# Positive Seedling-Shrub Relationships in Natural Regeneration of Ponderosa Pine[1]

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**Abstract**

An understanding of natural regeneration processes, and the stand structural features that influence those processes, is vital to attaining goals associated with natural regeneration. This paper discusses natural regeneration concepts and the interactions that occur between shrubs and natural regeneration of ponderosa pine. The interactions observed recently in a series of related seedling recruitment studies in central Oregon are summarized. Evidence suggests a positive relationship between shrubs and the occurrence of ponderosa pine seedlings during the first two years of the seedling establishment phase. The vast majority of germinant mortality occurs during summer months, and especially the weeks immediately after emergence. Shrubs do not enhance emergence rates, but do enhance overall recruitment rates by reducing rates of first-summer mortality. The mechanism driving these patterns appears to be microenvironmental amelioration by shrubs, abating germinant moisture stress and desiccation. The manifestation of this relationship is a positive spatial relationship between shrubs and small seedlings during this establishment phase.

## Introduction

For most forest management objectives, the recruitment of a cohort of seedlings is the first and most critical process following regeneration harvest or stand-replacing disturbance. The spatial and temporal patterns of seedling recruitment set the stage for all subsequent stand development patterns; hence, the seedling recruitment stage is the first step in determining future stand structures, habitat conditions, susceptibility to disturbances, and silvicultural options. An understanding of the natural regeneration processes in forests of ponderosa pine (*Pinus ponderosa* P. & C. Lawson), and the stand structural features that have bearing on those processes, is vital to manipulating controllable factors in order to successfully secure natural regeneration. This subject is particularly relevant under the current Forest Service paradigm of ecosystem management, wherein reliance upon natural processes in natural systems management is stressed, and funds for reforestation are scarce.

An understanding of regeneration processes is equally important for those management objectives wherein regeneration is undesirable. For example, managers may wish to maintain crown fire resistance by promoting ponderosa pine stands with

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open-understory structures that are free of ladder fuels. Currently, management and research in this region is directed toward dealing with the existing condition of dense ponderosa pine stands. However, it is worthwhile to analyze the processes that have contributed to the development of these dense stands in the era of fire suppression and exclusion. It is reasonable to theorize that the effects of fire exclusion on ponderosa pine regeneration have been both direct and indirect. If the relationship of shrubs to seedling recruitment is positive, for example, it then follows that one effect of fire exclusion may have been the indirect proliferation of pine seedlings by enabling dense shrub understories to establish and persist. An understanding of these and other potential indirect effects of fire exclusion on pine proliferation is essential to prescribing practices that will create and sustain stands with crown fire resistance.

Despite an abundance of previous research on the subject, the effects of shrubs on processes of ponderosa pine natural regeneration are still poorly understood. Research efforts have been geographically limited, short in duration, and restricted to a single stage of regeneration, a situation that is typical of regeneration research in other species and regions as well (Clark and others 1999). The result has been sometimes-conflicting and often-confusing advice for forest managers dealing with regeneration objectives. This paper addresses the relationship of shrubs to the establishment of ponderosa pine regeneration with a discussion of shrub effects within the context of recent conceptual models of facilitation and competition that have been applied in similarly xeric ecosystems. We also offer evidence of positive seedling-shrub relationships in a summary of the results of three integrated establishment-phase regeneration studies that were recently conducted in central Oregon.

## Constraints on Regeneration

Several ubiquitous biological and physical factors are capable of limiting seedling recruitment in ponderosa pine forests, and often do so (*table 1*). Many of these factors may occur simultaneously during any given year, thus severely curtailing opportunities for regenerating ponderosa pine without human intervention. Among those factors, moisture stress represents the most significant of practicably controllable factors. The potential roles of phytotoxins as chemical regeneration inhibitors have also been investigated (Kelsey and Harrington 1979), but were revealed to be absent.

In previous reviews of ponderosa pine regeneration processes, Heidmann (1992) and Barrett (1979) both identified aspects of climate having greatest influence on the establishment of seedlings from seedfall. Heidmann (1992) opened his review article, *Regeneration Strategies for Ponderosa Pine*, with the bluntly succinct statement, "Regenerating ponderosa pine (*Pinus ponderosa*) is difficult." He elaborated that,

> The primary obstacle to regeneration of this species throughout its natural range is drought… Annual precipitation in the western and southwestern United States is generally adequate for tree growth but erratic distribution during the year makes seedling establishment difficult.

***Table 1****—Factors that potentially limit ponderosa pine regeneration, the affected regeneration stages, and relevant literature specific to ponderosa pine (references not specific to ponderosa pine are denoted by parentheses).*

| Factor | Regeneration stage | Sample reference |
|---|---|---|
| Seed deficiency | flower, seed | Pearson 1923<br>Fowells and Schubert 1956<br>Daubenmire 1960<br>Curtis and Foiles 1961<br>Shearer and Schmidt 1970<br>Foiles and Curtis 1973<br>Dahms and Barrett 1975<br>Barrett 1979<br>McDonald 1992 |
| Molds | seed | Fowells and Schubert 1951<br>Wagg 1958<br>Roth 1970 |
| Predation | seed, germinant, seedling | Pearson 1913<br>Eastman 1960<br>Hooven 1966<br>Cochran 1970<br>Blake and others 1986<br>Blake and others 1989<br>Shearer and Schmidt 1971 |
| Damping-off fungi | germinant | Wagg and Hermann 1962<br>Roth 1970 |
| Unfavorable forest floor substrate | germinant | Larsen 1924<br>Foiles and Curtis 1965 |
| Litterfall burial | germinant | (Koroleff 1954)<br>(Tappeiner and Helms 1971) |
| Excessive heat | germinant | Baker 1929<br>Larson 1967 |
| Moisture stress, drought | germinant, seedling | Pearson 1923<br>Hermann 1968<br>Larson and Schubert 1969<br>Cleary 1970<br>Djavanshir and Reid 1974 |
| Frost heaving | germinant, seedling | Heidmann 1976 |
| Summer frosts | germinant, seedling | Cochran 1972<br>Cochran 1984 |
| Excessive shade | germinant, seedling | Pearson 1936<br>Atzet and Waring 1970 |

In his report, *Silviculture of Ponderosa Pine the Pacific Northwest*, Barrett (1979) summarized the primary constraints on ponderosa pine regeneration with the observations:

> Prolonged moisture for germination, growth, and life during the critical heat of July and August is critical… Germination usually occurs in early spring, but rapid drying of the germinating medium often causes death of the seedling… Because summers are usually dry, conservation of moisture is critical.

In the Pacific Northwest, 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 (*fig. 1*). On the east slope of the Cascade Range, these climatic conditions are exacerbated by the presence of relatively young, poorly developed, mineral deficient, and highly porous volcanic soil types that dominate the region. These climatic and edaphic conditions present, through the moisture stress they induce, significant environmental challenges to tree regeneration, survival, and growth.

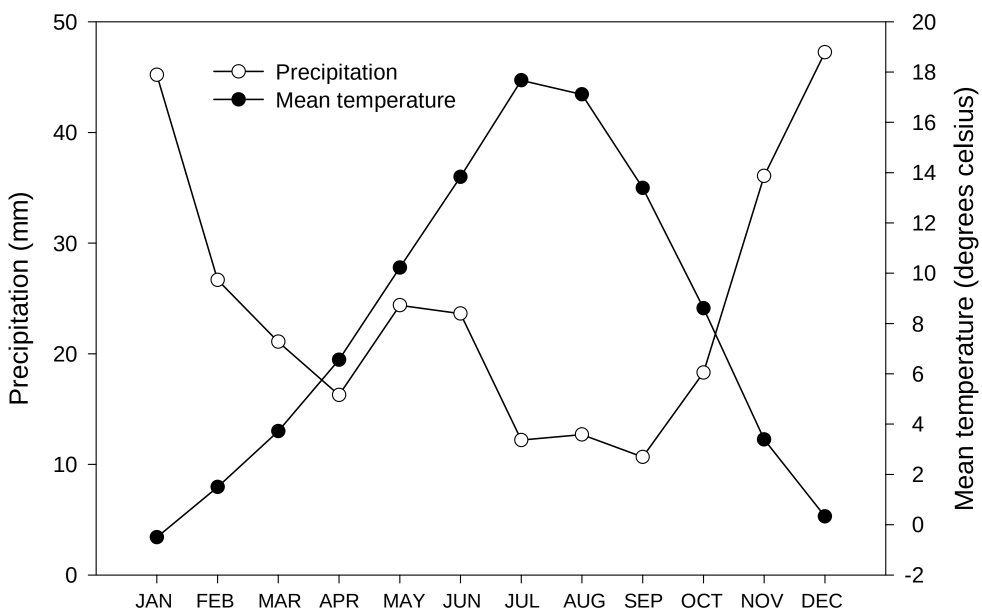


**Figure 1**—Climatic conditions in the central Oregon area illustrating the annual coincidence of high temperatures with low precipitation (1928-2004 mean values from National Climate Data Center cooperative station no. 350694 at Bend, Oregon).

Given these constraints, the microenvironments most favorable for seedling establishment will be those where moisture stress is abated. Moisture stress may be abated by a reduction in solar radiation, wind, soil temperature or ambient temperature; by an increase in relative humidity; and by retention of soil moisture near the forest floor surface further into the summer months.

## Shrub Influences on Regeneration

This challenging regeneration environment suggests the potential for positive effects of shrubs on ponderosa pine seedling recruitment by their microenvironmental influences and attendant effects on germinant and seedling moisture stress. Past observations of regeneration have provided indications of numerous influences of shrubs on ponderosa pine recruitment processes, both positive and negative (*table 2*).

**Table 2**—*Potential influences of shrubs on ponderosa pine seedling regeneration.*

| Positive influences | Negative influences |
|---|---|
| Enhanced soil fertility via N fixation | Accelerated soil moisture depletion |
| Extended soil moisture retention via shading | Excessive shade |
| Lower ambient temperatures via shading | Reduced seedling growth |
| Physical browse interference | Enhanced seed-predating mammal habitat |
| Enhanced soil moisture via hydraulic lift | Burial by litterfall |
| Improved seedling form | Consumption by fire (via fuelbed continuity) |
| Reduced thermal flux and frost heaving | |

But in some cases these influences are conflicting. On balance, 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? Moreover, do their effects change over the course of seedling establishment and growth? The situation is likely characteristic of the so-called ‘seed-seedling’ conflict described by Schupp (1995). Schupp determined that inter-specific conflicts and intra-specific conflicts had been well addressed in ecological literature, but that intra-individual conflicts had received considerably less attention. For trees, intra-individual conflicts occur when the conditions favorable for growth are diametrical to those favorable for establishment (*fig. 2*).

Such conflicts have been recognized for centuries by silviculturists and have been addressed operationally in the utilization of shelterwood regeneration systems. Shelterwood systems, which have been employed as formal systems since at least the $18^{th}$ century (Kostler 1956), were developed to balance the requirements for seedling establishment with those for seedling growth. Under these systems, partial live tree overstories are retained at harvest in order to facilitate regeneration by providing a seed supply and a shaded forest floor (ameliorated microenvironment); once an understory cohort has become established, the overstory is removed to maximize growth of the new cohort (Matthews 1989, Smith and others 1997). Although this concept is well known and understood by foresters, other potential intra-individual conflicts have not been widely recognized by foresters or adequately investigated by researchers. For ponderosa pine, investigations into seed-seedling conflicts during the periods of germinant emergence and establishment are absent.

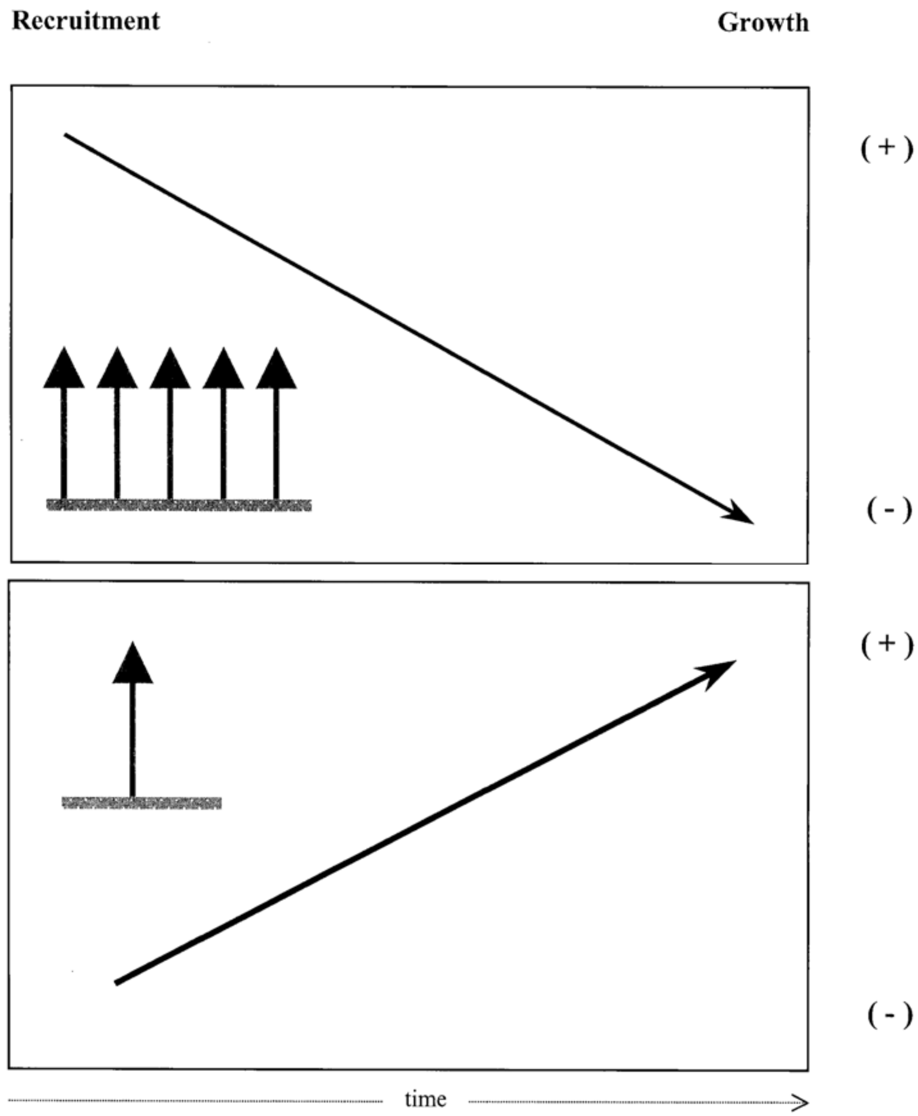


**Figure 2**—Illustration of intra-individual regeneration conflicts. Above, germinants recruited beneath partial live overstories have greater initial survival potential, but survivors of the establishment phase have reduced growth potential. Below, seedlings establishing in the open or beneath a sparse overstory have reduced survival potential, but survivors have greater growth potential.

In ecosystems where plants are similarly subjected to severe environmental stresses, evidence is mounting that positive interactions (facilitations) are common. Positive interactions and facilitated recruitment in vascular plants are most often observed in those natural communities where either physical stress is great or consumer pressure is intense (Bertness and Callaway 1994). For example, in many ecosystems where severe desiccating conditions are typical – including grasslands, tundra, sand dunes, deserts, salt marshes – positive interactions frequently occur (Holmgren and others 1997). All observed plant interactions can be generalized as the net result of co-occurring facilitation and competition (Callaway and Walker 1997). In xeric plant systems, facilitation is the dominant force when the costs associated with reduced light levels are more than offset by improved water relations (Holmgren and others 1997). This balance of competition and facilitation is dependent upon plant life stages, so the relationship between individuals may differ over time. Adapting these concepts to ponderosa pine systems, it is reasonable to theorize that ponderosa pine germinants may benefit from shrub presence during the establishment phase in a facilitative relationship that becomes competitive once seedlings become established and increase their demands for growth resources.

## Regeneration Field Studies

The relation of shrubs to ponderosa pine seedling regeneration was recently analyzed in a series of related field studies located in central Oregon (Keyes 2002, Keyes and Maguire 2000). The goal of the project comprising the studies was to quantify the relative effect of stand structural features on the earliest phases of seedling recruitment. An objective of each study was to determine whether the relationship of shrubs to seedlings was one of attraction (positive spatial association) or repulsion (negative spatial association). A summary of the relevant findings of the three field studies is presented here.

The first of these is a case study of regeneration in an old-growth ponderosa pine stand. The second is an observational study of ponderosa pine germinant emergence and 1-2 season survival, and the relationship of those processes to the presence of shrubs. The third is a seed-sowing experiment relating the presence of shrub cover to ponderosa pine germinant emergence and 1-season survival rates.

Each of the studies presented here was conducted in pure ponderosa pine stands on the lower east slope of the Cascade Range in central Oregon. All stands were at sites that were flat or nearly so. The case study was conducted in one undisturbed stand at the Metolius Research Natural Area, located 22 km northwest of the town of Sisters. The observational study was conducted in four stands at the eastern edge of the Deschutes National Forest southeast of the city of Bend. The experiment was conducted in four stands of the Deschutes National Forest; two were located on the forest's eastern edge, and two were located on the forest's western half, near the Pringle Falls Experimental Forest. The stands in the observational study and experiment had been subjected to operational regeneration harvests performed within the past 20 years, but retained partial overstories. The stands in the observational study had not been cut within the previous decade; the stands in the experiment had been cut more recently.

### *Case Study: Regeneration in an Old-Growth Stand*

In the first study, an analysis was conducted of the spatial relationships between ponderosa pine small seedlings (≤10 cm tall), large seedlings (10.1-140 cm tall), saplings (0.1-10 cm dbh), overstory trees (≥10 cm dbh), and shrubs (Keyes and others 2001). The study was conducted in a multi-cohort old-growth stand containing a range of tree sizes (including 4 or more trees in each 10-cm dbh class from 0-100 cm) and was virtually pure in ponderosa pine. A grid of 28 2-meter radius regeneration plots was installed within a 4.5-hectare study area. A tally was made of the number of seedlings and saplings in each plot. Percent shrub cover (primarily antelope bitterbrush; *Purshia tridentata* Pursh DC.) was visually estimated to the nearest five percent from illustrations of shrub cover drawn in the field. Local overstory basal area was calculated within a 5-m radius of each plot center. Simple and multiple Poisson regressions were used to identify significant relationships between seedling or sapling density (stems per hectare) and percent shrub cover. It was theorized that positive or negative spatial associations would be suggestive of facilitative attraction or competitive repulsion.

The analysis revealed that small seedlings were negatively related to local overstory basal area ($P$=0.0007) and sapling density ($P$=0.0029). Large seedlings were also negatively related to local overstory basal area ($P$=0.0043) and sapling density ($P$=0.0269). Shrub cover, however, was negatively related to saplings ($P$=0.0003), had no statistically-significant relationship to large seedlings ($P$=0.0888), and was positively related to small seedlings ($P$=0.0141). Consistent with these results, when local overstory basal area was included in two-factor models, positive relationships of shrubs to small seedlings ($P$=0.0005) and large seedlings ($P$=0.0070) were observed. These spatial associations suggest a facilitative relationship between shrubs and seedlings that yields to a competitive relationship between shrubs and saplings. They also suggest that the presence of shrubs benefits seedlings in a way that saplings and overstory trees do not.

## *Observational Study: Patterns of Recruitment*

In the observational study, the temporal patterns of seedling emergence and survival over two seasons (one winter) were addressed. All fresh germinants from natural seedfall were identified in 64 10-m$^2$ circular regeneration plots systematically located in grids within 1-hectare study areas in four stands. Germinants were labeled as shaded by live local vegetation, shaded by dead local vegetation, or unshaded. Shrubs were antelope bitterbrush and greenleaf manzanita (*Arctostaphylos patula* Greene). Two cohorts of germinants were tracked over the course of 1-2 years for patterns of mortality.

Only about 3 percent of viable seed resulted in emergents. A small fraction of emergents survived their first summer. Overall, most mortality occurred immediately after emergence, and nearly all mortality occurred during the summer months. Local shade did not improve emergence rates. Most germinants (72.4 % in 1999, 57.8% in 2000) emerged without understory shading, and in fact the proportion of shaded emergents during 1999 (27.6%) was significantly lower than the expected proportion assuming random germination and survival, and based on estimates of percent shrub cover (34.5%) (Fisher's Exact Test; $P$=0.0138). But although most new germinants were unshaded, few of those survived their first summer (0.8% in 1999, 4.4% in 2000). Most germinants surviving the first summer received local shade, and the only survivors of two summers were shaded germinants. During both years, the proportion of survivors within shade was significantly greater than the expected proportion (Fisher's Exact Test; $P$<0.0001 during 1999, $P$=0.0005 during 2000). This positive effect of shrubs on germinant survival were quantified in cumulative mortality distributions that differed significantly (at $\alpha$=0.05) among the three conditions of shading, with mortality extended furthest into the summer by live shade, and secondarily by dead shade.

## *Experimental Study: Shrub Effects on Recruitment*

The experimental study was a seed-sowing experiment consisting of ponderosa pine seed sown under controlled conditions to test for differences in germination and survival rates among shrub-shaded and unshaded locations. Shrubs were antelope bitterbrush, greenleaf manzanita, and snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex Hook.). Survival was monitored over one summer under conditions controlled by the split-plot design of the experiment. Whole plots tested caching and substrate treatments. Because mechanisms driving the germination and survival patterns were of interest in this experiment, measurements were taken to assess whether differences in relative humidity, air temperature, soil temperature, and light intensity existed between shrub-shaded and unshaded treatments.

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 ($P$=0.349). However, mortality to germinants under shrubs occurred at a slower rate than germinants in the open, and hence establishment rates were higher ($P$=0.032). At unshaded sites, the mortality rate was greatest immediately after germination, whereas the rate remained relatively constant throughout the summer at shrub-shaded sites. As a result, by midsummer the survival rate among shaded germinants was 2.2 times the survival rate of unshaded germinants; by November, nearly 4 out of every 5 germinants were shaded by shrubs. Shrub-sheltered germinants received about one-half to one-third the solar radiation received by adjacent unshaded germinants (data collected 31 July to 1 August 2000). 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 ($P$<0.05).

## Summary of Study Findings

The studies described above focused on establishment-phase regeneration processes during the first two growing seasons after emergence. They provide additional evidence supporting moisture stress as a major factor in ponderosa pine seedling recruitment. For this early phase of regeneration, the relationship of shrub presence to germinant recruitment is a positive one. Results from these studies can be summarized as follows:

- Seedling spatial patterns are positively associated with shrub cover and negatively associated with sapling and overstory tree density, suggesting that shrubs benefit seedlings in ways that saplings and overstory trees in the same stand do not.
- The positive spatial association of shrubs to regeneration does not persist once seedlings achieve sapling proportions (taller than 140cm). Adopting the conceptual model of Callaway and Walker (1997), this suggests that the relationship transitions from one of facilitation to one of competition between the seedling and sapling stages.
- Local shade increases recruitment rates over unshaded sites by reducing rates of germinant mortality. Desiccation is the primary source of mortality, and nearly all mortality occurs during summer (most during the first summer).

- Probability of germinant survival is high if desiccation can be avoided during the first weeks after germination. The germinant survival rate in the second season is higher than survival rate in the first season.
- Shrub cover is not associated with greater emergence rates but greatly improves germinant survival. Establishment from seeds sowed beneath shrubs was several times that from seeds sowed in the open.
- Shrub cover appears to indirectly reduce moisture stress in germinants. The specific mechanism by which shrub cover affects germinants may be by reducing soil temperature or by reducing solar radiation.

Taken together, these findings indicate that the objective of securing natural regeneration in this region will be best served by the retention of understory shrubs. They also indicate that by enabling dense shrub understories to establish and persist, the practice of fire suppression has had an additional (indirect) effect on the development of dense ponderosa pine stands in this region during the past century. Dense shrub understories are likely to continue contributing to the development of ladder fuels by their positive effect on seedling recruitment. Therefore, understory shrub structure should be taken into consideration by managers responsible for prescribing long-term silvicultural treatments to minimize fire behavior.

The time frame encompassed by these studies represents the period when natural regeneration is most strongly influenced by stand structural features, but the studies should be regarded as a foundation for further research into ponderosa pine regeneration processes. Monitoring of seedlings from germination onward is necessary to identify the long-term influences of shrubs on regeneration. This would serve to clarify the role of shrubs on survival of new seedlings beyond the first two seasons, as well as the effects of shrubs on seedling growth. It will probably be useful to analyze shrub cover as a quantitative variable (such as distance from dripline or distance from shrub center) to describe the range of conditions for seedling regeneration within the area of shrub crowns. Differences in regeneration effects among different species of shrubs common in ponderosa pine forests – including antelope bitterbrush, greenleaf manzanita, and snowbrush ceanothus – should be determined, if these differences can be assessed without being confounded by site quality.

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