
Long-Term Seedfall, Establishment, Survival, and Growth of Natural and Planted Ponderosa Pine in the Colorado Front Range

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ABSTRACT: Seedfall, natural regeneration establishment, and growth of planted seedlings was observed from 1981 to 2001 under shelterwood and seedtree overstories in a replicated study in ponderosa pine in the Manitou Experimental Forest in the Colorado Front Range. Good seed crops were produced only every 4 to 6 years, with almost no viable seed produced in intervening years. With seed predation, only 14% of total seedfall was available for germination. Shelterwood overstories containing between 6 and 14 m² ha⁻¹ stem basal area over scarified seedbeds provided optimal conditions for natural seedling establishment. Survival and growth of planted seedlings was much better than that of natural seedlings. However, poor survival and slow initial growth may require many years to establish a fully stocked forest of natural seedlings. *West. J. Appl. For.* 21(1):19–26.

Key Words: *Pinus ponderosa*, silviculture, regeneration, seed viability.

Regeneration of ponderosa pine (*Pinus ponderosa* Laws.) is of crucial interest in all areas of the west, especially in light of recent large wildfires. Understanding the regeneration dynamics of ponderosa pine is important not only in re-establishing forests that have been destroyed by fire, but is also essential in planning fuel treatments in fire-susceptible forests. Knowing how quickly and under what circumstances ponderosa pine will naturally regenerate and grow is critical in prescribing fuel reduction and forest restoration activities and estimating how long they will be effective. This is especially true in the urban interfaces of the Colorado Front Range and Southwest, where climates are dry and ponderosa pine regeneration has been historically sporadic (Schubert 1974). Research on regeneration and silviculture practices for ponderosa pine in the Front Range of the Rocky Mountains has been limited (Meagher 1950). Roeser (1955) outlined early studies undertaken in ponderosa pine silviculture, regeneration, and cutting methods. Unfortunately, these were not completed and cannot be used to formulate management guidelines. Silvicultural methods used in Front Range ponderosa pine were developed by Myers (1974) primarily from experience in the Black Hills and Southwest. He recognized three general stand struc-

tures, resulting from the effects of logging, diseases, insects, fires, and irregularities of reproduction: (1) areas large enough to be managed as uneven-aged stands with an irregular mosaic of small, even-aged groups (<0.4 ha) of trees; (2) stands consisting of irregular patches (0.4–2.0 ha); and (3) stand-size areas that are even-aged or two-storied as though regenerated by uniform shelterwood, seedtree, or clearcutting methods. This study was designed to examine and evaluate regeneration cutting methods applicable to situations 2 and 3 above.

In the Southwest and Black Hills, the shelterwood method has been favored to regenerate even-aged ponderosa pine stands (Boldt and Van Deusen 1974, Schubert 1974). Except where stand conditions warrant the preparatory cut of a three-cut shelterwood, a uniform, two-cut shelterwood is most efficient and effective. The seedtree method has also been used successfully in the Black Hills (Boldt and Van Deusen 1974) and in the Southwest (Pearson 1950). The clearcutting method of regeneration is not well suited to ponderosa pine because of limited seed dispersal distances from parent trees and adverse impacts on wildlife habitat, scenic, and recreational values when applied over large areas. Therefore, this study was limited to comparing shelterwood and seedtree regeneration methods.

Site preparation to expose mineral soil and reduce herbaceous competition is recommended in the Southwest and

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Black Hills (Pearson 1950, Boldt and Van Deusen 1974, Schubert 1974) when attempting artificial regeneration of ponderosa pine. Disturbance associated with logging activities may be sufficient for natural and artificial regeneration as observed from past cutting in the Colorado Front range. Site preparation, which removes all herbaceous competition, may not be desirable when dealing with highly erodible soils in the Front Range (Gary 1975).

In the past, planting ponderosa pine sites has been limited to clearcut areas where natural regeneration was unsuccessful or areas where stands were destroyed by fire, insects, or disease. To meet the standards of the National Forest Management Act, foresters must underplant shelterwood and seedtree residual stands if adequate restocking has not occurred within the specified 5-year regeneration period. Because of this, we designed another phase of this study to compare performance of planted trees under shelterwood and seedtree overstories.

Purpose and Objectives

The purpose of this study was to compare the effects of seedtree and shelterwood cutting methods along with scarification and nonscarification of the forest floor on the establishment and growth of natural and planted ponderosa pine seedlings. Specifically, we wanted to provide a basis for formulating cultural prescriptions and management guidelines to regenerate mature even-aged patches or stands in the Front Range of Colorado. This study had three objectives: (1) to quantify seed production under seedtree and shelterwood cutting methods; (2) to determine natural seedling establishment with scarification and nonscarification of the forest floor under seedtree and shelterwood reserve overstories; and (3) to compare the survival and growth of planted ponderosa pine seedlings with scarification and nonscarification of the forest floor with seedtree and shelterwood reserve overstories.

Methodology

Study Location

This study was established in 1981 at the Manitou Experimental Forest, centrally located in the Colorado Front Range ponderosa pine-bunchgrass type. The plots are located at latitude 39.14° N, longitude 105.12° W at 2,370 m elevation in an area of gentle slopes with east-facing aspects. The study site was occupied by an overstory of mature ponderosa pine of 150+ years of age. Basal areas of the stands at the time of establishment ranged from 11.5 to 16.0 m² ha⁻¹ with only sparse, scattered regeneration. Mountain pine beetle (*Dentroctonus ponderosae* Hopk.) is a recurring threat to the stands in the study area. Only a few trees with light dwarf mistletoe (*Arceuthobium spp.*) infection were present in the original forest. Annual precipitation averages 40 cm. The relatively permeable soils originated from gravely alluvium and outwash of Pikes Peak granite (Marcus 1973) and are classified in the Boyette-French Complex of loamy mixed Eutroboralfs, or Aridic Haploborolls (Moore 1992). The understory vegetation is typical of the central ponderosa pine-bunchgrass type. Grasses,

a variety of forbs, and low shrubs, including Arizona fescue, mountain muhly, blue grama, Parry oatgrass, sedges, geranium, pussytoes, fringed sagebrush, and bearberry, are the primary components of the understory (Currie 1975).

Design

Three identically designed experiments were conducted simultaneously on the same areas, but were analyzed separately. The design of each experiment was a split plot with replications in randomized blocks. The whole plots were the seedtree and shelterwood overstory treatments. Subplots under overstory treatments were site preparation treatments of scarification and nonscarification with removal of logging slash. The shelterwood cut in 1981 left 50 mature seedbearing trees per hectare and the seedtree cut left 12 trees per hectare. The site preparation treatments were each applied to one-half of the area of each overstory plot. One-half of each site preparation treatment area was then used to study natural regeneration to meet objectives 1 (seed production) and 2 (natural seedling establishment and growth), and the other one-half was used for planting ponderosa pine seedlings to meet objective 3 (survival and height growth of planted seedlings).

Study Layout

Seven blocks of two plot units each were established. Each plot unit was 91 m on a side to allow for a 14-m-wide buffer zone around the 4-ha plot (63.6 m on a side). Block boundaries and plot boundaries were surveyed using a transit. Block and plot corners were permanently marked with tagged orange metal fence posts. Figure 1 shows a typical block and plot layout.

The seedtree and shelterwood overstory treatments were assigned to plot units within each block at random. Leave trees were selected to be as free of dwarf mistletoe as possible, be full-crowned, and have a history of cone production as shown by cones on the ground. Leave trees were distributed as uniformly as possible over the plot units. Numbered metal tags were nailed to leave trees and dbh was measured (to the nearest 0.25 cm), as was total height and height to base of live crown, and crown widths (to the

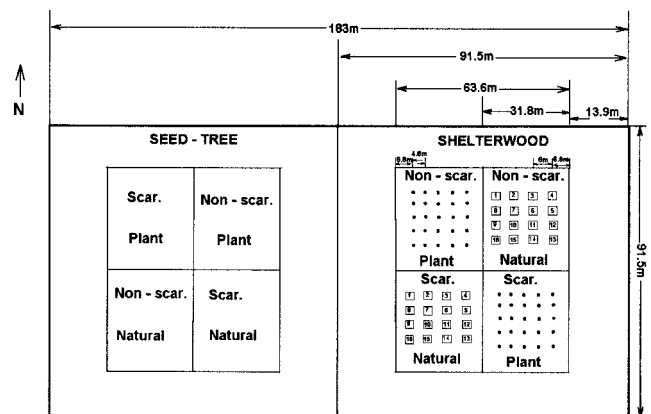


Figure 1. Typical block arrangement showing overstory and site preparation treatments with 4 m² natural regeneration subplots (numbered squares) and planted tree locations (dots).

nearest 0.5 m) were recorded for each leave tree. All livestock were excluded from the pasture containing the study units.

Study plots were logged during the 1980 to 1981 winter under contract administered by the Pikes Peak Ranger District, Pike, and San Isabel National Forest. All unmarked trees were cut and randomly skidded to designated landings with the butt ends raised to avoid excessive disturbance to unscarified plots. Logging slash was lopped and scattered according to standard timber sale contract guidelines. As soon as logging was completed, slash was removed from the subplots to be scarified, and the subplots were rototilled using a small rubber-tired tractor that could maneuver between subplots. All understory vegetation was completely removed from the scarified plots by the tilling treatment.

After tilling, 16 regeneration plots (4 m^2) and 25 seedling planting locations were staked with painted surveyor's stakes on each overstory treatment plot. Figure 1 shows details of the layout of regeneration plots and planting locations. Ponderosa pine 2-0 planting stock from the local seed zone (obtained from Pikes Peak Ranger District) was planted within 1 foot of the stakes and a numbered tag was assigned to each seedling. Planting holes were dug using a chainsaw-powered auger and they were backfilled by hand. The height of each seedling (measured from ground surface to terminal bud tip to the nearest centimeter) was recorded.

In the spring after logging and site preparation, two 25.4×25.4 -cm square wire mesh seed traps were positioned next to each 4-m^2 regeneration plot. One of the two seed traps was covered with a hardware cloth lid and the other was left uncovered to allow seed predation by birds and animals. The bottoms of the seed traps were constructed of aluminum window screen. Lids were made of 8.4-mm mesh hardware cloth. Traps were installed in a shallow pit so the top of the trap was flush with the ground surface. Two wire pins were driven into the ground to secure the trap and anchor the top. Livestock was excluded from all sites for the duration of the study.

Data Collection

At the end of each growing season (the last week in September and first week in October), the 4-m^2 natural regeneration plots were examined, and the number of live seedlings that were present was recorded. Each live seedling was labeled with a plastic tag giving the year of germination. Yearly survival checks of planted seedlings were also made. Periodic height (groundline to terminal bud tip) measurements were obtained for each live seedling and were recorded to the nearest centimeter.

Seed traps were emptied each year after seedfall was completed. The contents of each seed trap were placed in a small paper bag, air-dried if necessary, and stored in a freezer until the seeds could be counted. After seed counts were completed, seed was separated by block and overstory treatment, soaked in water for 1 to 2 days, stratified in plastic bags held at 2°C for 40 days, and then germinated on moist blotting paper using 8 h of light at 30°C and 16 h of dark at 20°C for 21 days (Krugman and Jenkinson 1974).

Continuous weather records for this study were obtained from the Manitou Experimental Forest weather station, located approximately 5 km from the study site.

Data Analysis

Seedfall and germination capacity were compared under seedtree and shelterwood treatments by block and year using analysis of variance techniques. Analysis of variance was also used to compare seedling establishment, survival, and height growth on scarified and unscarified seedbeds under seedtree and shelterwood overstories by block and year. Survival and height growth data of natural seedlings were also combined in chronological sequences by seedling ages and regression techniques used to construct growth and survival models under the various treatment combinations.

Results

Seedfall

The 21 years of seedfall collection in this study have revealed several trends. Total seedfall per hectare has varied considerably from year to year. Seedfall has exceeded 500,000 seeds ha^{-1} in only 4 years: 1983, 1986, 1990, and 1994 in the shelterwood overstory treatment (Figure 2). Intervening years have shown a pattern of decreased seedfall for several years after a good seed year. Less than 100,000 seeds ha^{-1} were produced in 12 of the 21 years of record. Seed production in a year before a good year was usually quite low. The periodicity of good seed crops was quite consistent from 1981 to 1994, but no good seed years have occurred since. Note that seed production data presented here is from thinned stands and therefore considerably less than what would be expected in fully stocked ponderosa pine forests in the Colorado Front Range. However, year-to-year variation in seed production is probably valid over a wide range of forest densities.

Shelterwood overstory treatments consistently produced more seed than seedtree treatments (Figure 2) because of the greater number of trees left after harvest. Although these seedfall trends were consistent across all blocks, plotting seedfall averaged overall years of this study against the

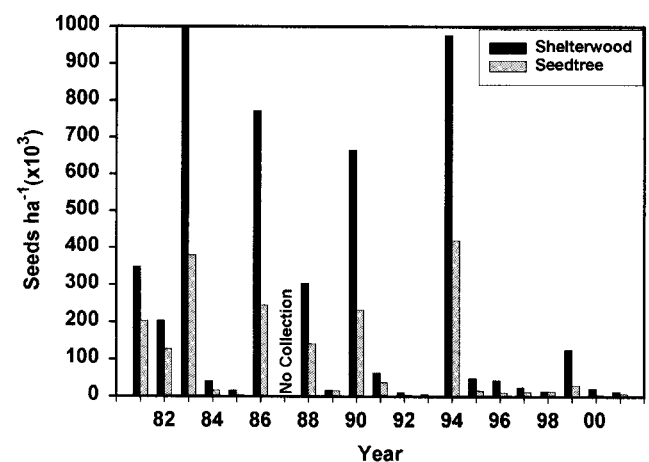


Figure 2. Annual seed production per hectare under shelterwood and seedtree overstories.

basal area in the seven shelterwood and seven seedtree blocks (Figure 3) revealed considerable variation of both variables among blocks within the two overstory treatments. However, Block 5 in the seedtree treatment and Blocks 3 and 5 in the shelterwood treatments exhibited inordinately high seed production for their basal areas (Figure 3). We investigated this phenomenon by comparing individual seed trap counts with overstory tree maps, and we found that the high seed counts were a result of inordinate seed production from individual “super trees” in these respective blocks.

Seed viability also varied from year to year. Yearly germination tests of seed collected from covered traps revealed that very few seed are viable in years that have produced less than 200,000 seed ha^{-1} (Figure 4). Seed viability in years producing more than 200,000 seed ha^{-1} ranged from 27% to 51%, (mean, 42%) with no apparent relationship between viability and seed production.

A consistent pattern of seed consumption by small mammals and birds is revealed by a plot of the number of seeds collected from covered traps against the difference in number of seed that was collected from uncovered traps (Figure 5). A linear equation fit to a zero intercept for this data has a slope of 0.48 ($R^2 = 0.92$), indicating that on average about 48% of the total seedfall was consumed by animals, regardless of the total seed production in a given year. However, this relationship does not account for the ability of animals to differentially select viable seed. To estimate that effect, we compared the germinative capacity of seed collected from uncovered traps with that collected from covered traps and found that uncovered traps consistently contained a lower percentage of viable seed (Figure 6). A linear equation fit to a zero intercept for this data ($R^2 = 0.82$) indicates that seed in uncovered traps had only 66% of the germinative capacity of that in covered traps, clear evidence that predatory animals can distinguish viable from nonviable seed. The cumulative effect of seed viability and predation by seed-eating animals can be summarized as follows: Of every 100 seeds produced in good seed years ($>200,000$

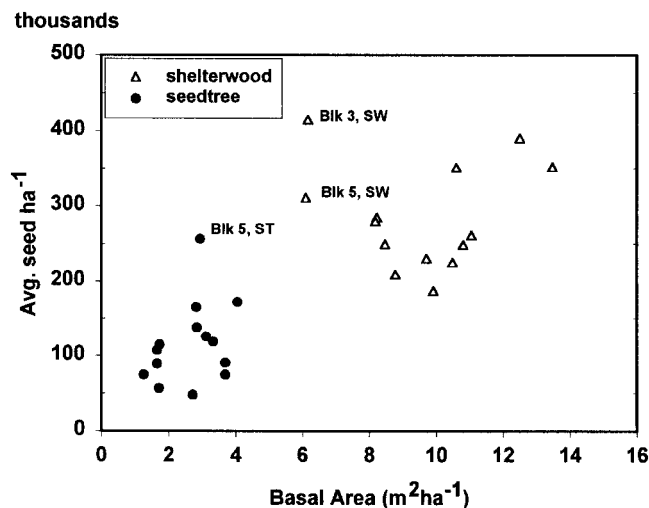


Figure 3. Mean seedfall per hectare as a function of basal area within the seven shelterwood and seedtree overstory blocks.

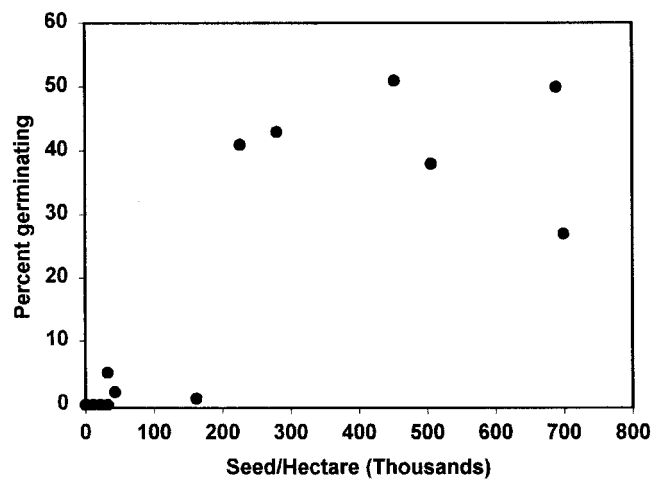


Figure 4. Germination capacity of seed collected from covered traps ($n = 16$ years).

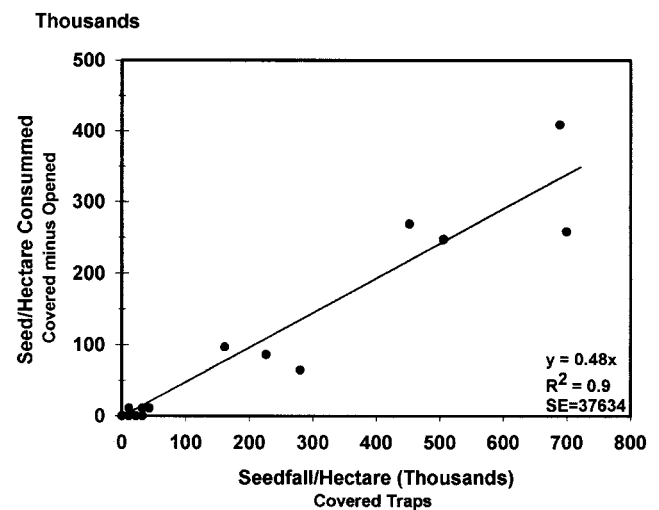


Figure 5. Linear regression of total seedfall against seed consumed by birds and animals. About 48% of seedfall was consumed by animals, regardless of the total seed production.

seed ha^{-1}), only 40 were viable. Animals consumed 48% of these, leaving 21 seeds. Because animals could distinguish viable from nonviable seed without eating them, only 66%, or 14, of these seeds remained capable of germinating. Therefore, only 14% of the average total seedfall remained available to germinate after accounting for all of these factors.

Seedling Germination and Establishment

In spite of the clear differences in seedfall between seedtree and shelterwood overstories, natural seedling establishment was more complicated. Overall, more seedlings germinated under shelterwood overstories than under seedtree overstories, regardless of seedbed treatment (Table 1). However, this effect was primarily a result of differences that occurred in 1982 and 1995, years that had the highest numbers of seedlings germinating. Significantly more seedlings germinated on unscarified seedbeds in 1982 than on scarified seedbeds, and significantly more seedlings germinated on the shelterwood/scarified treatment combination in

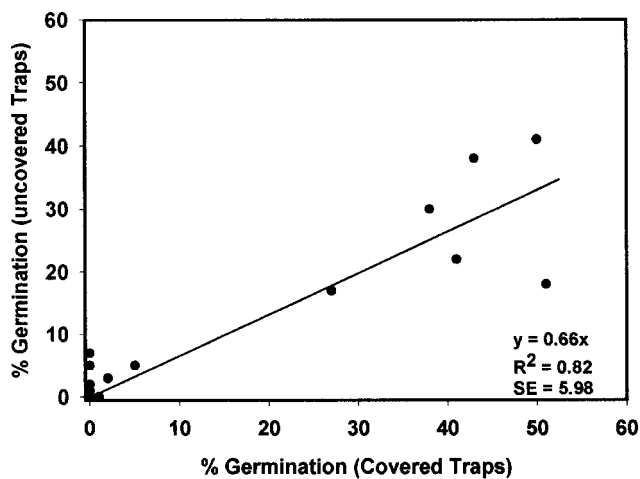


Figure 6. Seeds collected from uncovered traps had 66% of the germinative capacity of those in covered traps, indicating that predatory animals can distinguish viable seeds.

1995. Otherwise, seedbed treatment had no apparent effect on germination.

Survival of naturally germinating pine seedlings in this study followed a consistent pattern, regardless of the year of germination. Only a small portion of naturally germinating seedlings survived for more than a few years, with most mortality occurred during the first 2 years after germination (Figure 7). Overstory and site preparation treatments strongly influenced survival of seedlings that originated in 1982, 1989, and 1995, but not other years. Generally, more seedlings survived under shelterwood overstories and on scarified seedbeds for the above 3 years (Table 1). These data suggest that denser overstories and scarified seedbeds help promote seedling survival in years with abundant seed germination. However, confounding effects of the treatments from year to year negated the overall effects of overstory and site preparation treatments on natural seedling survival in this study (Table 1).

Planted seedlings survived much better than naturals (Figure 8). Overall, 62% of the seedlings planted in 1982

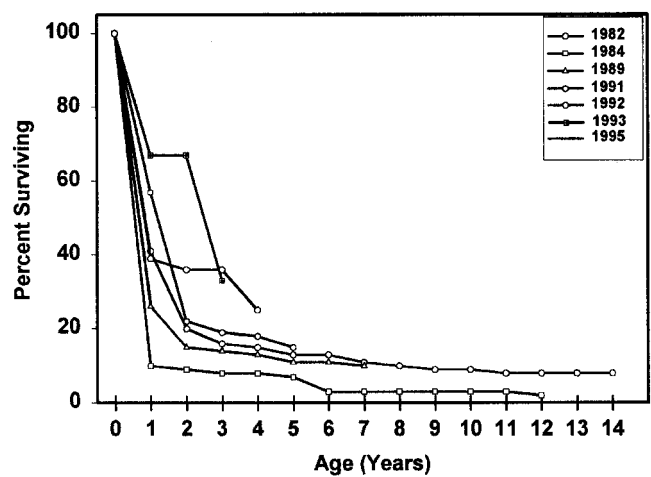


Figure 7. Percentage of germinated natural seedlings surviving to a given age.

are still alive, compared with 8% of the natural seedlings that germinated in 1982. There were no significant differences in survival of planted trees among overstory and scarification treatments.

Growth Rates

Planted trees grew much better than naturally germinating seedlings, regardless of the overstory or scarification treatments. In 1998, (the last year that all seedlings were measured), the average height of planted trees ranged from 1.2 m in shelterwood/unscarified treatments to 1.8 m in seedtree treatments (Figure 9). Natural seedling heights in 1998 ranged from 0.1 m in seedtree/unscarified treatments to 0.9 m in seedtree/scarified treatments (inspection of Figure 9).

Height growth rates for all natural seedlings in this study are shown in Figure 10. An exponential growth model fit to this data and projected to a height of 1.4 m (breast height) indicates that about 22 years are needed for a typical seedling to reach this height. To determine whether this projection is reasonable, we excavated 52 open-grown ponderosa

Table 1. Mean germination and seedling survivals per hectare ($\bar{X} \pm \text{SE}$) recorded in the year 2002 by Over-Story and site preparation treatments located at the Manitou Experimental Forest. Dissimilar superscripts within Over-Story and site preparation treatments are significantly different at $\alpha = 0.05$.

		Germination													
OVSTY	SPREP	1982		1984		1989		1991		1992		1995		Overall	
Trts	Trts	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Shelterwood	Unscarified	11,357.6 ^a	1,275.4	3,749.1 ^a	982.2	2,425.9 ^{ab}	530.7	2,315.6 ^{ab}	513.1	352.9 ^a	98.4	7,454.1 ^b	1,159.2	4,609.2 ^c	379.8
	Scarified	3,418.3 ^{bc}	462.8	2,249.5 ^{ab}	266.9	3,837.3 ^a	718.4	3,308.0 ^a	472.6	286.7 ^a	111.8	19,605.6 ^a	3,768.5	5,450.9 ^c	694.2
Seedtree	Unscarified	5,248.8 ^b	622.0	1,279.1 ^b	290.5	1,455.5 ^b	272.3	1,543.7 ^b	311.9	264.6 ^a	79.0	2,492.1 ^b	565.2	2,047.3 ^{ab}	174.3
	Scarified	1,587.9 ^c	263.7	705.7 ^b	127.0	1,212.9 ^b	271.3	2,095.1 ^{ab}	420.6	242.6 ^a	121.2	4,653.3 ^b	764.7	1,749.6 ^a	170.0
		Survival													
OVSTY	SPREP	1982		1984		1989		1991		1992		1995		Overall	
Treatments	Treatments	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Shelterwood	Unscarified	441.1 ^{ab}	109.5	44.1 ^a	31.0	198.5 ^{ab}	77.6	330.8 ^{ab}	115.1	66.2 ^a	37.9	816.0 ^{ab}	286.1	296.1 ^{bc}	52.1
	Scarified	595.4 ^a	141.0	0.0 ^a	0.0	419.0 ^a	120.9	573.4 ^a	162.7	66.2 ^a	37.9	1,587.9 ^a	378.4	636.4 ^c	122.0
Seedtree	Unscarified	22.1 ^c	22.1	22.1 ^a	22.1	44.1 ^b	31.0	88.2 ^b	53.6	44.1 ^a	31.0	88.2 ^b	43.5	47.3 ^a	12.9
	Scarified	176.4 ^{bc}	68.0	22.1 ^a	22.1	66.2 ^b	49.1	242.6 ^{ab}	103.7	66.2 ^a	49.1	352.9 ^b	139.6	151.2 ^b	29.1

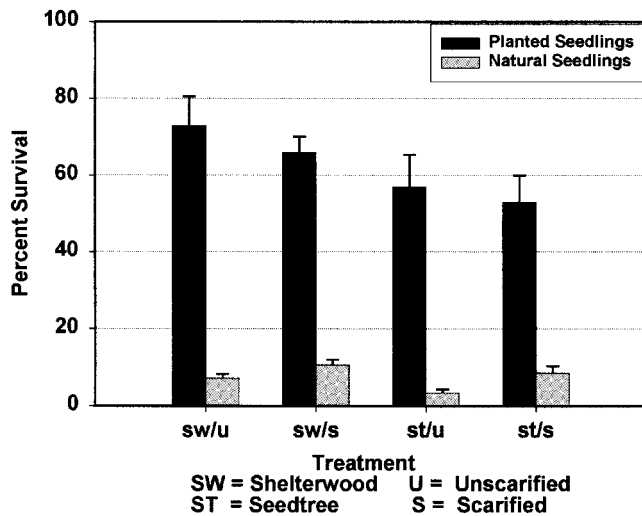


Figure 8. Natural and planted seedling survival (recorded in 2002) with SE bars.

pine saplings from nearby areas, split them at the groundline to expose the root collar, and then aged them at 10, 30, 50, and 137 cm above that point. Figure 11 shows the ages of each open-grown tree at those heights, along with the average age at each height and the observed seedling height growth model from Figure 10. The growth rate of open-grown seedlings is generally faster than that of seedlings that established under seedtree and shelterwood overstories. However, it seems reasonable to conclude that about 20 to 25 years are needed for naturally establishing ponderosa pine to grow to breast height in this ecosystem.

Growth Environment

Average hourly temperature records obtained on-site during the 1999 growing season are summarized in Figure 12. The apparent differences in temperatures among overstory and seedbed treatments may explain some of the variation in growth and survival that have been observed in this study. Daytime air temperatures measured at 1.4 m above the ground appeared considerably cooler than surface temperatures under any treatment combination. Peak daytime surface temperatures reached 36° C on scarified seedbeds under the open seedtree overstory. Average peak surface temperatures under the seedtree/unscarified treatment appeared cooler, averaging about 34° C. Peak surface temperatures under the shelterwood overstory appeared still cooler, averaging 27° C to 29° C on scarified and unscarified seedbeds respectively. Note that dips in average daily temperature curves occurred when tree crowns shaded sensors.

Precipitation, measured at Manitou Experimental Forest Headquarters approximately 5 km from the study site at the same elevation, has been quite variable over the past 60 years, but has averaged about 40 cm year⁻¹ (Figure 13). Overlaying 5-year natural seedling survival data on the precipitation graph reveals that all but one of the successful surviving seedling cohorts in this study established during periods of above average precipitation (Figure 13). The

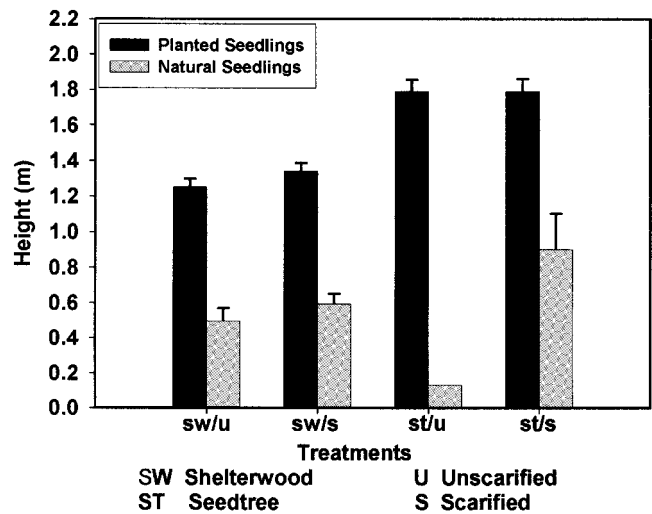


Figure 9. Average heights of natural and planted seedlings under shelterwood and seedtree overstories (measured in 1998) with SE bars.

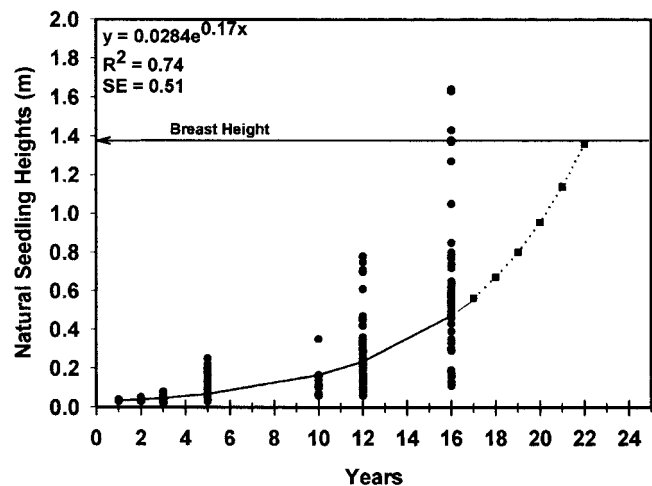


Figure 10. Measured heights of natural seedlings (age 1–16 years) with fitted model projecting years needed to reach dbh.

recent severe drought may be responsible for the poor survival of 1995 seedlings.

Discussion

This study has provided a unique opportunity to observe the long-term pattern of ponderosa pine seed production, as well as to follow the establishment, growth, and survival of natural and planted ponderosa pine seedlings in the harsh environment of the Colorado Front Range.

Seed Production

Ponderosa pine seed production in the Colorado Front Range is quite variable. Good seed crops are produced only every 4 to 6 years, with almost no viable seed produced in intervening years. Seed viability is nominally less than one-half of the total seed production. Predation by small mammals further reduces the seed available for germination to the point that only 14% of total seed production is available to germinate in good seed crop years. No seedlings

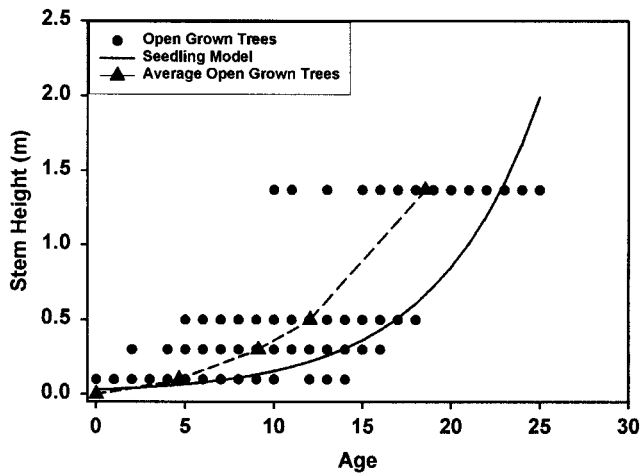


Figure 11. Observed ages at four stem heights for open-grown of ponderosa pines collected on the Manitou Experiment Forest with average ages at each height. The natural seedling height growth model from Figure 10 is included for comparison.

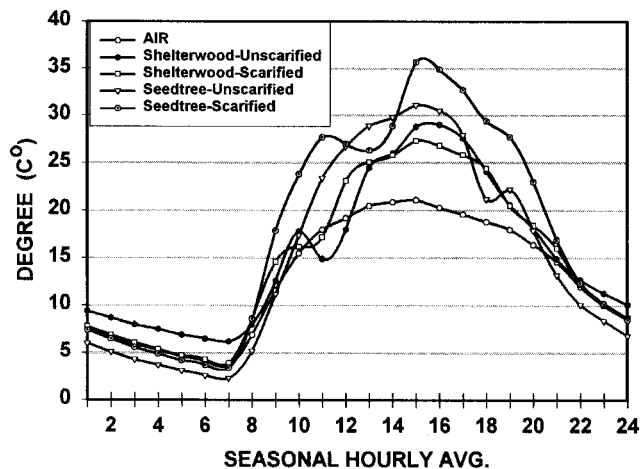


Figure 12. Surface temperatures of scarified and unscarified seedbed treatments under shelterwood and seedtree overstories.

can be expected to establish in the intervening years between good seed crops. Denser overstories generally produce more seed than sparse overstories.

Seedling Establishment and Growth

Planted trees grew taller under seedtree overstories than under shelterwood overstories (Figure 9). This indicates that the higher light environment of the open seedtree overstories favored the height growth of those planted ponderosa pine seedlings. The tallest natural seedlings also occurred under seedtree overstories, but only on scarified seedbeds. Unscarified/seedtree treatments contained the shortest natural seedlings, indicating that scarification is an important factor in the successful establishment of natural seedlings.

Based on observed height growth rates, it appears that natural seedlings have lagged 10 to 15 years behind planted seedlings. Data from excavated natural saplings suggests that much of this lag was due to slow height growth early in the life of the seedlings. Once natural seedlings reach 20 to 30 cm in height, their height growth rates improve dramat-

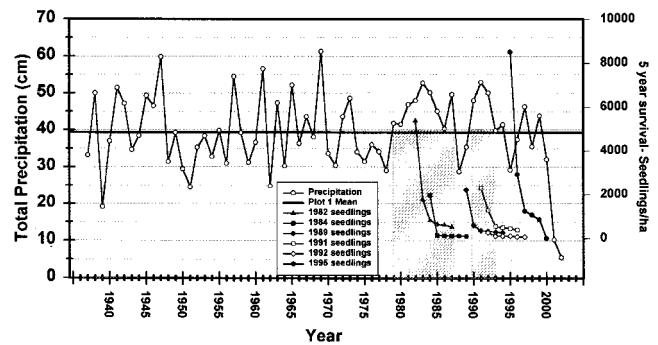


Figure 13. Total yearly precipitation and 5-year natural seedling survival. The shaded area indicates periods of above-average precipitation during this study.

ically. About 20 to 25 years are needed for naturally establishing ponderosa pine to grow to breast height in this ecosystem.

Further investigation of the scarification phenomenon is needed. Although the microplots in this study were scarified only once in 1982, the effects of that scarification have persisted through the years. In 1995, significantly greater numbers of seedlings germinated on scarified seedbeds than on unscarified seedbeds, indicating that the 1982 scarification treatment still influenced establishment of natural seedlings 13 years later.

Recommendations

Shelterwood overstories containing between 6 and 14 m² ha⁻¹ stem basal area over scarified seedbeds provide optimal conditions for natural seedling establishment and growth in the Colorado Front Range. However, fickle climatic conditions and the intermittent occurrence of good seed crops may require many years to establish a fully stocked forest of natural seedlings. Exceptions would be the occurrence of "super trees" in the overstory that produce disproportionate numbers of viable seed. Several such trees in this study clearly contributed to the successful establishment of numerous nearby seedlings. Identifying such trees and planning for their use as seed sources would be a priority when using natural regeneration silviculture.

Planting seedlings appears to be a much more reliable method of quickly re-establishing new ponderosa pine forests in the Front Range. Although initial costs are high, survival and growth of planted seedlings in this study was much better than that of natural seedlings. Planted seedlings survived best on scarified seedbeds under shelterwood overstories, but height growth was best under seedtree overstories. This implies that optimal conditions for survival and growth of planted seedlings might be under intermediate overstories containing basal areas of 5 to 6 m² ha⁻¹ (the most open of our shelterwood blocks). These conditions would provide sufficient protection for survival, yet allow adequate light for optimal growth.

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