nutrients. Surface soils in this area are derived from air-lain pumice parent material erupted from Cascade volcanoes

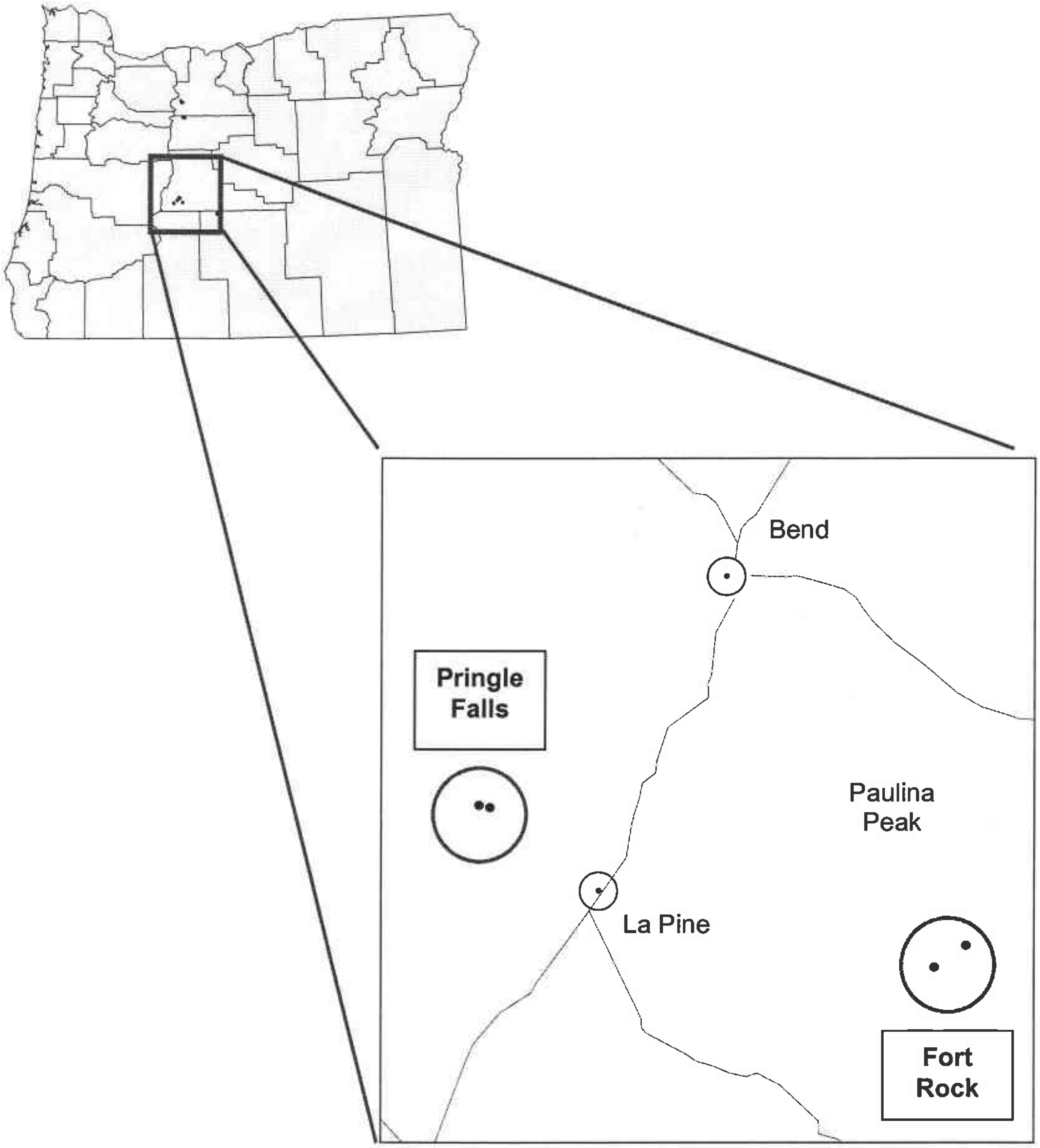

FIGURE 6.1. Location of the two sites and four stands used in the study.

and are poorly developed, sandy-textured and highly porous. A NOAA climate station in the nearby city of Bend, Oregon reports an annual precipitation average (1961-1990) of 29 cm, mostly occurring during the winter months. Less than 4 cm of rain falls between June and October.

Two sites were located on the Deschutes National Forest: a western site near the Pringle Falls Experimental Forest, and an eastern site on the former Fort Rock Ranger District. The sites represent two levels of site quality. The Pringle Falls site is more mesic, and ponderosa pine may occur in mixtures with, and is often replaced by, *Pseudotsuga menziesii* and *Abies concolor*. Plant associations at the Pringle Falls stands are in the mixed-conifer forest community series described by Volland (1985). The Fort Rock site is at a dry extreme for ponderosa pine, and at drier sites ponderosa pine is replaced by *Juniperus occidentalis*. Stands at the Fort Rock site are within the ponderosa pine forest community series (Volland 1985).

The study was conducted in four stands of ponderosa pine that had previously been partially harvested. The appearance of the stands ranged from a seed-tree harvest to a heavy low thinning, with large, mature residual trees. Table 6.1 lists some structural attributes of the overstory and understory components at the four stands. Stand densities ranged from 18 to 77 trees per hectare, and from 4.2 to 19.3 m^2/ha. Dominant understory vegetation at the Pringle Falls site comprised the shrubs *Ceanothus velutinus*, *Arctostaphylos patula*, and *Purshia tridentata*. At the Fort Rock site, *Purshia tridentata* and the graminoid *Festuca idahoensis* were dominant. Understory vegetation density varied among stands

TABLE 6.1. Attributes of stand structure for the four stands used in the study. Qmd is quadratic mean diameter at breast height. LCR is live crown ratio. Shrub cover is percent of forest floor surface area covered by shrub foliage. Understory Veg. codes: CEVE=*Ceanothus velutinus*, PUTR=*Purshia tridentata*, FEID=*Festuca idahoensis*.

Site	Stand	Trees / Ha	Basal Area (m^2/Ha)	Qmd (cm)	Ave. Ht. (m)	Ave. LCR (%)	Shrub Cover (%)	Understory Veg. (spp.)
Pringle Falls	201	77	19.3	56.5	32.7	50	33	CEVE, PUTR
	204	39	10.8	59.3	31.7	44	77	CEVE
Fort Rock	301	18	4.2	54.8	21.8	61	38	PUTR, FEID
	304	47	13.2	59.8	24.4	62	40	PUTR, FEID

due to differences in site quality, stand structure, and time since thinning or harvest, but within stands it was relatively uniform.

Data Collection

Germinant Emergence and Survival

Ponderosa pine seeds were sowed under specified conditions at 5 plots on each of 2 stands at the Pringle Falls and Fort Rock sites (n=20 plots). Within each stand, the plots were located at the center and at each corner of a square sampling grid. The treatment design was split-plot with splitting at 3 levels within each plot. Eight different treatment combinations were conducted at each plot representing differing conditions for germinant emergence and survival.

The effect of shrub shading was tested by sowing seeds within the crown area and as close as possible to the center of a representative individual shrub ("shaded" treatment). Seeds were sown at an adjacent location outside the shrub crown ("unshaded" treatment). Since all four stands had large trees in the overstory, the "unshaded" seeds were not completely free of shade, but rather represented an environment beneath a partial overstory that is free of shrub cover. At Fort Rock, shrubs were all *Purshia tridentata*, whereas at Pringle Falls they were mostly *Ceanothus velutinus* with some *Purshia tridentata*. The total number of experimental units was 40.

Two substrates tested the effect of forest floor litter on germination and survival. In the "bare soil" treatment, litter was brushed aside to expose mineral soil (the soil itself was undisturbed). In the “litter” treatment the litter was undisturbed. Litter within the shrub-shaded treatments consisted of a mix of pine needles and shrub leaves, whereas litter in the unshaded treatments was mostly pine needles. The total number of experimental units was 80.

The final treatments were designed to replicate two different seed dispersal mechanisms. In the “cached” treatment, which simulated the activity of seed-caching rodents, individual seeds were buried 1-cm into mineral soil. For “cached” treatments within “litter” treatments, the litter was gently pushed aside and then replaced after seeds were buried. In the “uncached” treatment, which simulated wind-dispersed seed deposition, seeds were placed on top of mineral soil or litter. The total number of experimental units was 160.

Sowing was conducted on October 30-31, 1999 using seed from the Deschutes National Forest’s Pine Nursery in nearby Bend, Oregon. Seeds were from local stock at elevations of 5,500 to 6,500 ft. For each treatment combination, five seeds were sowed 5 cm apart in rows. To protect them from predation or other disturbance, seeds were covered by a 30x30x5 cm frame of hard wire mesh with openings of 25x12 mm.

Sites were revisited during spring 2000 to record germinant emergence. Five of the mesh cages had been disturbed (presumably by large mammals) and had to be discarded from the analysis, reducing the number of treatments by 10 to a total 150. Emergence was determined by tallies at all sites on June 19-20, 2000; no seedlings emerged after that date. The mesh cages were removed on those dates to prevent interference with germinant cotyledon elongation. Survival patterns were observed with periodic tallies throughout the summer and fall. The final tally was made on November 6-7, 2000.

Microenvironment

At stations near each of the 20 plots, measurements were taken in a chronosequence to identify diurnal differences between shrub-shaded and unshaded microenvironments (Figure 6.2). Relative humidity and air temperature were measured at 10-cm above the forest floor using a portable digital thermo-hygrometer (Hanna Instruments, model HI93640). Soil temperature at a depth of 10-cm was recorded using an analog Weksler soil probe thermometer. Measurements were taken at each plot over two consecutive 20-hour periods during the summer drought period (July 31 - August 1, 2000). Measurements were taken every four hours starting at 12 a.m.

During the same period, maximum light intensity was measured using the method described by Friend (1961). This method addresses the spatial scale of germinants by capturing the sun flecks and diurnally-changing light conditions on the forest floor. The number of sheets exposed by sunlight correlates well to the maximum instantaneous photosynthetic photon flux density (PPDF) received over the time period (Bardon et al. 1995).

Sealed plastic light registers containing 10-sheet stacks of ozalid blueprint paper were constructed in the lab and were distributed among the field sites after dusk. Registers were placed flat on the ground adjacent to the microenvironment station. At each plot, two subsamples were placed at a shrub-shaded location and

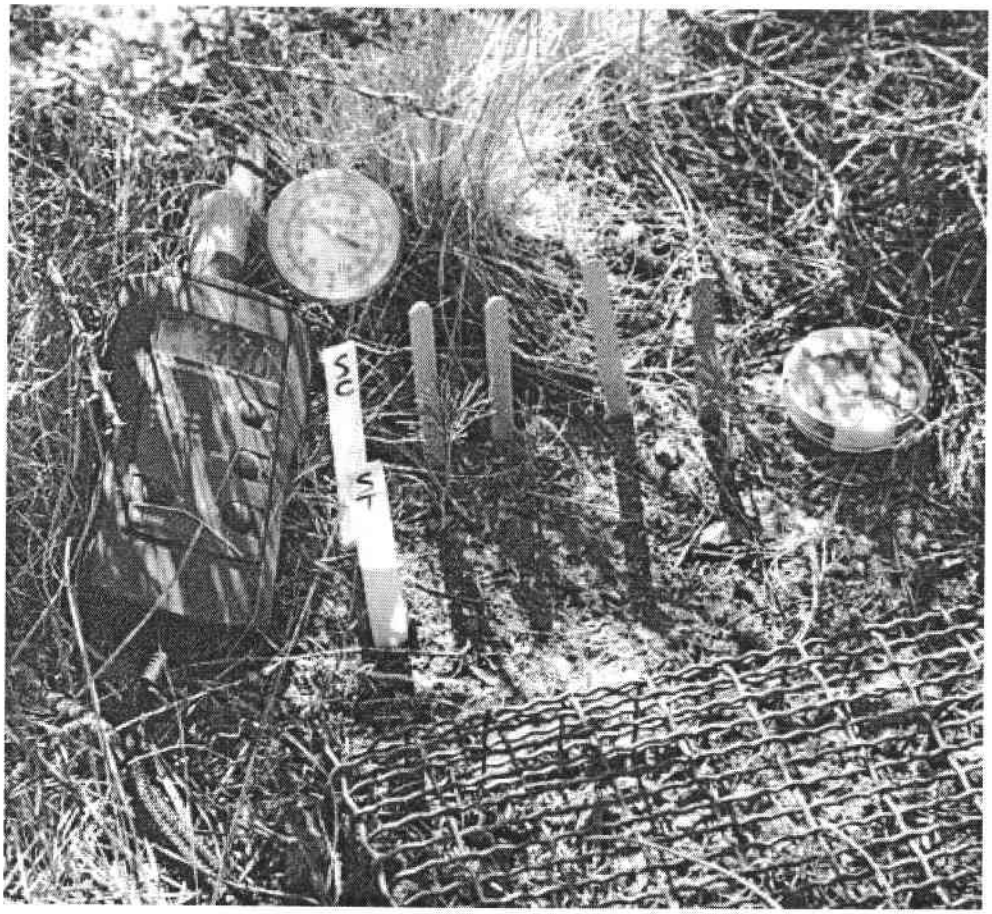

FIGURE 6.2. Layout of the sowing experiment, with instruments used to measure microenvironmental conditions (air and soil temperature, relative humidity, and solar radiation). Shown here is a bitterbrush-shaded treatment at one of the Fort Rock sites.

an unshaded location. The amount and intensity of light received by each register was partly due to its shrub status and partly to the presence of overstory trees. The registers were stored in black plastic bags during transport to and from the sites. Registers were collected after dusk the following day. The blueprint stacks were developed in a lab by exposing them for one hour in a glass chamber containing commercial-grade ammonia.

Once developed, the number of sheets with evidence of light exposure was tallied for each stack. Two methods of tally were made for comparison: 1) only those sheets that were completely exposed were counted (the traditional technique; "Method 1"), and 2) all sheets with evidence of any amount of exposure were counted ("Method 2"). The two subsamples taken at each location were averaged to produce a single estimate of light exposure. At each site, counts of exposed sheets at an open location (no shrub cover and no overstory tree cover) represented the baseline, or fully-exposed, condition. Following the method used by Friend (1961), the percent of that maximum light intensity was estimated at each plot as the relative difference between the number of sheets exposed at the shrub-shaded or unshaded treatment and the open location ($100(e-t)/e$, where e is the number of sheets exposed at the open location, and t is the number of sheets exposed from a treatment [shrub-shaded or unshaded] location).

Analysis

Data were analyzed using analysis of variance (ANOVA) F-tests. Treatments were tested with a mixed-effect model using the GLM (generalized linear models) procedure in SAS. Site (n=2, Pringle Falls v. Fort Rock) was tested as a fixed effect to distinguish between the mixed-conifer (Pringle Falls) and true ponderosa pine (Fort Rock) sites. Random effects included Stand (n=2 per Site) and Plot (n=5 per Stand). Fixed treatment effects included Shrub Cover (n=2, shaded v. unshaded), Substrate (n=2, bare soil v. litter), and Dispersal Method (cached v. uncached). Animal damage to 10 of the sowed-seed replicates made the design unbalanced. Statistical significance was tested at α=.05 and was based on Type III sums of squares. Analyses of variance were conducted to test for differences in microenvironment between sites and between shaded and unshaded treatments within sites. The tests were conducted for air temperature, soil temperature, and relative humidity at each measurement period.

RESULTS

Germinant Emergence and Establishment

Overall, less than 30 percent of the seed sowed in fall resulted in spring germinants (emergents). Neither the site nor the shrub treatment had any effect on emergence rates, but the substrate and caching treatments were significant (Table 6.2). Bare soil substrates resulted in 78 percent more emergence than litter substrates (Figure 6.3, middle). Of all germinants, 88 percent emerged from seeds receiving the “cached” treatment (Figure 6.3, bottom). Half of all cached seed emerged as germinants, whereas less than 7 percent of uncached seed resulted in germinants.

TABLE 6.2. Analysis of variance table showing results of F-tests when the response variable is a function of percent of seeds resulting in live germinants on June 6-7.

		Type III		Sum				
Source	**DF**	**SS**	**MS**	**SSe**	**DFe**	**MSt, MSe**	**F-stat**	**P-value**
SITE	1	0.0135	0.0135		1	0.0135	0.0098	0.9301
STAND(SITE)	2	2.7428	1.3714		2	1.3714	8.8146	0.0026 **
PLOT(SITE*STAND)	16	2.4893	0.1556		16	0.1556		
SHRUB	1	0.1302	0.1302		1	0.1302	0.9256	0.3488
SITE*SHRUB	1	0.1125	0.1125		1	0.1125	0.7998	0.3830
STAND*SHRUB(SITE)	2	1.0322	0.5161					
PLOT*SHRUB(SITE*STAND)	15	1.3880	0.0925	2.5327	18	0.1407		
DUFF	1	1.7570	1.7570		1	1.7570	12.9243	0.0010 **
SHRUB*DUFF	1	0.0494	0.0494		1	0.0494	0.3632	0.5507
SITE*DUFF	1	0.3292	0.3292		1	0.3292	2.4218	0.1289
STAND*DUFF(SITE)	2	0.1928	0.0964					
PLOT*DUFF(SITE*STAND)	16	2.1718	0.1357					
SITE*SHRUB*DUFF	1	0.1641	0.1641					
STAND*SHRUB*DUFF(SITE)	2	0.0067	0.0034					
PLOT*SHRUB*DUFF(SITE*STAND)	12	1.7574	0.1465	4.6221	34	0.1359		
CACHE	1	13.4515	13.4515		1	13.4515	126.3757	<.0001 ***
SHRUB*CACHE	1	0.0128	0.0128		1	0.0128	0.1202	0.7298
DUFF*CACHE	1	0.4183	0.4183		1	0.4183	3.9297	0.0513 (*)
SHRUB*DUFF*CACHE	1	0.0395	0.0395		1	0.0395	0.3712	0.5443
SITE*CACHE	1	0.0230	0.0230					
STAND*CACHE(SITE)	2	1.4684	0.7342					
PLOT*CACHE(SITE*STAND)	16	2.3046	0.1440					
SITE*SHRUB*CACHE	1	0.0222	0.0222					
STAND*SHRUB*CACHE(SITE)	2	0.1478	0.0739					
PLOT*SHRUB*CACHE(SITE*STAND)	15	0.7884	0.0526					
SITE*DUFF*CACHE	1	0.2769	0.2769					
STAND*DUFF*CACHE(SITE)	2	0.0885	0.0443					
PLOT*DUFF*CACHE(SITE*STAND)	16	1.3394	0.0837					
SITE*SHRUB*DUFF*CACHE	1	0.0596	0.0596					
STAND*SHRUB*DUFF*CACHE(SITE)	2	0.0239	0.0120					
PLOT*SHRUB*DUFF*CACHE(SITE*STAND)	12	1.0145	0.0845	7.5573	71	0.1064		

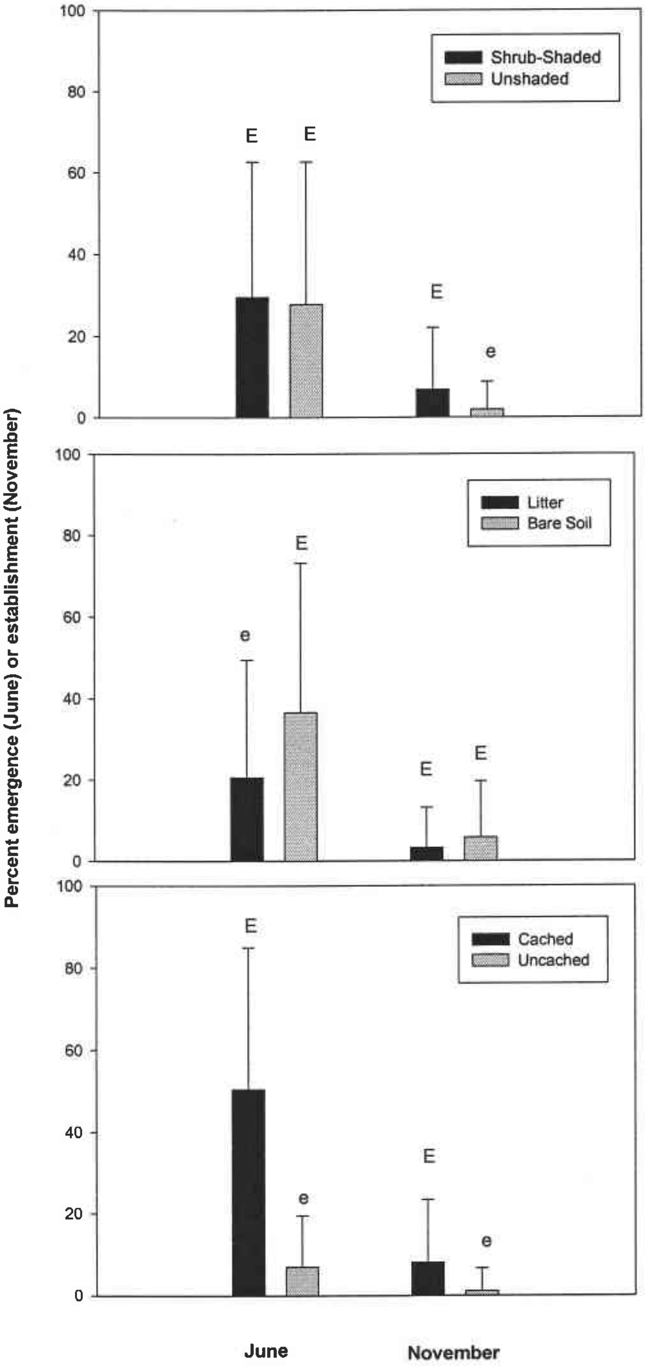

FIGURE 6.3. Effects of shading, substrate, and caching on percent emergence (June) and establishment (November). Paired upper-case letters indicate a non-significant difference at α=.05.

The (substrate)*(dispersal method) treatment interaction term was significant for germinant emergence. This finding is illustrated in Figure 6.4, which shows that caching was especially effective at enhancing emergence rates on bare soil substrates. Cached seed beneath litter produced germinant emergents at a higher rate (37.3 percent) than uncached seed on bare soil (10.0 percent). Emergence rates were lowest from uncached seeds on litter. Other interaction terms tested in this analysis proved non-significant for both emergence and establishment.

Within sites there was a significant difference in germinant emergence among stands, with the higher emergence rate associated with the stand of greater density (stems per hectare, basal area). Because the two stands at each site were topographically and edaphically similar, this result suggests the possibility of an overstory effect on emergence rates. To illustrate this effect, percent emergence (June) and percent establishment (November) were calculated on a stand-average basis (Figure 6.5). Although just the four stands are represented, the figure suggests that within a site, emergence and to a lesser degree establishment are enhanced by greater overstory density (for the range of densities represented by these four stands of partial overstories). An estimate of overstory density more local to each sowing plot would have enabled a more precise assessment of the overstory effect on emergence and establishment.

Due to summer mortality, less than 5 percent of all seed sown in fall 1999 resulted in established (live) germinants in fall 2000. Among spring germinants emerging from the sowed seed, more than 84 percent were dead by November.

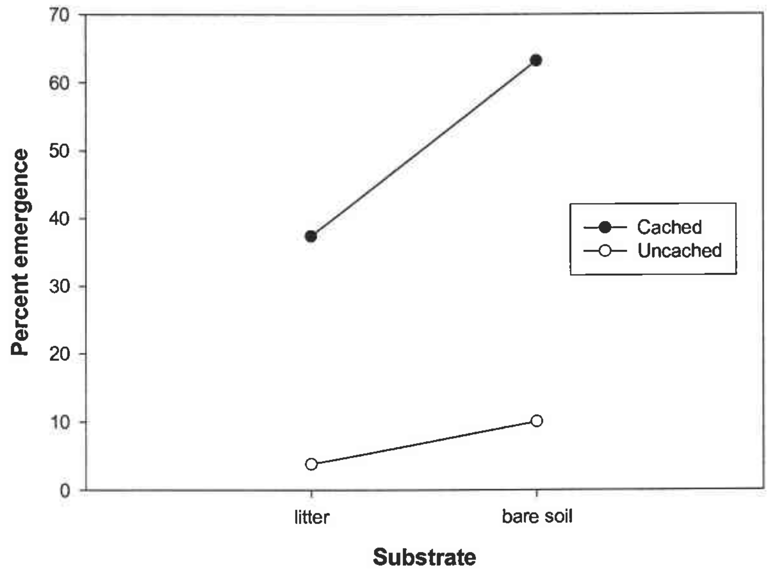

FIGURE 6.4. Relationship of the significant cache*substrate treatment interaction for percent emergence (June). The effect of caching was most pronounced on bare soil substrates. Other interaction terms were non-significant.

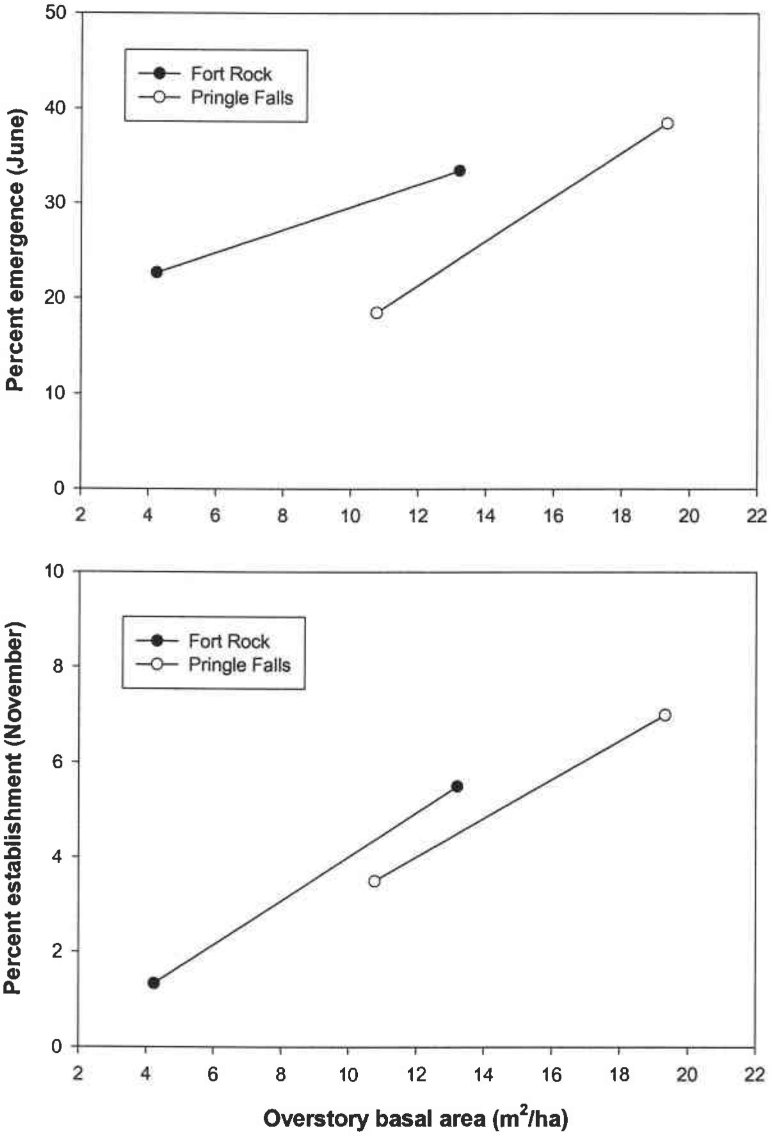

FIGURE 6.5. Effect of overstory density on stand-average percent emergence (June; top) and percent establishment (November; bottom).

Although the cause of mortality was not recorded, observations indicated that virtually all mortality was due to desiccation.

Net germinant recruitment measured at the end of the fall was significantly improved by shrub shading and by seed caching, and was unaffected by site or substrate (Table 6.3). Among seeds that emerged as germinants in June, more survived under shrubs than away from shrub canopy (Figure 6.3, top). At unshaded sites, the mortality rate was greatest immediately following germination, whereas it remained relatively constant throughout the summer at shrub-shaded sites (Figure 6.6). At midsummer, the survival rate among shaded germinants was 2.2 times the survival rate of unshaded germinants. By summer's end, the survival rate among shaded germinants was 4.1 times that of unshaded germinants. There was no difference in mortality rates between cached and uncached seed, thus the higher emergence rate of cached seed (7.3 times that of uncached seed) resulted in 7.5 times more germinants recruited (Figure 6.3, bottom). Despite the early advantage of the bare soil substrate on emergence rates, there was no significant difference in net recruitment between the litter and bare soil substrate treatments.

Microenvironment

Relative humidity and air temperature fluctuated substantially, and soil temperature fluctuated moderately, over the 20-hour period of measurement. There were clear site-related differences for relative humidity and air temperature, but a significant shrub effect was present only for soil temperature.

TABLE 6.3. Analysis of variance table showing results of F-tests when the response variable is a function of percent of seeds resulting in live germinants on November 6-7.

		Type III		Sum				
Source	**DF**	**SS**	**MS**	**SSe**	**DFe**	**MSt, MSe**	**F-stat**	**P-value**
SITE	1	0.0655	0.0655		1	0.0655	0.6205	0.5134
STAND(SITE)	2	0.2111	0.1056		2	0.1056	2.0762	0.1579
PLOT(SITE*STAND)	16	0.8136	0.0508		16	0.0508		
SHRUB	1	0.2377	0.2377		1	0.2377	5.4065	0.0320 *
SITE*SHRUB	1	0.0646	0.0646		1	0.0646	1.4696	0.2411
STAND*SHRUB(SITE)	2	0.0310	0.0155					
PLOT*SHRUB(SITE*STAND)	15	0.6959	0.0464	0.7915	18	0.0440		
DUFF	1	0.0588	0.0588		1	0.0588	1.9503	0.1716
SHRUB*DUFF	1	0.0378	0.0378		1	0.0378	1.2523	0.2710
SITE*DUFF	1	0.0030	0.0030		1	0.0030	0.0998	0.7540
STAND*DUFF(SITE)	2	0.0087	0.0043					
PLOT*DUFF(SITE*STAND)	16	0.5429	0.0339					
SITE*SHRUB*DUFF	1	0.0027	0.0027					
STAND*SHRUB*DUFF(SITE)	2	0.0641	0.0321					
PLOT*SHRUB*DUFF(SITE*STAND)	12	0.4043	0.0337	1.0257	34	0.0302		
CACHE	1	0.4938	0.4938		1	0.4938	11.5733	0.0011 **
SHRUB*CACHE	1	0.0668	0.0668		1	0.0668	1.5655	0.2150
DUFF*CACHE	1	0.0208	0.0208		1	0.0208	0.4864	0.4878
SHRUB*DUFF*CACHE	1	0.0107	0.0107		1	0.0107	0.2503	0.6184
SITE*CACHE	1	0.0002	0.0002					
STAND*CACHE(SITE)	2	0.1397	0.0699					
PLOT*CACHE(SITE*STAND)	16	0.6441	0.0403					
SITE*SHRUB*CACHE	1	0.0007	0.0007					
STAND*SHRUB*CACHE(SITE)	2	0.0343	0.0172					
PLOT*SHRUB*CACHE(SITE*STAND)	15	0.5449	0.0363					
SITE*DUFF*CACHE	1	0.0020	0.0020					
STAND*DUFF*CACHE(SITE)	2	0.0570	0.0285					
PLOT*DUFF*CACHE(SITE*STAND)	16	0.9814	0.0613					
SITE*SHRUB*DUFF*CACHE	1	0.0191	0.0191					
STAND*SHRUB*DUFF*CACHE(SITE)	2	0.0807	0.0403					
PLOT*SHRUB*DUFF*CACHE(SITE*STAND)	12	0.5253	0.0438	3.0293	71	0.0427		

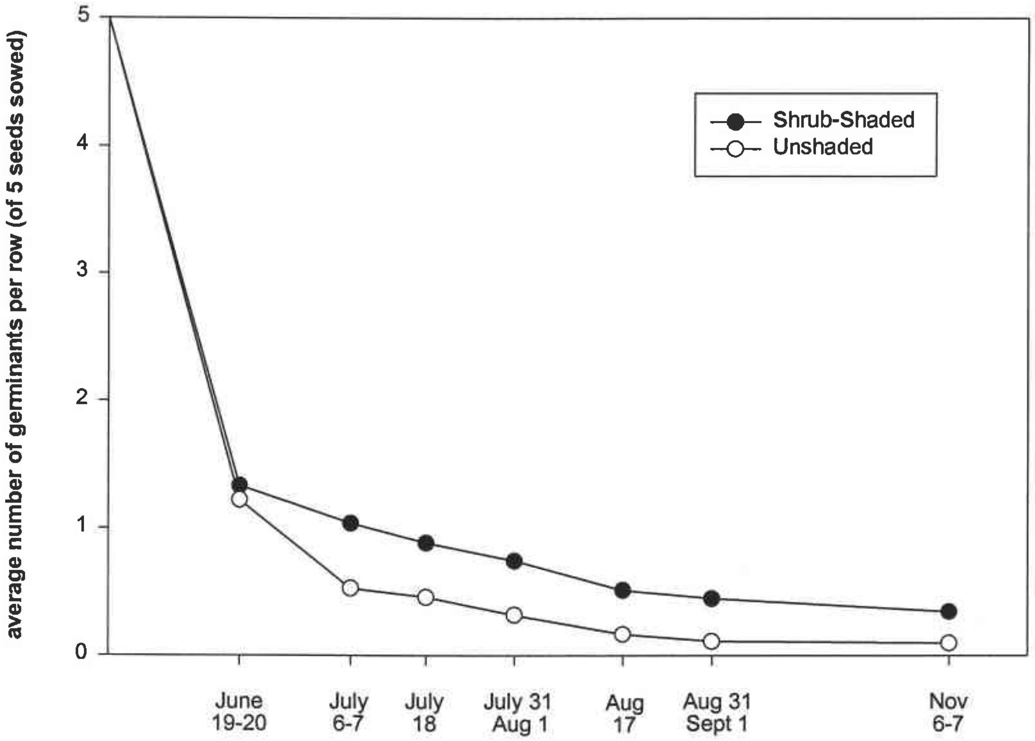

FIGURE 6.6. Germinant emergence and temporal patterns of germinant mortality among shrub-shaded and unshaded sites.

Relative humidity ranged from an overall average high of 86.5 percent at 4 a.m. to an overall average low of 12.1 percent at 12 p.m. (Figure 6.7, top). Relative humidity was consistently lower at the Fort Rock site than at the Pringle Falls site at each period ($P<.05$). The minimum average difference between the two sites was 5.6 percent, and occurred at 4 a.m. The maximum average difference of 22.4 percent occurred at 8 p.m. Shrub cover did not result in any significant differences in relative humidity at any stage ($P>.05$).

Flux in air temperature was great over the 20-hour period, with an overall average high temperature of 38.7°C, and an overall average low of 8.3°C (Figure 6.7, middle). The flux was greater at the Fort Rock site than the Pringle Falls site. Temperatures at the Fort Rock site ranged from an average low of 5.2°C at 4 a.m. to an average high of 39.9°C at 12 p.m. The Fort Rock site was warmer than the Pringle Falls site for most of the day, between 8 a.m. and midnight. Between approximately 1 a.m. and 8 a.m., the Fort Rock site was colder. The maximum differences between the two sites occurred at 4 a.m., when Fort Rock was 6.1°C colder, and at 8 p.m., when Fort Rock was 5.1°C warmer. Shrub cover resulted in no differences in air temperature at any time during the 20-hour period ($P>.05$).

Flux in soil temperature was much less than air temperature, and site differences were less pronounced (Figure 6.7, bottom). Coldest temperatures were identified at 4 a.m., with Fort Rock Sites averaging 15.0°C, and Pringle Falls sites averaging 17.1°C. Maximum soil temperatures lagged behind air temperature, occurring at 4 p.m. rather than 12 p.m. At 12 p.m. and 4 p.m. significant site differences did not exist ($P>.05$). Shrub cover was a significant

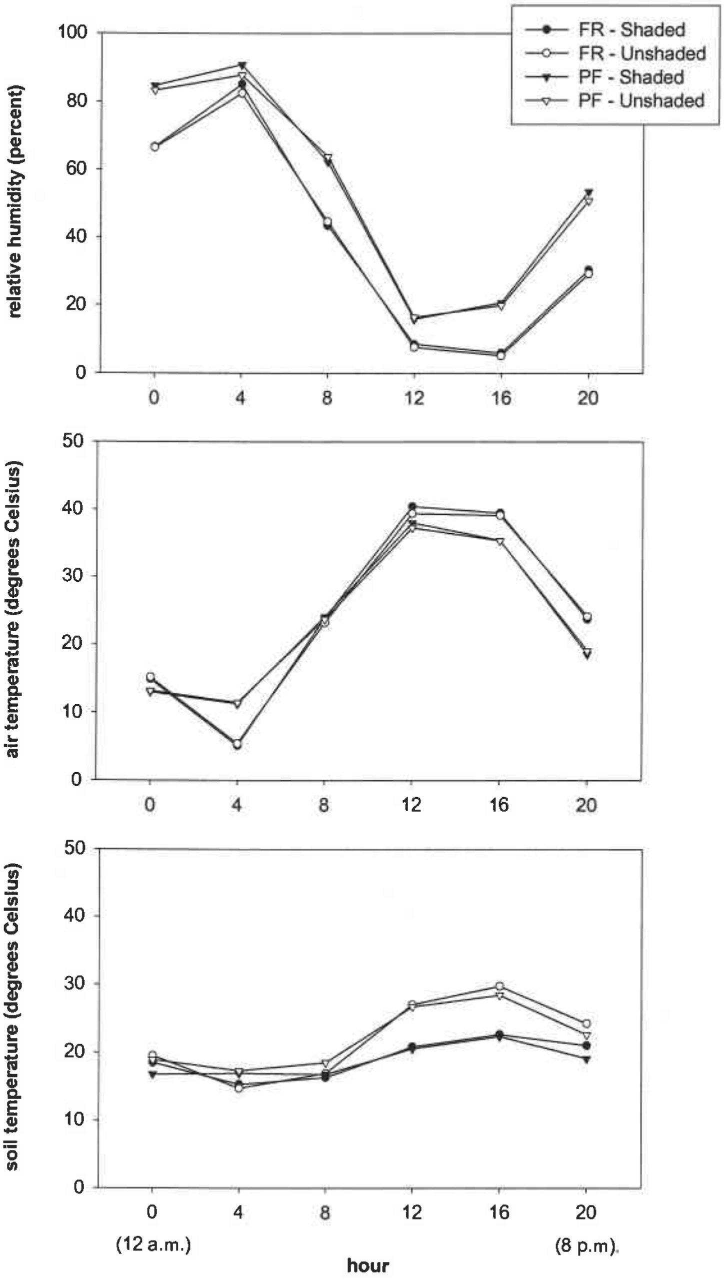

FIGURE 6.7. Changes in relative humidity (top), air temperature (middle), and soil temperature (bottom) over one 24-hour period. Shrubs had a substantial impact on soil temperature; site had a more dominating influence on relative humidity and air temperature.

factor (P<.05) from noon to dusk, and its effect on soil temperature over that period was substantial. Unshaded sites averaged 26.9°C at 12 p.m. and 29.1°C at 4 p.m. In contrast, shrub-shaded sites averaged 6.2°C cooler than unshaded sites at 12 p.m., and averaged 6.6°C cooler at 4 p.m. Soil temperature differences between shaded sites and unshaded sites continued after dusk. As late as 8 p.m., shaded sites were cooler than unshaded sites by 3.2°C at Fort Rock and 3.5°C at the Pringle Falls sites.

Shrubs had a moderate shading effect on the forest floor light environment (Figure 6.8). Based on the standard method of interpreting diazo paper exposure (Method 1), the intensity of solar radiation at shrub-shaded locations was 23.3 percent less than open sky at Pringle Falls, and 27.5 percent less than open sky at Fort Rock. Locations not shaded by shrubs received 10.0 percent of open sky at Pringle Falls and 9.2 percent of open sky at Fort Rock, indicating the effect of the partial tree overstory on the forest floor light environment. Shrubs supplemented the mild shading effect contributed by the partial overstories that were present at all four stands. Light intensity averaged 17.5 percent less among shrub-covered treatments than among adjacent treatments away from shrubs. There was no significant difference between sites (P=.496; T-test).

The estimate of shading did not differ substantially depending on whether it was calculated based on fully-exposed sheets (Method 1) or partially-exposed sheets (Method 2). The magnitude of shading differed between the two methods of calculation (note y-axes on Figure 6.8 charts), but correlation of shading values between the two methods produced an r-value of 0.899.

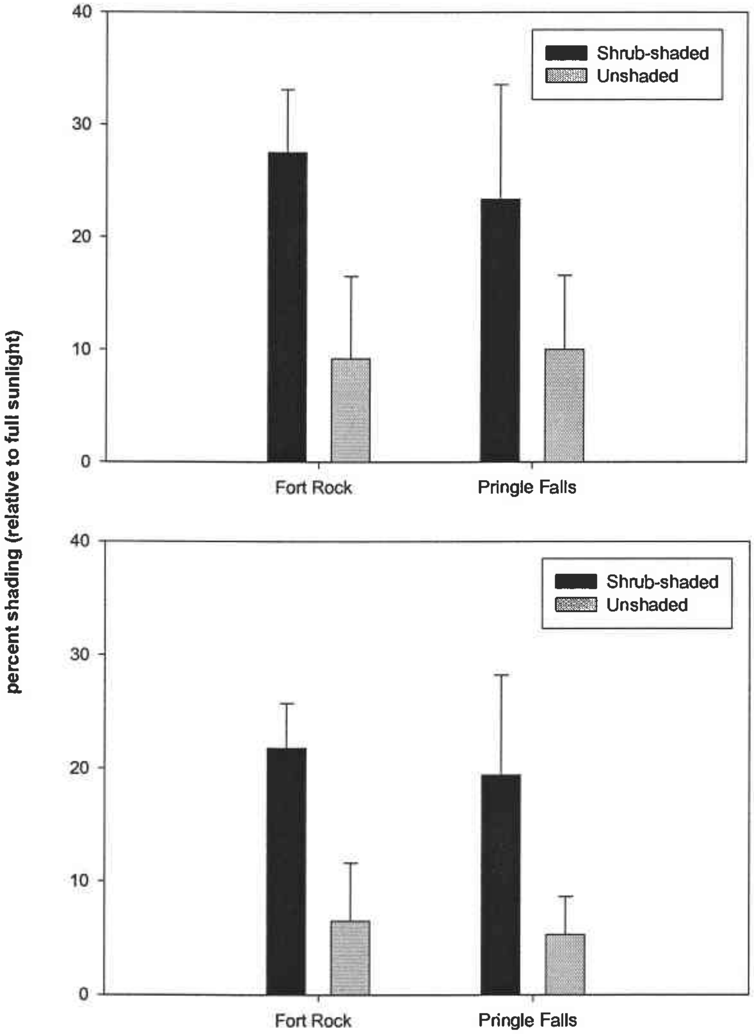

FIGURE 6.8. Effect of shrubs on microsite solar radiation in stands with partial live overstories. Percent shading is relative to a fully-exposed location at the same site. Under Method 1 (top), only fully-exposed ozalid sheets were counted; under Method 2 (bottom), all partially-exposed sheets were counted. The two methods yield comparable results.

DISCUSSION

The experiments in this study provide evidence supporting the hypothesis that ponderosa pine seedling recruitment is facilitated by the presence of shrubs. Less than 30 percent of all seed sown in fall resulted in live germinants the following spring, and just 5 percent resulted in live germinants by the following fall. There was greater germinant recruitment under shrubs than in the open. Shrubs had no effect on germinant emergence rates, but germinants under shrubs succumbed to apparent desiccation at a slower rate than did germinants in the open. Nearly 4 of 5 germinants that survived their first summer were beneath shrubs.

These findings provide stronger evidence of a positive regeneration/shrub association than has been reported in past observational studies by other workers in central Oregon. Dyrness (1960) observed that 60 to 85 percent of *Pinus ponderosa* seedlings and saplings occurred within cover of *Ceanothus velutinus*, *Arctostaphylos patula*, or *Purshia tridentata*. Dahms (1950) observed that *Ceanothus* and *Arctostaphylos* cover disfavored *Pinus ponderosa* seedling height growth, but acknowledged that seedling establishment was unaffected by cover of those species. This study's findings also lend support to the arguments of Youngberg (1966), who contended that in the harsh conditions of the central Oregon pumice zone, shrub cover was critical in ameliorating extremes of soil moisture and temperature, improving soil fertility, and providing mechanical protection to young seedlings. Wollum and Youngberg (1964) supported the theory with a greenhouse study in which *Pinus ponderosa* seedlings growing beneath *Ceanothus* possessed more fine roots and higher foliar nitrogen content than open-grown seedlings.

This paper's findings are in agreement with those of other studies in similar arid and semi-arid ecosystems, providing evidence that the presence of shrub cover can ameliorate harsh summer conditions and facilitate establishment of tree seedlings (Holmgren et al. 1997). In coastal California chaparral, for example, Dunne and Parker (1999) related the greater emergence and first-year survival of *Pseudotsuga menziesii* germinants under two *Arctostaphylos* species to higher soil water potential. Show (1924) found that brush cover increased ponderosa pine seedling survival in California, especially at poorer sites. Facilitative effects may have been responsible for spatial patterns in an old-growth ponderosa pine stand in central Oregon, where germinant and small seedling densities were positively associated with *Purshia tridentata* cover (Keyes et al. 2001).

In this study, the primary effect on recruitment was shading by shrubs, and the effect of shrub shade in summer was to reduce solar radiation and soil temperatures. Shrub-sheltered germinants 17.5 percent less solar radiation than adjacent germinants away from shrubs, and 25.4 percent less radiation than germinants under open sky. This moderate shading was not reflected in increased relative humidity or reduced air temperatures, but it did result in cooler soil temperatures, especially during the hottest parts of the day (12 pm to 4 pm).

Heat did not appear to operate as a direct cause of seedling mortality in this study. Excessively high temperatures have been demonstrated as a direct agent of seedling mortality by causing heat lesions at the base of seedlings

(Hartley 1918). In this study, however, heat lesions were not identified on seedlings. Baker (1929) identified 54° Celsius as an upper temperature limit for western conifers, but in this study the highest temperatures recorded did not exceed 47° Celsius. The periodic nature and limited duration of temperature measurements in this study limits inferences to maximum temperatures, however weather during the experiment was typical of mid-summer conditions in this region.

The combination of higher soil temperatures and greater solar radiation could explain the higher mortality rates of unshaded germinants via higher transpiration rates. Since contributors to seedling moisture stress include air vapor pressure, wind speed, leaf temperature, soil temperature, and soil properties (Cleary 1970), shrub cover appears especially important to ponderosa pine recruitment in the droughty climate and pumice soil conditions typical of central Oregon. Excessive shading is only a direct mortality problem for seedlings when light is reduced to low levels. For example, Atzet and Waring (1970) showed that ponderosa pine seedlings can persist at light levels as low as 20-30 percent of full sunlight. Pearson (1936) showed that seedlings were substantially weakened at light intensities below 50 percent of full sunlight but that mortality did not occur above 10 percent of full sunlight. With the partial-overstory stands in this study, light levels beneath shrubs averaged 74.6 percent of full sunlight, well above the thresholds identified by those authors. Germinants not covered by shrubs received 90.4 percent of full sunlight, a condition attributed to the scattered overstory trees in each stand.

Because the effect of shrubs on available soil moisture was not measured, it is not possible to infer the effect of shrub cover on this important factor. Such measurements in this experiment might have helped clarify past discrepancies on the effect of shrub cover on soil moisture availability. For example, Tarrant (1957), found that the seasonal soil moisture depletion rate beneath *Arctostaphylos patula* was 2-3 times the depletion rate beneath dead brush or in the open. Also, Barrett and Youngberg (1965) showed that soil water use in thinned stands receiving shrub control was 30% less than in stands without shrub control. In that study, canopy leaf area accumulated more rapidly in the stands receiving vegetation control, and vegetation control improved growth efficiency in the treatments with low leaf area index (Oren et al. 1987). In contrast, Dyrness (1960) found that soil nutrient contents and moisture depletion patterns were more favorable under *Ceanothus velutinus* than in the open.

Neither relative humidity nor air temperature were influenced by shrubs. In a comparison of regeneration microsites in the Sierra Nevada, Tappeiner and Helms (1971) found that first-summer survival of white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) germinants was greater within *Ceanothus prostratus* cover. They attributed this result to the significantly reduced potential evaporation at seedling height above *Ceanothus prostratus*, which is a low, creeping shrub with a dense canopy. In contrast, the primary shrub in this study, *Purshia tridentata*, has a relatively porous canopy with a low foliar density, as evidenced by the relatively high light levels recorded beneath those shrubs. *Purshia tridentata*'s low foliar density and open crown morphology likely enabled greater air flow in the shaded area, resulting in no detectable differences in air temperature or humidity among shaded and unshaded areas. Hence it appears that shrubs at these sites have an effect on microenvironment (light intensity and soil temperature) that differs little from the effect of overstory trees and other shading structures (such as dead shrubs).

Ponderosa pine germinants must first germinate and emerge in spring before they can be favorably influenced by shrub shading. This study found that seed caching and mineral soil substrate were important factors in germinant emergence; hence they were important factors on the year's crop of available germinants. With nearly 9 of 10 of spring germinants emerging from "cached" seeds, the potential influence of rodents on seedling recruitment in central Oregon appears substantial. Although it cannot be inferred from these numbers the extent to which seed caching contributes to each year's germinant crop, they do show that seeds in unrecovered caches are much more likely to germinate than seeds that are not buried in caches.

Observational works suggest that seed caching may indeed play an important role in the recruitment of ponderosa pine and similar species. In Vander Wall's (1992) work in Nevada, the majority of new Jeffery pine (*Pinus jeffreyi*) seedlings originated from unrecovered rodent caches. Caches were responsible for half of ponderosa pine regeneration seedlings in Saigo's (1968) central Oregon study. At another central Oregon location, West (1968) estimated more conservatively that 16-18 percent of ponderosa pine emergence sites were attributed to seedling clusters (assumed to have originated from seed caches).

Caching may be a more important natural regeneration factor in the pumice zone than in other areas. The loose, deep pumice soils are highly amenable to digging and burial. The difference in soil types between Cascades and Sierra Nevada ponderosa pine forests is a reason why outbreaks of defoliating pandora moths (*Coloradia pandora*), which require loose soil in order to bury themselves for overwinter pupation, are common in central Oregon but not California (Furniss and Carolin 1977). Additionally, pumice soils appear to dry out more rapidly at the surface than other soil types, partly because of better airflow and partly because of less upward water movement by capillary action. Caching places the seeds in the more favorable germinating environment just below the surface.

This study addressed seedling mortality during the first summer months following emergence. Although not recorded, observations suggested that seedling mortality was due almost exclusively to desiccation. Notably, emergence rates, which averaged less than 30 percent, were significantly enhanced by the two treatments (bare mineral soil, “caching”) that minimized the exposure of seeds to duff. The negative effect of duff was most likely associated with the inability of seeds to imbibe water when in poorer contact with moist mineral soil. Duff also provides habitat for damping-off fungi, including *Pythium*, *Rhizoctonia*, *Fusarium*, *Corticum*, and *Cylindrocladium* species, which cause seedling mortality (Farmer 1997). Damping-off fungi were not a factor reducing survival of those seedlings that emerged, but they may have helped reduce seedling emergence rates.

Predation of ponderosa pine seeds by birds and small mammals is great in central Oregon (Eastman 1960, Cochran 1970, Hooven 1966). However, observations showed that over-winter seed predation in this study was successfully prevented by the screen exclosures. Most non-germinated seeds could be clearly seen on the forest floor in spring in the same place where they had been placed during the previous fall. After the screens were removed following spring emergence, damage by clipping or grazing damage was evident for only a few seedlings.

Due to the limited time frame of this study, the effects of other seedling mortality agents were not addressed. Frost-heaving and autumn litterfall, for example, are two agents of new seedling mortality that have been shown to be significant factors in other studies (Heidmann 1976, Christy and Mack 1984, Tappeiner and Helms 1971). In a two-year observational study of emergence and survival related to this study, however, most ponderosa pine germinant mortality occurred during the first few weeks after emergence in June (Chapter 5 of this dissertation). Over the 15-month period of that study (June 1999 to November 2000), only 2 germinants died (0.6 percent of all mortality) during the winter and spring months (December 1, 1999 to June 6, 2000). Those findings suggest that in the pumice zone, winter mortality agents are less influential on ponderosa pine seedling recruitment than the summer mortality agents that germinants were exposed to in this study.

This study regarded shrub cover as a discrete factor (either present or not present). However, the effects of shrub shading on several important variables can probably be observed on a continuum from the inside out, or from a shrub's center outward to its dripline and beyond. This study's findings suggest that light intensity and soil temperature are two variables that may increase with increasing distance from shrub center. Competition for below-ground resources (e.g. soil moisture) might also occur on a continuum from shrub center outward, with spatial relationships differing by shrub species, height, and width. For a better understanding of shrub influences on natural regeneration processes related to the forest floor microenvironment, future studies should attempt to more precisely quantify these spatial relationships.

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CHAPTER 7

SUMMARY

The pumice zone of central Oregon possesses climatic, edaphic, and vegetative qualities that uniquely influence the natural regeneration of ponderosa pine. The objective of this project was to investigate the fate of ponderosa pine regeneration from seed to established seedling, and to determine the relative influences of stand elements on those fates. The project was carried out in observational and experimental recruitment studies in six stands of varying overstory density levels at two sites on the Deschutes National Forest. Because the studies addressed a limited recruitment period of approximately two years, an additional study at the Metolius Research Natural Area was conducted to examine the relationship of stand characteristics to the density of older, more established seedlings.

The analysis of seedling spatial patterns at the Metolius Research Natural Area (Chapter 3) found evidence of relationships between ponderosa pine regeneration and adjacent vegetation. Overstory trees were negatively related to the density of regeneration in smaller size classes (less than 140 cm tall). The overstory effect operated at a small spatial scale (5-m radius) but not at a larger scale (15-m radius). Like overstory trees, saplings adversely impacted the occurrence of germinants and seedlings. Shrub cover was negatively related to saplings, but was positively related to germinants and seedlings. Quadrat-based spatial analyses revealed that regeneration in each size class was aggregated, and that aggregation was greatest at smaller regeneration sizes. The relationships observed in this study indicated the need for additional studies to clarify the relationship of overstory trees, shrubs, and other stand factors to the seedling recruitment process in ponderosa pine stands.

An analysis of the temporal and spatial patterns of seedfall in stands with partial overstories was presented in Chapter 4. As the first step in the seedling recruitment process, the absolute amount of seedfall that occurs in a given year determines the maximum number of seedlings that can establish. Seed traps were used to collect 2,166 seeds of the 1999 crop in four stands at two sites in central Oregon. Viable seeds accounted for 62-73 percent of all seeds (72-86 percent of all intact seed), and seed density across stands averaged more than 1 million per hectare. There was a strong site effect on seed quantity (the less mesic of two sites produced more seed) that was not accounted for by overstory density. Within each site, however, the denser stand yielded more seed. More than half of all viable seeds fell within the first 30 days of collection. The rate of seedfall was more rapid at the more mesic site.

Spatial patterns of seedfall set the stage for subsequent recruitment stages, and directly influence the spatial distribution of seedlings that are recruited from the year's seed crop. In this study, seedfall patterns within each stand were not spatially uniform. At the two stands of highest and lowest overstory density (18 and 80 trees per hectare), seedfall patterns were not associated with the spatial distribution of seed-bearing trees. At the two stands of moderate densities (39 and 47 trees per hectare), the relationship of seed density to distance from trees followed a negative binomial distribution.

The observational study in Chapter 5 led to several findings about the role of seed caching, substrate, and understory shade on the emergence and early survival of ponderosa pine germinants in central Oregon. Only about 3 percent of viable seed resulted in emergents, the remainder presumably succumbing to seed predation, molds, or damping-off fungi. A small fraction of emergents survived the first summer. Overall, most mortality occurred immediately after emergence, and nearly all mortality occurred during the summer months. Most emergents were from caches, and germinants in clusters from caches remained a substantial portion of the cohort after two seasons. Large clusters were reduced to small clusters or individuals shortly after emergence, but the mortality rate for germinants in clusters was not different than individual germinants. More germinants emerged on a thin litter substrate than a mineral soil substrate, and mortality rates were higher for seedlings emerging on mineral soil. Woody debris produced few germinants, and fewer yet survived on that substrate. Most germinants emerged without understory shading, but very few of those survived. Mortality rates were far lower for seedlings emerging beneath live vegetation (mostly shrubs), and most germinants alive after one year, and especially two years, had emerged beneath live cover.

The seed-sowing and microenvironment experiments in Chapter 6 provide additional evidence supporting the hypothesis that ponderosa pine seedling recruitment is facilitated by the presence of shrubs. Less than 30 percent of all seed sown in fall resulted in live germinants the following spring, and just 5 percent resulted in live germinants by the following fall. Shrubs had no effect on germinant emergence rates, but germinants under shrubs succumbed to desiccation at a slower rate than did germinants in the open. Nearly 4 of 5 germinants that survived their first summer were beneath shrubs.

Shrubs supplemented the mild shading effect contributed by the partial overstories that were present at all four stands. Germinants beneath shrubs received 17.5 percent less radiation than germinants that were away from shrubs, and 25.4 percent less solar radiation than germinants beneath open sky. This shading was not reflected in relative humidity or air temperature differences, but did result in cooler soil temperatures, especially during the hottest parts of the day. The exposure of unshaded germinants combination to higher soil temperatures and greater solar radiation could have produced the observed higher mortality rates by increasing transpiration rates.

Ponderosa pine germinants must first germinate and emerge in spring before they can be favorably influenced by shrub shading. Simulated seed caching (burial to 1-cm depth in soil) and mineral soil substrate increased germinant emergence rates. With nearly 9 of 10 of spring germinants emerging from cached seed, the potential influence of rodents on seedling recruitment in central Oregon appears substantial.

The studies in this dissertation set a foundation for further research into ponderosa pine regeneration processes in central Oregon. Subsequent studies in these stands, and others that have been established for the long-term project, will provide additional information about the fate of seedlings under the conditions tested here. Inclusion of the sites located at the Warm Springs reservation will provide another level of site quality, different understory plant communities, and a broader range of overstory densities.

The studies in this dissertation analyzed processes up to the initial establishment of seedlings (first two years). The first of future studies will address the spatial relationships of seedlings that have established beyond their second year. Further studies are required to determine how the spatial distributions of those seedlings change as the stand ages. They are also required to determine how well seedlings grow in the presence of retained partial overstories. It is anticipated that the density and distribution of overstory trees will play a greater role in ponderosa pine seedling growth than in the studies of emergence and establishment presented here.

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