

Naturally Seeded versus Planted Ponderosa Pine Seedlings in Group-Selection Openings

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ABSTRACT

The purpose of this article was to determine whether natural regeneration or planted seedlings should be used in group-selection openings. The answer depends on the survival and growth rate of both types of seedlings, and that could depend on the size of the openings and the effect of trees on their edge. In this side-by-side study, the natural pine seedlings originated from the 1988 seed crop and the 1–0 nursery-grown seedlings were outplanted in spring 1989. Openings ranged from 0.01 to 0.65 ha. The plant community consisted of many species of shrubs, forbs, and grasses with manzanita having the highest density and greatest development. After 9 years, manzanita had an average density of 13,870 plants/ha, 2,050 m²/ha of foliar cover, and was 125 cm tall. From 1990 to 1997, planted ponderosa pine seedlings were taller ($P < 0.05$) than natural seedlings, and from 1995 to 1997, mean stem diameter at 30 cm of planted seedlings was larger than natural counterparts ($P < 0.05$). Development for 1 year in the nursery apparently gave the planted seedlings a growth advantage over the natural seedlings. For natural seedlings, distance from opening edge had little effect on pine height or diameter growth regardless of opening size. Planted seedlings, however, appeared to increase in height and diameter growth with both opening size and distance from edge.

Keywords: ponderosa pine, natural and planted seedlings, group selection, distance from edge, north central California

Sustaining ecosystems and not chronically disrupting ecosystem processes are the key features of modern forestry. The group-selection regeneration cutting method has some of these attributes. Indeed, Smith et al. (1997) noted that for this method “it becomes possible to accommodate the ecological requirements of almost any tree species.” The group-selection method gives the appearance of continuous forest cover because the small openings created by timber harvest mimic natural disturbance caused by small high-intensity fires within a matrix of low-intensity surface fires (Fiske et al. 1992). In the northern California mountains, Weatherspoon and Skinner (1996) noted that group-selection silviculture promotes the process of maintaining a mostly ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*) forest having many ages. In the mixed-conifer forests of the Sierra Nevada in California, group-selection management also created species richness values that had a high proportion of late seral species and a low proportion of introduced exotic species when compared with even-aged or shelterwood regimes (Shlisky et al. 1999). Results from a large growth-model study in California suggested that uneven-aged management could match the productivity of even-aged systems (Liang et al. 2005). Slocum (1979) noted that owners of large or small amounts of land should consider group selection if looking for a sound investment that requires low capital expenditure, offers a periodic income and a respectable return, and benefits recreation and wildlife habitat.

Planted ponderosa pine seedlings are known for their ability to establish and grow well on a wide variety of sites, especially in environments that have full sunlight and are subject to drought (Laacke and Fiske 1983). But how well will they develop in small openings, typical of group-selection cutting, that have less than full sunlight and with competition from roots of surrounding trees? Will they

grow faster than natural seedlings having an equal number of growing seasons in the field in this environment? The answer could partly depend on the early vigor of the seedlings, their adaptation to the environment, and how they interact with other species in the plant community. The answer, along with costs, also could help silviculturists decide, when dealing with small openings, whether to depend on natural regeneration or to plant.

In California, ponderosa pine seedlings typically direct most of their early energy toward developing a taproot (US Forest Service 1965) that often penetrates 75 cm or more into the soil the first growing season and gives access to a zone of adequate soil moisture. Natural seedlings in group-selection openings are likely to develop this taproot. Planted ponderosa pine seedlings, however, have at least one-third of their taproot removed when lifted from the nursery bed. They tend to develop a more fibrous root system than their natural counterparts.

In addition to the more shady environment in group-selection openings, another factor that differs somewhat from that in plantations in full sunlight is the plant community. In a clearcutting, for example, the first seed crop generally stocks the land and successive crops contribute few seedlings because most favorable microsites are already occupied. In group-selection openings and specifically in this study, several ponderosa pine seed crops occurred and seedlings become established each year. In group-selection openings, more plants in most categories of vegetation originate from root crowns or dormant seeds in the soil and fewer plants originate from wind-blown seeds. Consequently, fewer ephemeral forbs are present in group-selection openings than in larger disturbed areas. With time, the proportion of annual forbs in the openings decreases and that of perennial forbs increases (McDonald and Reynolds 1999).

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Published literature on the development of natural and planted ponderosa pine seedlings having the same date of origin is scant for the group-selection cutting method in the Western United States. On the University of California's Blodgett Forest Research Station in central California, Heald (R.C. Heald, Blodgett Experimental Forest, pers. comm., May 1999) compared the growth of natural and planted ponderosa pine seedlings on prepared ground in a range of openings similar to those in this study. The 1st year of growth for natural seedlings corresponded to the 1st year of growth for out-planted seedlings, which had spent the prior year in a nursery bed. At age 9 years, the height of natural and planted seedlings did not differ statistically ($P > 0.05$).

Literature on the effect of edge vegetation within group-selection openings in the Western United States also is scant. In a preliminary report on this study, McDonald et al. (1997) reported results from various categories of vegetation in two broad zones, measured in 1992. These were near the forest edge and near the opening center. In general, mean density of natural pine seedlings, manzanita (*Arctostaphylos* spp.), and forbs was higher near the edge, and that of other shrubs, ferns, and graminoids was higher near the center. Mean height of all categories of vegetation except manzanita was highest near the plot center.

On the Blodgett Forest Research Station in north central California, York et al. (2003) quantified the mean height of six planted conifer species and found after 3 years that a 10-fold increase in the area of the opening corresponded to a 34% increase in mean height of all six species combined. Seedlings also were taller near the centers of openings and shorter near the edges with height being correlated to light and water supply.

The objectives of this study were to document the plant community in the group-selection openings, to quantify the development of naturally seeded and planted ponderosa pine seedlings in a range of opening sizes typical of the group-selection cutting method, and to determine the effect of opening size and distance from edge on seedling growth.

Methods

The study site is located in the Boggs Mountain State Forest, about 24 km southeast of Lakeport, in north central California. Before harvest in 1987, the forest was comprised of mostly young-growth (40 and 85 years old) ponderosa pine, scattered sugar pine (*Pinus lambertiana* Dougl.), and coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) with occasional hardwoods such as canyon live oak (*Quercus chrysolepis* Liebm.) and California black oak (*Q. kelloggii* Newb.). In terms of ecological subregions of California, the area corresponds to section M 261Be and the Konocti Flows subsection (US Forest Service 1997). The Society of American Foresters forest cover type is Pacific ponderosa pine (McDonald 1980) and stand basal area averaged about 40 m²/ha. A few shrubs of the genera *Arctostaphylos* and *Rhamnus* were scattered in more open places along with a few forbs, grasses, and ferns.

The climate of the study site is typically Mediterranean with long, hot, dry summers and cool, wet winters (Major 1977). The growing season occurs from April to mid-June or as long as soil moisture is available. Site quality of the study area is above average (20 m in 50 years; Dunning and Reineke 1933); annual precipitation is 1,803 mm, mostly as rain; the elevation is 1,083 m; aspect ranges from northwest to southwest; and slopes range from 4 to 23° (Table 1). The soil is of the Aiken series (Xeric Haplohumult),

Table 1. Characteristics of group-selection openings, Boggs Mountain State Forest, 1997.

Opening size (ha)	Slope (°)	Aspect (°)
0.01	9	220
0.08	5	232
0.20	12	199
0.22	14	235
0.22	16	311
0.28	21	250
0.29	7	275
0.32	23	205
0.65	4	242

which grades in texture from loam to clay-loam with depth and is deep, moderately well drained, and quite fertile.

The number and size of openings in this study were created by removing clumps of even-aged trees. Nine different-sized, approximately circular openings in the range of 0.01–0.65 ha constituted the study sites. Openings were devoid of trees and spanned the operational range of sizes used in group selection in this forest type. They were randomly located on land that could be logged by a tractor and were 0.4–1.6 km apart. In June 1988, the logging slash was piled in nearby skid roads with a brushrake-equipped bulldozer and burned in the fall.

Ponderosa pine seedlings from a local seed source were grown for 1 year in a nursery bed and then planted with a bar in February 1989 at a 4.6-m spacing. Their growth was compared with ponderosa pine seedlings from the 1988 seed crop. Thus, both natural and planted seedlings were in place in the study plots in spring 1989. Deer (*Odocoileus* spp.) and dwarf mistletoe (*Arceuthobium* spp.) were possible threats to the pines. Seedlings in both types (natural and planted) were considered as established (having a good chance of survival) after one growing season.

Within each opening, 15 seedlings of each type were randomly chosen in summer 1989, permanently tagged, evaluated for damage, and measured each year. Thus, the pine sample consisted of 270 seedlings (135 natural and 135 planted). Chosen seedlings were well distributed and no concentration of either type of seedling was located at the edge or in the middle of the plots. A few seedlings that regenerated in 1989 within a 1.5-m radius of tagged seedlings were hand pulled to ensure early development free of intraspecific competition. Pine stem diameter was measured at 30 cm above mean groundline. A slope-correcting laser instrument was used to measure the distance from each seedling to the opening edge. Distance ranged from 1 to 22 m. The edge was defined by the crowns of mature trees around each opening, and no natural or planted seedlings beneath the drip line were sampled.

Although vegetation had been intensively measured on transects since the beginning of the study (McDonald et al. 1997), a special sample was taken in August 1997 after nine growing seasons. The sample was centered around the pine seedlings to better evaluate direct competition to them. Of the 15 tagged seedlings in each type, 9 in each were randomly chosen for measurement of competing vegetation. Each of the 162 seedling-centered plots (81 natural and 81 planted) had a 1.5-m radius and contained about 7.1 m² of area. Vegetation was measured for density, foliar cover (the sum of shadows that would be cast by leaves and stems of the vegetation in each category expressed as a percentage of the land surface; Daubenmire 1968), and average dominant height (average of three tallest stems).

Table 2. Average density, foliar cover, and height of several categories of vegetation, Boggs Mountain State Forest, 1997.

Vegetation category	Density (plants/ha)		Foliar cover (m ² /ha)		Height (cm)	
	Mean	SE	Mean	SE	Mean	SE
Pine wildlings	13,924	166	370	7	63	18
Manzanita	13,870	98	2,050	18	125	8
Other shrubs	918	62	102	17	47	20
Forbs	1,513	41	50	1	20	3
Fern	26,123	410	400	9	37	4
Grasses	3,544	110	18	1	52	14

SE, standard error.

For analyzing ponderosa pine height and diameter growth at age 9 years, many models were tested, and that which gave the best fit incorporated Akaike's Information Criterion (AIC; Bozdogan 1987) into a mixed effects model using both distance from edge and opening size. The model was

$$Y_{ij} = B_0 + B_1 D_{ij} + B_2 I_{p_{ij}} + B_3 D_{ij} \times I_{p_{ij}} + B_4 D_{ij} \times O_j \times I_{p_{ij}} + (b_{0j} + b_{1j} D_{ij}) + e_{ij}$$

in which Y_{ij} = mean annual pine height increment (centimeters per year), or ending diameter (centimeters) for tree i and opening j ; D_{ij} = distance from edge; O_j = $\ln$ (opening size); $I_{p_{ij}}$ = 1 for planted and 0 for natural seedlings; $B_{0,1,2,3,4}$ = fixed effects parameters; b_{0j} , b_{1j} = random effects parameters; $e_{ij} \sim N(0, \sigma^2 D_{ij}^2)$.

Results

The Plant Community

Revegetation from dormant seeds in the soil, from those that blew in on the wind, and from rhizomes was rapid and abundant. Four complete growing seasons after site preparation (1992), the number of species on transect plots was 81 and consisted of 54 forbs, 12 graminoids (including 1 sedge), 8 hardwoods and conifers, 6 shrubs, and 1 fern (*Pteridium aquilinum* [L.] Kuhn var. *pubescens*) (McDonald et al. 1997).

In 1997, hardwoods and conifers other than ponderosa pine were too few to analyze, and no sedges were found in the seedling-centered plots. Thus, data are presented for ponderosa pine seedlings (untagged natural seedlings from the 1988 seedcrop and subsequent crops, hereby designated as "pine wildlings"), manzanita, shrubs other than manzanita, forbs, ferns, and grasses.

Mean density of pine wildlings that had accumulated from 1989 through 1997 was 13,924/ha with only a small amount of cover and little height (Table 2). Manzanita, which consisted of two species (*Arctostaphylos canescens* Eastw. and *A. manzanita* C. Parry), had more foliar cover than all other categories of vegetation combined and almost twice the mean height of vegetation in any other category. Other shrubs and forbs tended to be few and short with little foliar cover. Ferns (fronds) had high density but little foliar cover, and grasses tended to be few and short.

Natural and Planted Ponderosa Pine Seedlings

No sampled natural or planted pine seedlings died during the study and annual damage from deer and dwarf mistletoe was minimal. Diary records indicated that deer browsing took place as early as 30 days after planting. Damage from browsing peaked during the third growing season at 18% (natural, 24%; planted, 12%), decreased to 4% the fourth season, and was negligible through the ninth season. In spite of

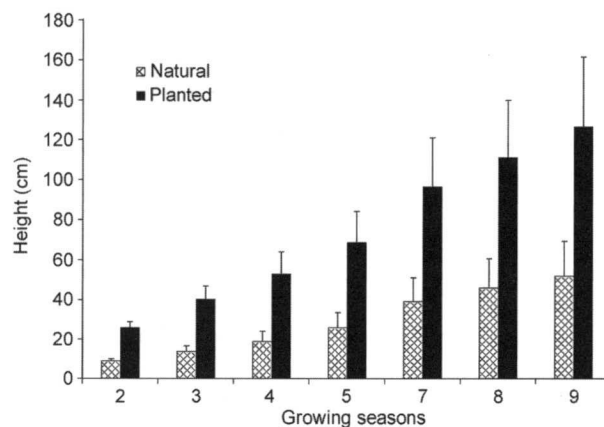


Figure 1. Mean stem height of natural and planted ponderosa pine seedlings in all openings for growing seasons two to nine, Boggs Mountain State Forest. Bars show standard errors.

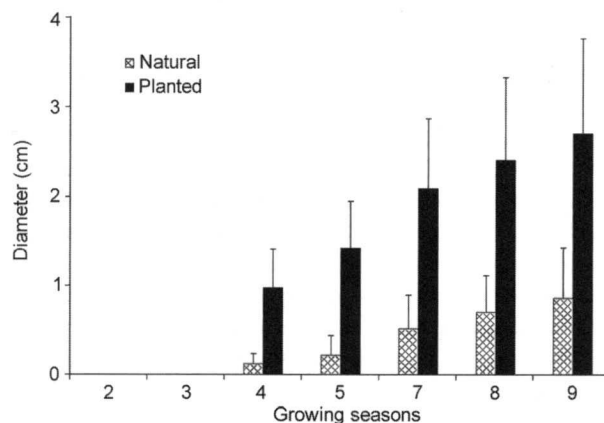


Figure 2. Mean stem diameter at 30 cm for natural and planted ponderosa pine seedlings in all openings for growing seasons two to nine, Boggs Mountain State Forest. Bars show standard errors.

this damage, seedlings recovered quickly and little effect (e.g., forking) could be seen. Dwarf mistletoe infection increased slowly from less than 1% the third season to 7% (natural, 6%; planted, 8%) the ninth season. However, for the length of the study, it likely had a negligible effect on pine seedling growth.

To portray the overall difference between natural and planted pine seedlings, the height and diameter of all seedlings in each type was averaged over all openings. Average height of natural seedlings was consistently less than that of planted counterparts based on t -tests that became statistically meaningful ($P < 0.05$) after the second growing season and continued through the ninth season (Figure 1). After the ninth season, average height of planted seedlings was 2.4 times that of natural seedlings. A few natural seedlings were sufficiently tall to have a measurable diameter (at 30 cm) after the fourth growing season and enough were large enough to statistically analyze after the sixth season. After the seventh season, mean diameter of natural seedlings was smaller ($P < 0.05$) than that of planted seedlings (Figure 2). After the ninth season, the mean diameter of planted seedlings was 2.7 times larger than that of natural seedlings.

Growth Relationships

Many variables can affect the growth of conifer seedlings in group-selection openings. Size of opening, distance from edge, slope, aspect,

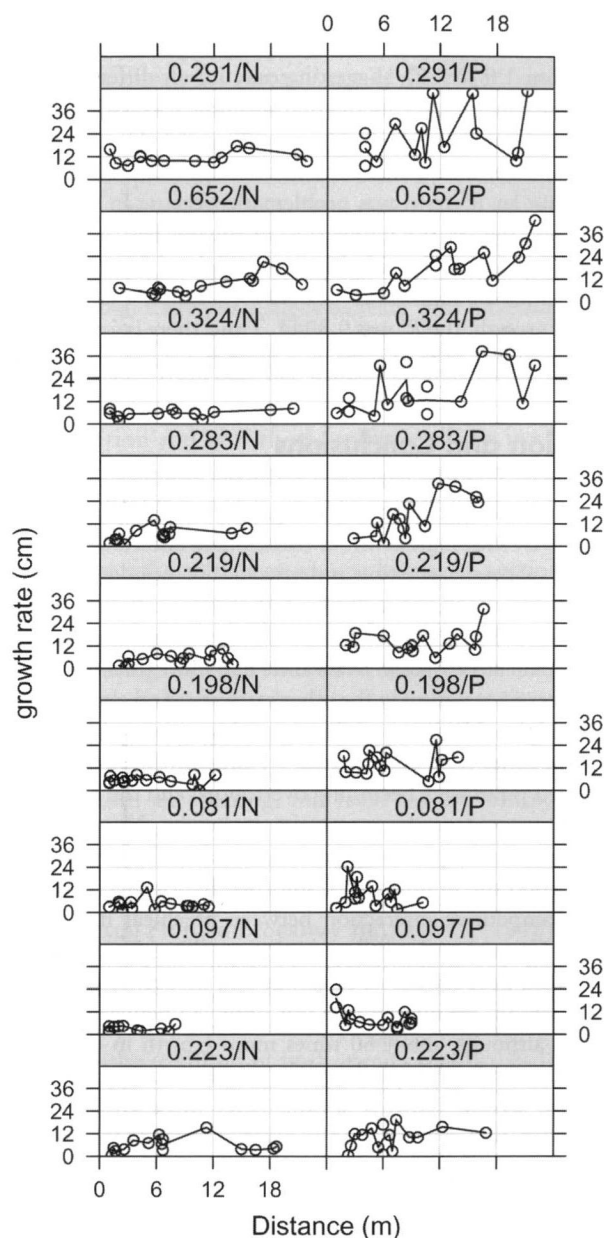


Figure 3. Height growth rate for naturally seeded and planted ponderosa pine seedlings relative to distance from opening edge, displayed by opening size, age 9 years.

sun angle, competition, roots from edge vegetation, height of edge trees, and distance of trees from the outer edge of the opening are some of them. Slope and aspect are particularly important because the amount of shade cast by border trees on a north slope would have a much different effect than the amount of shade cast by trees bordering a south slope. Consequently, we examined slope and aspect in this study and found that AIC decreased by dropping both variables. The lack of applicability of these variables probably was caused by their narrow range and the small number of openings.

To illustrate the relationship of pine seedling development to distance from edge and opening size, we graphed height growth rate and stem diameter at age 9 years of naturally seeded and planted seedlings relative to distance from edge for each opening size and arrayed the opening sizes from small to large (Figures 3 and 4). Estimates for several variables pertaining to both are shown (Table 3).

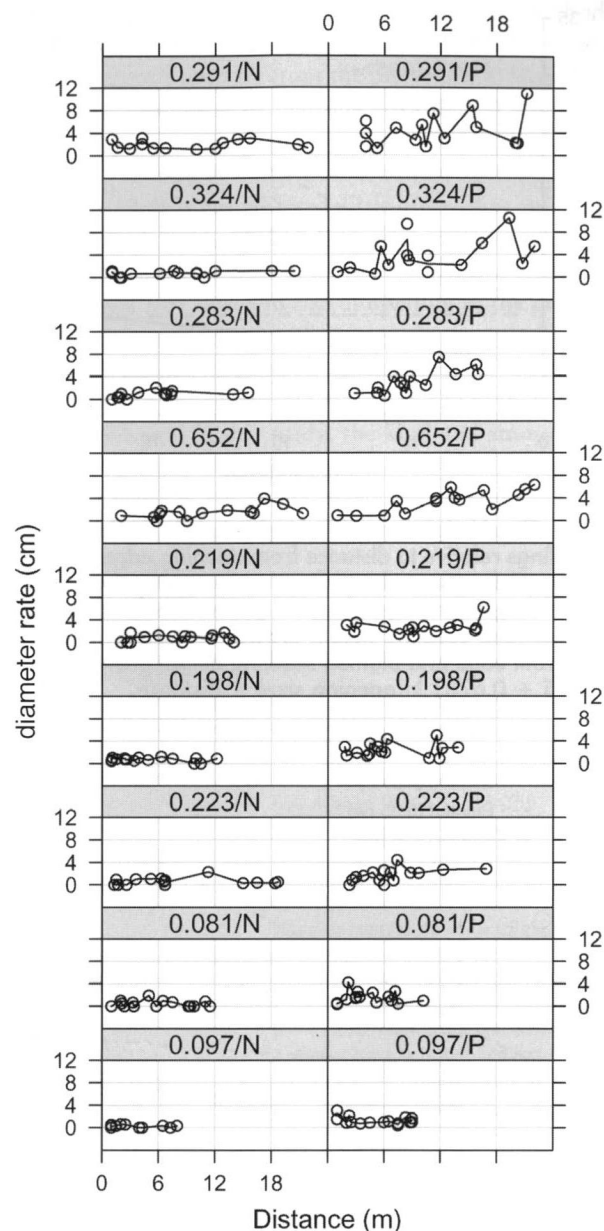


Figure 4. Stem diameter at 30 cm for naturally seeded and planted ponderosa pine seedlings, relative to distance from opening edge, displayed by opening size, age 9 years.

Table 3. Fixed effect estimates (model) for ponderosa pine height growth rate and diameter, age 9, Boggs Mountain State Forest, Lake County, CA.

Variable	Height growth		Diameter	
	Estimate	SE	Estimate	SE
Intercept	4.6503	1.085	0.6255	0.218
D_{ij}	0.2335	0.117	0.0328	0.025
Ip_{ij}	4.2011	1.628	0.7907	0.326
$D_{ij} \times Ip_{ij}$	1.3384	0.262	0.2838	0.058
$D_{ij} \times O_j \times Ip_{ij}$	0.6781	0.168	0.1224	0.036

SE, Standard error.

The mixed effects model indicated large differences in pine seedling height growth rate between naturally seeded and planted seedlings relative to opening size and distance from edge (Figure 5).

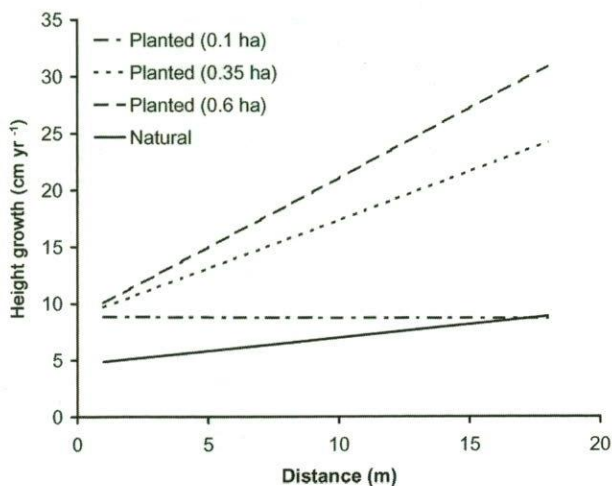


Figure 5. Fitted height growth rate of naturally seeded ponderosa pine seedlings relative to distance from opening edge for all opening sizes and for planted seedlings in representative small, medium, and large openings at age 9 years. The fitted models are naturally seeded seedling height growth = $4.6503 + 0.2335 \times \text{distance from edge}$ and planted seedling height growth = $8.8514 + (1.5715 + 0.6781 \ln \text{opening size}) \times \text{distance}$.

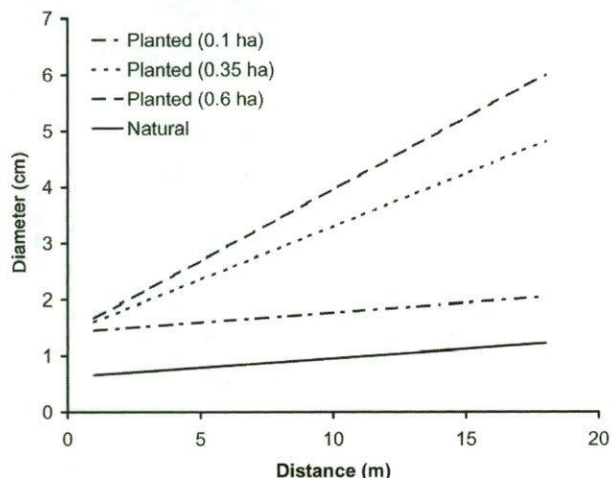


Figure 6. Fitted diameter of naturally seeded ponderosa pine seedlings relative to distance from opening edge for all opening sizes, and for planted seedlings in representative small, medium, and large openings at age 9 years. The fitted models are naturally seeded seedling diameter = $0.6255 + 0.0328 \times \text{distance from edge}$ and planted seedling diameter = $1.4162 + (0.3167 + 0.1224 \ln \text{opening size}) \times \text{distance}$.

Opening size had little effect on natural seedling height growth regardless of distance from opening edge. However, for planted seedlings, the interaction of opening size and distance from edge was important. Seedlings in larger openings had a progressively higher growth rate than seedlings in medium-sized and smaller openings and the effect was stronger as distance from edge increased. The fitted response for pine stem diameter almost mirrored that of height growth (Figure 6). This suggests that both pine stem height and diameter are responding in a similar manner to location within the opening as well as to the size of opening.

We did not include a *P* value in our results because it is inconsistent with use of AIC for model selection. Among the diameter

models considered, AIC ranged from 877.1 to 888.1. Several models with one less parameter were slightly higher (change in AIC ranged from 1.0 to 2.2), suggesting only minor differences among them. Consequently, the model that we chose had both the smallest AIC and was similar to the height growth model. The variance term for the diameter model was 0.5682.

Deriving an R^2 term was problematic because in the weighted mixed effect model, the model sum of squares has more than one potential definition. Considering an unweighted fixed effect contribution yielded an adjusted R^2 of 0.4241. Using the same approach for height growth, the R^2 was 0.3944. Thus, there is a slightly better fit for diameter than for height, but the difference is negligible.

Discussion and Conclusions

The small openings characteristic of the group-selection cutting method are considered to be advantageous for colonization by many species, often with high densities (McDonald and Abbott 1994). In this study, natural vegetation and, specifically, ponderosa pine, two species of manzanita, other shrubs, forbs, grasses, and a fern, totaled 59,892 plants/ha, 2,990 m²/ha of foliar cover, and ranged from 20 to 125 cm tall after 9 years. Manzanita had more than five times the foliar cover of vegetation in the other categories and almost twice the average height. After two or three growing seasons, its height and that of the pines were about equal. By the fourth season, the naturally seeded pines were becoming overtopped and the planted pines were about equal to the manzanita in height. Not until several seasons later did the planted pines become taller than the manzanita.

On a good site in northern California, Radosevich (1984) studied the competitive interaction between greenleaf manzanita (*A. patula* E. Greene) and ponderosa pine seedlings in an experiment with varying proportions of seedlings and shrubs. During the first growing season, no interference was observed between shrubs and seedlings, although about 60 times more growth in biomass took place on the shrubs than on the pines. Interference apparently began during the second growing season. After three growing seasons, shrub growth was still about 35 times that of pine seedling growth. Pine growth had decreased on all plots where manzanita was present. After three seasons, manzanita was beginning to limit its own growth, especially where it was more abundant.

In general, the environment of the group-selection openings is neither too shady nor too sunny. However, it is far from being homogeneous. Variables such as slope and aspect, height and size of adjacent vegetation, and proximity of adjacent vegetation to the opening can affect the environment in each opening. Crowns of adjacent trees influence the amount of light that reaches an opening, and the roots of these trees deplete soil moisture for some distance into the opening. Thus, it is no surprise that vegetation tends to develop better in that portion of each opening where adjacent trees have little or no influence (McDonald and Fiddler 1991, York et al. 2003).

Because of the summer-dry climate and moisture limit on growth, plants tend to grow as soon as possible and as fast as possible until the moisture is gone. Thus, becoming established and growing well the 1st year after site preparation, when competition is low, is critical. Growing for a year in the nursery probably gave the planted pine seedlings enough biomass, vigor, and perhaps type of root system to grow rapidly after planting. The natural pine seedlings, however, began from a small seed and lacked the energy to compete as effectively as the planted seedlings the 1st year. At the end of the

second growing season in 1990, the planted seedlings had a 16-cm gain in average height over natural seedlings. By the end of the study in 1997, this gain had increased to a 74-cm advantage. It also allowed the planted seedlings to be slightly taller than the abundant and vigorous manzanita. The natural seedlings were not as tall as the manzanita and probably had been stressed by it for several years.

Opening size and distance from forest edge are two primary variables that can influence the growth of ponderosa pine seedlings. If the seedlings were naturally seeded, early growth was relatively stable, although there was a slight increase with increasing distance from edge. Planted seedlings generally grew faster than natural seedlings and distance from edge had a much stronger effect, particularly in larger openings.

Regeneration and growth of conifer seedlings in small openings in the forest have been studied for several species at different locations in North America. In the cool, moist mountain ranges of coastal Oregon and Washington, the amount of natural regeneration of several conifer species was lowest in portions of large openings that were exposed to direct solar radiation (Gray and Spies 1997). However, seedling development increased with increasing opening size and decreased with increasing shade. In southern coastal British Columbia, Lertzman (1992) examined relations between "gap-maker" and "gap-filler" tree species. Four species of conifer seedlings were studied. Neither opening size, location within an opening, nor local canopy composition appeared to affect the species composition or regeneration in the opening.

In the longleaf pine (*P. palustris* Mill.) forest in the sandhills of north central Florida, Brockway and Outcalt (1998) noted the lack of longleaf pine and wiregrass (*Aristida stricta*) in all but the centers of 12 representative canopy openings. They concluded that the root systems of mature trees were denying nearly all site resources to the seedlings of both species within 12–16 m of the opening edge.

Plainly, the effect of opening size and environment differs among regions for conifer seedling survival and growth. If a common thread were discernible, it would be that seedlings are more numerous and grow better near the centers of openings. In terms of distance from the opening edge, that was true for ponderosa pine seedlings in this study.

Results from this study are not replicated in time or space and they pertain to a specific stand in a specific range of slopes and aspects in a forest type. Deviation from these variables may limit the application of results.

Because natural regeneration tends to be frequent and abundant in group-selection openings, to plant or rely on natural regeneration is often an option. Planting gives a significant early growth advantage but is more costly. Planting costs (1999 basis) were

Seedlings (1–0) @ \$214/1,000	\$104
Plating (contract) @ \$11.62 per hr	126
Total per ha	\$230

Planting genetically superior stock is another option. Although it presently is slightly more costly than nursery-run stock, the higher seedling growth rate that it provides should more than compensate for the additional cost.

An ongoing question with the group-selection method concerns limits on the size of opening. At some point an opening becomes too small to differ from the forest and so large as to be a clearcutting. The range of opening sizes in this study did not allow an answer to this question. However, McDonald and Reynolds (1999) found that vegetation in an opening size of 9 m in diameter (0.007 ha) differed little from that in the uncut forest, and York et al. (2004) presented information that suggested little additional effect of increasing opening size above 0.6 ha. We suggest that limits to size of opening in the group-selection method depend on the environment in the opening and that too depends on the interaction of many of the variables mentioned earlier. In the meantime, based on the pine development relationships found in this study, the kind and amount of vegetation in the plant community, and the relative costs of planting and natural seeding, the forest manager can now make a more enlightened choice for natural regeneration or planting in group-selection openings.

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