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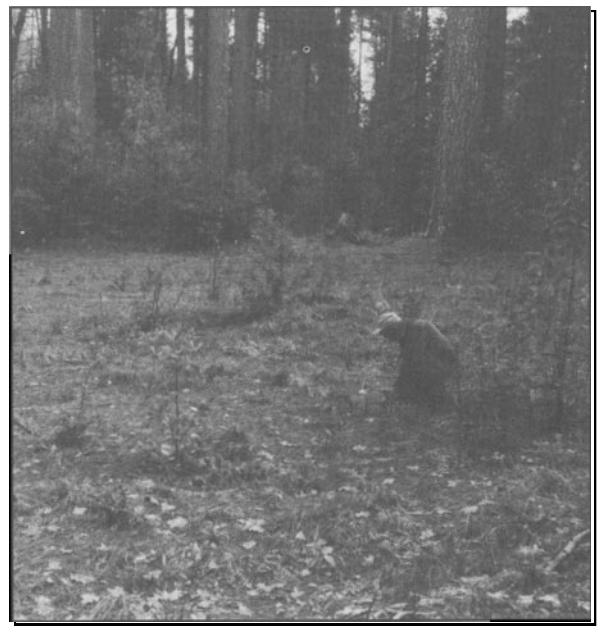
Seedfall, Regeneration, and Seedling Development in Group-Selection Openings

Philip M. McDonald   Celeste S. Abbott

1965



1970

1973

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Forty-eight openings of 30, 60, and 90 feet in diameter were created in previously unmanaged mixed conifer-hardwood stands on a high-quality site in northern California in 1963. They were an attempt to convert an essentially even-aged forest to an uneven-aged arrangement and comprised the initial cut in the group-selection system. Five conifers and three hardwoods produced 36 seed crops that ranged from very light to heavy during the 10-year study period (1964-1973). Sound seed for four conifer species combined (not sugar pine) for 10 years amounted to the equivalent of more than 302,900 seeds per acre and, in general, did not differ significantly among opening sizes. Shade and roots from bordering trees were major influences on seedling survival and development in the openings. Density of established conifer and hardwood seedlings (at least 4 years old) ranged from 12 per acre for incense-cedar in 90-foot openings to about 9,600 ponderosa pines per acre in 60-foot openings after 10 years, and did not differ significantly among opening sizes. Conifer seedling heights ranged from 0.8 to 1.7 feet after 9 years. Average height of ponderosa pines and hardwoods differed significantly between the largest and smallest opening size with height being best in the largest. Normally multi-stemmed and wide-crowned shrubs were conspicuous by their single spindly stems.

Retrieval Terms: conifers, hardwoods, seed crops, seedling density, seedling development, management implications

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Philip M. McDonald **Celeste S. Abbott**

Contents

In Brief . . .

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The group-selection cutting method promotes a landscape that has the appearance of continuous forest cover. Closer examination, however, reveals a number of small openings created by timber harvest. These are scattered throughout, at least initially, and suggest small-scale natural disturbances such as those caused by small hot fires. In this study on the Challenge Experimental Forest in northern California, 48 openings—30-, 60-, and 90-feet in diameter—were created in 1963. These openings were located such that groups of mostly mature trees were harvested along with some individuals of poor form, slow growth, and low development potential. After site preparation by bulldozer, the mineral soil seedbed provided an excellent medium for conifer, hardwood, and shrub seeds to become hidden, germinate, and reproduce the stand.

Once the seedlings are present, however, the environment in which they grew was characterized by shade and a soil moisture regime influenced by the roots of trees adjacent to the openings. For those species whose seedlings are intolerant of shade, like whiteleaf manzanita, deerbrush, California black oak, and ponderosa pine, growth will be curtailed. Some species, like tanoak, which is adapted to shady situations, will grow well. The other tree species that are common in the study area (sugar pine, California white fir, incense-cedar, Douglas-fir) tolerate shade, but will not grow as well as they would in more sunlit environments.

The five conifer and three hardwood species surrounding the group-selection openings produced 36 seed crops during the 10-year study period—4 heavy, 9 medium, and 23 light and very light. Total sound seed for 10 years from the four conifer species that were quantified averaged more than 302,900 seeds per acre in each opening. After 10 years, the equivalent of more than 9,800 conifer and 1,450 hardwood seedlings per acre, at least 4 years old, were present in each opening. Every seed crop contributed to the total. Height of 9-year-old seedlings from lowest to highest was incense-cedar, ponderosa pine, sugar pine, Douglas-fir, California white fir, hardwoods, and shrubs. Ponderosa pine seedlings were significantly larger in 90-foot diameter openings than in 30-foot openings, and combined hardwoods in 60- and 90-foot openings were significantly larger than counterparts in 30-foot openings. Plants of all species were generally taller in the largest openings because of better development near the center.

Although the opening sizes studied here are at the lower end of the size range associated with group selection, findings from them should contribute to the practice of this regeneration cutting method. Stands can be regenerated with a diversity of species while maintaining high forest cover; the reproduction, although too numerous and developing slowly, should continue to grow and even accelerate in growth in the future—forming a spatially distinct age class; and the normally aggressive shrub species, which are negatively affected by the shady environment, pose little threat to the survival and growth of the conifer and hardwood seedlings.

Introduction

Forest managers have, and always will, need to choose among different silvicultural and management systems to achieve a desired mix of commodities and amenities for an ever-changing and ever-more-complicated society. Today, as never before, sentiment is shifting away from clearcutting toward the application of systems that people perceive to be more "gentle" on the land, its vegetation, and its creatures. Proposed alternatives include managing for multiple-aged, multiple-species stands (Beuter 1992) and having an ecosystem perspective that provides a wide array of values and products (Salwasser 1992).

The group-selection method, which is part of an uneven-aged silvicultural regeneration system, involves the removal of groups of trees to create small openings that range from 0.02 to 2.0 acres. Several of these openings, scattered throughout a stand, usually are harvested together on a cyclic basis. The cycle often is 10 or 15 years. There is no rotation, and cutting continues in perpetuity, always removing clusters of mature trees. Initial and early entries into the stand, however, often have an element of "improvement" in them, whereby trees of younger ages are removed (Hawley 1946). This gives opportunity to lower the proportion of less desirable species, trees with poor growth, those that interfere with the growth of better trees, and poorly formed, slow-growing, and diseased individuals (Smith 1962). This cyclic cutting creates a stand of many age classes, often with several species, whose crowns and roots fill nearly all available space. If an equal proportion of all age classes is present throughout the stand, a condition called a balanced stand is achieved, and productivity is considered to be close to the inherent capacity of the site. It has been proposed that this system is particularly adapted to (i) maintaining the health and resistance to damage of the forest; (ii) producing the highest possible volume of valuable timber; (iii) promoting the protective effect of the forest in the widest sense (protecting the soil, scenery, and native flora and fauna); and (iv) functioning like a bank (being in a position to supply critical material when needed without jeopardizing productive capacity) (Hann and Bare 1979).

In addition, the periodic creation of small openings, with their particular environment, is one technique that aids conversion from an even-aged stand of primarily one species to an uneven-aged arrangement with several species.

Uneven-aged silviculture is more an art than a science (Hann and Bare 1979). Implementing it on a broad scale, particularly where stands are even-aged, leads to significant administrative, financial, and biological problems (Fiske and others 1992). A major need is for knowledge on the species composition, magnitude, persistence, and development of regeneration and competing vegetation in group-selection openings (McDonald and Fiddler 1991, Phares 1978). A crucial question is whether the desired species become established and develop satisfactorily under the imposed treatments (Guldin 1991).

This paper reports results 10 years after the first entry in group-selection cutting. It quantifies sound seed from 20 seed crops of four conifer species and relates subsequent seedling survival, density, and development to small openings of three different sizes. Establishment and development of three hardwood and two shrub species also are quantified. Results from this study indicate remarkable similarity in seedfall and regeneration among the three sizes of openings, but striking differences in conifer and hardwood seedling height. They have strong ecological and silvicultural implications.

Methods

Species and Site

The study was located on the Challenge Experimental Forest in north central California. Here, site quality is high and the dominant species, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), will average about 95 feet in height in 50 years (Powers and Oliver 1978). Other tree species scattered over the Forest are Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), sugar pine (*Pinus lambertiana* Dougl.), California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), and incense-cedar (*Libocedrus decurrens* Torr.). Hardwoods, principally California black oak (*Quercus kelloggii* Newb.), tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.), and Pacific madrone (*Arbutus menziesii* Pursh), are present throughout as individual trees, clumps, or groves. Altogether, trees larger than 3.5 inches in diameter at breast height (d.b.h.) number over 245 per acre and contain about 270 ft^2/acre of basal area. The forest is a mosaic of even-aged stands, depending on fire history, with the oldest dominant and codominant trees being about 100 years old and averaging about 140 feet tall. Trees 170 feet and taller at the same age are not unusual. Those in the dominant and codominant crown classes average about 35 per acre, 70 percent of which are ponderosa pines. In general, many trees of the more shade-tolerant species (Douglas-fir, California white fir, incense-cedar, sugar pine, and tanoak) are younger, reflecting a decreasing incidence of fire in the area. Dormant but viable seeds of whiteleaf manzanita (*Arctostaphylos viscida* Parry) and deerbrush (*Ceanothus integerrimus* H. & A.) are abundant in the soil almost everywhere on the Experimental Forest. Apparently, these species were abundant in the past in many areas where not a trace above ground remains today.

Herbivores, chiefly deer (*Odocoileus* spp.), woodrats (*Neotoma* spp.), and deer mice *(Peromyscus maniculatus)*, are plentiful throughout the Experimental Forest.

Summers on the Experimental Forest are hot and dry; winters cool and moist. The average midsummer maximum temperature, based on 43 years of record, is 90 °F; the midwinter minimum is 30 °F. The growing season is about 200 days. Precipitation averages 68 inches with 94 percent falling between October and May. Moisture is the limiting factor and drought the primary cause of mortality for conifer and hardwood seedlings. Aspects are mostly northeast and southwest, and slopes vary from 3 to 30 percent. Soils are of clay loam-clay texture, deep, moderately well drained, and quite fertile.

The overall environment of the small openings is quite similar. Other than for occasional sunflecks, the sun shines in the openings only when directly overhead. Trees on the border cast shade, ameliorate temperatures, and lessen the amount of wind in the openings. Warm temperatures, in general, would not get as high, and cold temperatures would not get as low as in less sheltered environments. Peak summer temperatures may be reduced by as much as 9 °F and winter extremes by an equal amount (Geiger 1966). Snow accumulates in the openings and, because of shade, remains longer than in more open stands. Relative humidity tends to be higher in small openings, and the moisture content of the surface soil may remain higher later into the summer. Because of cold air ponding in the openings, late spring frosts sometimes occur.

Treatments, Measurements, and Analysis

Groups of large and small trees in a natural stand were harvested in the fall of 1963 to create openings of about 30, 60, and 90 feet in diameter (crown dripline to crown dripline). The smallest size of opening was created by removing several medium to small trees, the largest by removing several large and medium trees. Each opening size was replicated 16 times, and all openings were located within 1 mile of each other on relatively homogeneous ground having similar soil and growth potential. Location of openings was random with the restriction that they be within 150 feet of skid roads. Opening size was randomly assigned to the 48 chosen locations. In May 1964, unmerchantable conifers and hardwoods were pushed over and the ground scarified by a bulldozer. The scarification pattern resembled spokes radiating from a central hub with a small flat pile of material located at the end of each spoke. In only a few openings was the slash heavy enough to require piling in the adjacent skid road for eventual burning. Consequently, the surface in all openings was mostly bare mineral soil with little or no competing vegetation.

Seed traps were made of two sizes of galvanized wire screen and were about 1-foot square *(fig. 1)*. The 0.25-inch top mesh often excluded sugar pine seed and was too small to reliably sample seeds of hardwoods. For smaller seeds from the other conifer species, this size of trap has provided reliable estimates of seedfall (McDonald 1973, Roy 1959). Number of randomly located seed traps in the 30-, 60-, and 90-foot openings was 5, 8, and 10, respectively. Collections from the traps were made in late fall or early winter after most seeds had been disseminated, and again in the subsequent summer when winter- and spring-fallen seeds were collected. Seeds from these two collections made up the sample for the preceding seed year. Contents of each trap were placed in paper sacks. After drying, seeds were sorted from the litter and the total number tallied. A cutting test on all seeds determined soundness. Seedfall was quantified every year in the study period (1964 through 1973).

Conifer and hardwood seed crops were evaluated over the entire Forest and surrounding area during the study period by means of a visual rating system *(table 1)* based on the proportion of trees with fruit and the number of fruit per tree (McDonald 1992). This system generally identified the medium and heavy seed crops of the conifer species on the Forest, but occasionally missed the light and very light crops of species that produce small cones.

Conifer, hardwood, and shrub seedlings were surveyed in late spring on randomly located, circular quarter-milacre (0.00025-acre) plots from 1965 through 1974. Sampling intensity reflected the variation in seedling density that occurred in similarly treated stands (McDonald 1966). Number of plots for each 30-, 60-, and 90-foot opening was 9, 17, and 20, respectively. To trace the fate of each species of seedling from each seed crop, a colored (for species) and coded (for seed crop) plastic stick was placed next to each seedling when initially surveyed. The plastic stick remained with the seedling until it died. Individual seedlings were tracked each year through age 4 and then considered as established. Established seedlings from the 1964-1970 seed crops were then accumulated and the total reported for each species for the 10-year study period. Whiteleaf manzanita and deerbrush were tallied as "shrubs," and only presence was recorded from 1964 to 1970. Height of all species was recorded to the nearest 0.5 inch in 1973.

Experimental design was completely randomized, and analysis was by analysis of variance (ANOVA) and Tukey test (Wilkinson 1989). Data on shrub presence were first transformed (arc sine) to produce an approximately homogeneous variance before analysis by ANOVA. Significance in all tests was at $\alpha = 0.05$. Because information was gathered from permanent plots measured each year, the data are not truly independent from year to year. The α levels or type I errors given for various tests apply to each measurement and year separately.

Results

Seed Crops

Seed production during the 10-year study period ranged from very light to heavy for conifer and hardwood species *(table 1)*. Ponderosa pine was the most reliable producer,

Figure 1—Three seed traps are visible in part of this 30-foot diameter opening. Note the center pin that anchors them to the ground.

Table 1—***Periodicity and magnitude of conifer and hardwood seed crops on the Challenge Experimental Forest, 1964-1973***

	Seed crop rating[x]									
Species	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Ponderosa pine	M	-	L	H	L	-	H	VL	-	M
Douglas fir	L	L	L	VL	L	-	-	VL	-	H
California white fir	M	-	-	M	-	-	-	-	-	M
Incense cedar	-	VL	-	-	-	-	-	L	-	VL
Sugar pine	M	-	-	L	-	-	M	-	-	VL
California black oak	-	-	-	M	L	-	-	-	-	-
Tanoak	L	-	L	L	-	H	-	L	VL	-
Pacific madrone	-	VL	-	-	M	VL	-	VL	-	-

[x]Seed crop ratings: VL = very light, L = light, M = medium, H = heavy

yielding medium and heavy seed crops every third year with at least one smaller crop in intervening years *(fig. 2)*. Douglas-fir and tanoak tended to produce frequent, but light and very light crops. Ponderosa pine, Douglas-fir, and tanoak yielded the most crops and California black oak the fewest. All species except incense-cedar bore at least one medium seed crop during the period. Little synchrony existed between conifer and hardwood species. No stimulation of reproductive material due to group-selection cutting was observed.

Seed Production

Sugar pine seed and the fruits of hardwoods were too large to fit in the small seed traps. For the four species that were sampled (ponderosa pine, Douglas-fir, California white fir, and incense-cedar), the amount of sound seed ranged from more than 124,000 per acre for ponderosa pine in a heavy seed year in a 60-foot opening to no sound seed for incense-cedar in any opening in the very light seed year of 1965 *(table 2)*. When seeds were totaled for all conifer species in all openings over the 10-year period and averaged, each opening received the equivalent of slightly more than 302,900 sound seeds per acre. Ponderosa pine constituted 87 percent of total sound seeds.

Amount of sound seed varied with opening size, but only for the low-rated ponderosa pine seed crop of 1966 was a statistically significant difference among opening sizes found. For other seed crops, whether heavy or light, no significant differences among opening sizes were discernible.

Survival and Density of Early Seedlings

To ascertain trends in survival and establishment, numbers of conifer and hardwood seedlings of each species in each size of opening were averaged and compared. Only minor differences were found. Numbers of seedlings of each species then were averaged over all openings combined, and their densities plotted each year until they were considered as established (after four growing seasons). Seedling mortal-

Figure 2—Numerous ponderosa pine cones in part of this 30-foot wide opening indicate heavy seed fall from this species.

Table 2—***Average number of sound seeds by species and size of group-selection opening, Challenge Experimental Forest, 1964-1973***

Opening size	Number per acre							
	1964	1965	1966	1967	1968	1970	1971	1973
ft								
	Douglas-fir							
30	2,725	1,090	545	4,355	1,090	1,090	1,090	23,413
60	1,020	0	680	340	0	340	680	22,461
90	2,725	250	740	745	495	250	495	22,770
SE[x]	979	450	553	1,757	472	493	543	6,835
	Ponderosa pine							
30	15,790	0	545	37,570	3,270	119,795	545	86,031
60	24,495	0	1,360	54,780	1,700	124,185	4,424	77,591
90	19,555	265	4,700[y]	36,140	2,475	105,445	4,207	65,092
SE[x]	5,572	144	1,048	1,757	472	22,956	1,257	10,754
	California white fir							
30	2,180	0	0	545	0	545	0	1,634
60	4,925	0	0	6,805	340	0	0	2,723
90	2,225	0	0	1,980	250	745	0	1,238
SE[x]	1,608	-	-	10,737	243	442	-	1,259
	Incense-cedar							
30	0	0	0	0	0	0	545	0
60	0	0	0	340	0	0	1,020	340
90	0	0	0	250	0	0	495	250
SE[x]	-	-	-	470	-	-	565	243

[x]SE = standard error.

[y]Differs significantly at 5 percent level from values in 30- and 60-foot opening sizes. This was the only significant difference observed.

ity, mostly from drought, followed the general trend of being highest the first year or two and then leveling off. Consequently, with time, the trend in seedling density formed a steep-to-shallow descending pattern *(fig. 3)*. California white fir, for example, numbered almost 1,540 seedlings per acre in 1965 and about 850 seedlings per acre in 1968; tanoak numbered 200 seedlings per acre in 1965 and 173 four years later. Because ponderosa pine produced so much seed and so many seedlings *(table 3)*, density values are presented for three seed crops *(fig. 4)*. They give insight to regeneration trends in group-selection cutting, especially for small openings with site preparation.

The most important trend was that every seed crop resulted in many additional seedlings, which became established and accumulated to the point that each opening became over-stocked with conifer and hardwood seedlings. We noticed that the whole opening became a favorable microsite that stayed favorable until the mineral soil was covered with organic material. In addition, the environment of the openings was such that the number of shrubs, forbs, and grasses were few and their development slow. Over 40 species of plants, including conifer and hardwood seedlings, were present in the openings after 10 years.

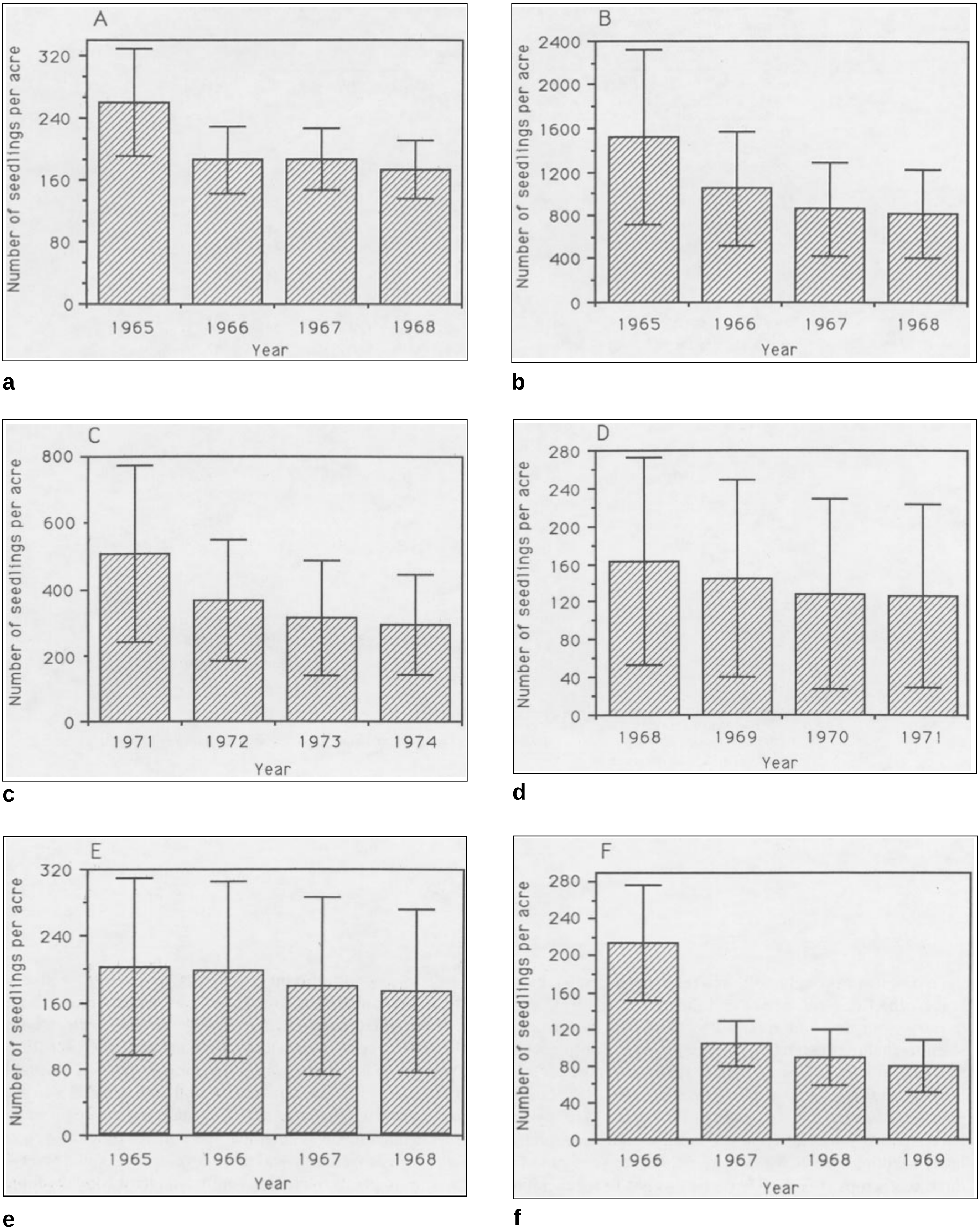
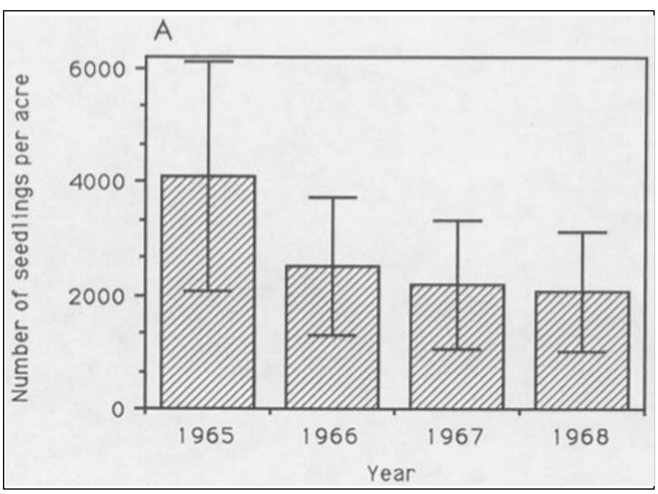


Figure 3—Average number of conifer and hardwood seedlings plus standard errors for first 4 years in group-selection openings, Challenge Experimental Forest, for Douglas-fir (A); California white fir (B); sugar pine (C); California black oak (D); tanoak (E), and Pacific madrone (F).

Table 3—***Average number of established conifer and hardwood seedlings by species and size of group-selection opening, Challenge Experimental Forest, 1974***

Species	Opening size (ft) 30	60	90	SE[x]
	----------- *Number per acre* -----------			
Conifers				
Douglas-fir	250[y]	279	264	88
Ponderosa pine	6,379	9,625	8,244	1,972
California white fir	805	1,589	388	555
Incense-cedar	83	103	12	44
Sugar pine	778	441	274	202
Hardwoods				
California black oak	166	588	550	209
Tanoak	1,111	544	550	330
Pacific madrone	222	500	175	143

[x]SE = standard error.
[y]No significant difference was found among opening sizes for any species.



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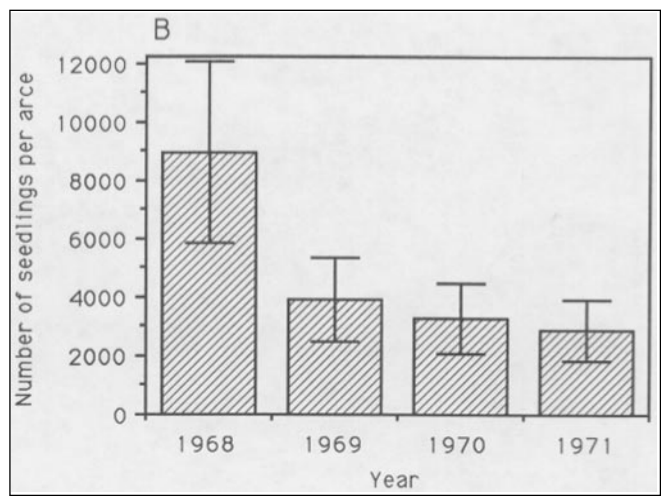

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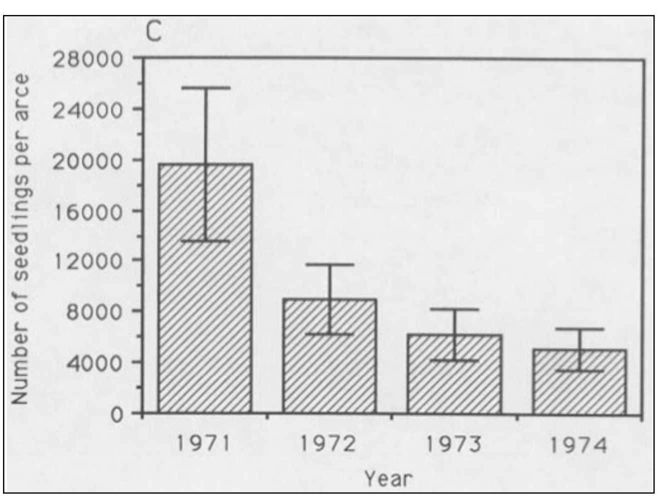

c

Figure 4—Average number of ponderosa pine seedlings plus standard errors in group-selection openings for seed crops of 1964 (A), 1967 (B), and 1970 (C), Challenge Experimental Forest.

Density of Established Seedlings

Number of established conifer seedlings ranged from an average of 12 incense-cedar per acre in 90-foot openings to about 9,600 ponderosa pine per acre in 60-foot openings *(fig. 5)*. Similarly, an average of 166 California black oak seedlings per acre became established in 30-foot openings and 1,111 tanoak seedlings per acre in openings of similar size. No significant difference among opening sizes was detected for any species. A similar finding resulted when aspect (north vs south) was included in the analysis. When all seedlings of all species were averaged over all opening sizes, the number of seedlings in each opening in 1974 was very large—the equivalent of more than 9,800 conifers and 1,450 hardwoods per acre *(fig. 6).* Although ponderosa pine constituted 82 percent of established seedlings, the more shade-tolerant conifers and hardwoods were almost always represented in each opening *(fig. 7)*. If the species composition of the future forest was based solely on conifer and hardwood seedling density after 10 years, it would closely resemble that of the original stand.

Presence of combined whiteleaf manzanita and deerbrush plants on the regeneration plots was 15, 27, and 24 percent on the 30-, 60-, and 90-foot openings, respectively. No statistical difference among opening sizes was found. Because no plants of either species were present before logging, it is likely that most plants originated from dormant seeds in the soil. Almost all plants became present soon after site preparation.

Seedling Growth

Mean height of established conifer, hardwood, and shrub seedlings, measured in fall 1973 or after 9 years, ranged from 0.8 feet for ponderosa pine in 30-foot openings to 3.8 feet for shrubs in 90-foot openings *(table 4)*. No damage

Figure 5—Abundant California white fir and ponderosa pine seedlings are visible in part of this 60-foot wide opening.

a

b

Figure 6—(A) Ponderosa and sugar pines are becoming visible in part of this 90-foot opening in 1973. (B) Hardwoods and ponderosa pines occupy most of this 90-foot opening in 1973. Note the heavy litter on the ground in both photos.

Figure 7—This quarter-milacre circular plot in part of a 60-foot opening in 1973 contains 10 living and one dead (horizontal stick) ponderosa pines, and one each of Douglas-fir, sugar pine, and California white fir. Note the relative heights of the seedlings and specifically the taller Douglas-fir (upper left) and sugar pine (upper right).

from browsing animals was noted. Analysis by size of opening revealed that ponderosa pine seedlings were significantly larger in 90-foot openings than in 30-foot openings, and hardwoods in 90- and 60-foot openings were significantly larger than counterparts in 30-foot openings. In general, plants of all species were tallest in 90-foot diameter openings, largely because of taller plants near the centers.

Relative height by species in descending order was shrubs, hardwoods, California white fir, Douglas-fir, sugar pine, ponderosa pine, and incense-cedar. This ranking reflects the various species response to the environment of the small openings, and specifically to the lower levels of light available there. It may or may not relate to seedling vigor. For the shade-tolerant hardwoods like tanoak, and to a lesser extent for Pacific madrone, their ranking accurately reflects the natural ability of the seedlings to grow well in shady environments. The poor development of ponderosa pine (many seedlings were only 5 inches tall at age 9) well portrays its response to an inhospitable environment. The ranking of the tolerant conifers (sugar pine, Douglas-fir, incense-cedar, California white fir) reflects both good adaptation to the

Table 4—***Average height of established seedlings by species or by combination of species and opening size, Challenge Experimental Forest, 1973***

Species	Opening size (ft) 30	60	90	SE[x]
	Height (ft)			
Ponderosa pine	0.8 a[y]	1.0 ab	1.3 b	0.2
Sugar pine	0.9 a	1.5 a	1.5 a	0.3
Douglas-fir	1.3 a	1.0 a	1.6 a	0.3
California white fir	1.2 a	1.5 a	1.7 a	0.2
Incense-cedar	-	-	0.9 a	-
Hardwoods	1.5 a	2.5 b	2.8 b	0.2
Shrubs	2.6 a	2.2 a	3.8 a	0.3

[x]SE = standard error.

[y]For each species, treatment means followed by the same letter do not differ statistically at the 0.05 level.

environment of the openings and to an inherently slow growth habit as seedlings. The shrubs, however, almost all consisted of a single spindly stem that reflected poor vigor. In a more open sunlit environment they would be much taller, have multiple stems, and be almost as wide as they were tall (Cooper 1922, Hellmers and others 1955).

Summary and Discussion

The environment of 30- to 90-foot diameter openings in a mixed-conifer and hardwood stand on a good site in northern California, cut as the first entry in a group-selection regeneration system, is modified both above and below ground by the adjacent trees. Above ground, the forest floor of the openings is shaded and showered by needles, twigs, and other organic material; below ground, roots of large trees extend into the openings and probably intensify in volume after harvest as roots capture at least some of the space formerly occupied by cut trees (Smith 1962). In general, soil moisture and light are less available to seedlings near the forest edge and become more available with distance toward the center of the openings.

Although the general environment of the small openings may be similar, the specific environment actually differs, depending on the size of the opening. In general, more light is available in 90-foot openings than in 30-foot openings and increases as aspect becomes more southerly. In a separate study on a nearby area on the Experimental Forest, Ziemer (1968) measured soil moisture around a forest-grown, but isolated (all other trees removed), 28-inch diameter sugar pine. He found that “soil moisture depletion extended outward to a distance of slightly over 20 feet from the base of the tree and somewhat deeper than 15 feet under the tree.” Presumably, this zone of depletion was caused by moisture-absorbing tree roots. Consequently, tree roots probably extend throughout the 30-foot diameter openings, through most of the 60-foot openings, and in all but the center of 90-foot openings. Less soil moisture would be available to seedlings in areas where the roots were present.

Years of observation have indicated that most seeds are distributed in the fall on days when winds are from the northeast and the atmosphere is warm and dry (McDonald 1983, 1992). When warm temperatures and low humidity combine to lower the moisture content of cones and scales and acorn cups, a shower of seeds takes place. If this weather continues, most of the seeds fall, often within a week. If it does not last, remaining seeds dribble out in warm weather between storms, which are usually from the southwest, or again are distributed under the influence of northeasterly winds.

During the 10-year study period, 24 seed crops were produced on five conifer species and 12 seed crops on three hardwood species. Ponderosa pine, Douglas-fir, and tanoak each produced six seed crops that ranged from very light to heavy. All other species yielded at least two crops during the study period. Ponderosa pine bore more medium to heavy seed crops (four) than any other species and had the most even periodicity (every third year).

Sound seeds were quantified for four conifer species and, when totaled for all species over the study period, amounted to the equivalent of more than 302,900 sound seeds per acre in every opening. Eighty-seven percent of it was ponderosa pine.

Because of bare mineral soil and the shade-ameliorated environment of the small openings, the entire area of each opening became a favorable microsite for the establishment of conifer and hardwood seedlings. Consequently, each seed crop contributed to the pool of established seedlings to the point that too many seedlings became present.

The survival pattern of seedlings of all species for the first 4 years was descending and steep to shallow depending on the species and timing of seed crop relative to amount of organic material on the forest floor. Shade-tolerant species and those from large seeds (acorns) in general had a less rapid rate of mortality than intolerant species.

Established conifer seedlings (at least 4 years old) averaged more than 9,800 per acre and hardwoods over 1,450 per acre in each opening. Eighty-two percent were ponderosa pine. Virtually no statistically significant differences among opening sizes were found for seed fall, survival and early seedling density, and established regeneration of any conifer, hardwood, or shrub species.

Because conifer and hardwood seedlings were abundant, few site resources will be available for the establishment of future seedlings. Consequently, the odds are that these seedlings will be the only age class that will be present in all these openings.

In general, the largest opening size was more amenable to height growth for all species than was the smallest opening size. Height of seedlings was significantly greater for ponderosa pine and combined hardwoods in larger openings. But the overall height growth of ponderosa pine seedlings was poor, which leads to the question of this species representation in future stands. In a longer-term study with single-tree selection in the central Sierra Nevada, in a forest type where the majority species of dominant trees were shade tolerant, Lilieholm and others (1990) noted that shade-tolerant species comprised the bulk of seedlings, but “selection harvests have resulted in adequate quantities of seedlings of all five conifer species, including pines.”

In the shady environment of the small openings, whiteleaf manzanita and deerbrush seedlings were tall and slender rather than “bushy”—their traditional form in areas with more sunlight.

Because large ecological and silvicultural differences exist between group selection and clearcutting in terms of the survival, density, and development of conifer, hardwood, and shrub seedlings, the two methods are compared. In general, in small openings cut as the initial entry in group selection, shade-tolerant species are better represented, and more tree seedlings per unit area become established. However, the shrub and herbaceous plant community is much less diverse and less developed in group-selection openings than in clearcuttings.

In clearcuttings, after site preparation by windrow and burn or broadcast burn, vegetative reoccupation is much more dynamic in terms of rapidity, diversity of species, and plant density. In nearby clearcut areas on the Experimental Forest, for example, plant species numbered more than 100 with a mean density of more than 57,500 per acre 5 years after site preparation by windrow and burn (McDonald 1983). Most favorable microsites became occupied by vegetation after 1 year. After 3 years, few areas remained that were receptive to the survival and establishment of conifer seedlings. Consequently, in clearcuttings, it is the first conifer seed crop that provides seedlings for the future forest—subsequent seed crops almost always are in vain. If no conifer seeds fall for 3 or 4 years after site preparation, the chance for acceptable conifer seedling establishment is low.

Height (in feet) of 9-year-old shrub, hardwood, and conifer seedlings in clearcuttings was 7.8 (shrubs), 12.6 (hardwoods), 4.0 (California white fir), 4.2 (Douglas-fir), 5.5 (sugar pine), and 6.2 (ponderosa pine) (McDonald 1976), or 3 to 6 times taller than seedlings in group-selection areas.

Can these small openings contribute to the practice of group selection in the future, given their size and their unique (shady) environment? More specific questions are: (1) will the newly established conifer and hardwood species grow to maturity as a spatially distinct age class, (2) will intolerant species be present in the future, and (3) will the normally-aggressive shrubs be a threat to the conifer seedlings?

Although these questions cannot be answered directly by this study, the data and relationships suggest possible answers: (1) Although the uncut forest and the small openings are best described as “shady,” a critical, higher amount of sunlight is present in the openings. This, plus the mineral soil present there, promulgates seedling establishment and slow but steady height growth. That the seedlings will continue to grow and form a distinct age class is likely. (2) The high proportion of ponderosa pine seedlings, their relatively low heights, and poor development potential suggest high mortality and a much-reduced presence in the future. It is likely that the more shade-tolerant species will replace ponderosa pine in all but the centers of the largest openings. (3) Although the growth of both shrubs and tree seedlings, with the exception of tanoak, is reduced greatly in the small openings, the spindly nature of the shrubs suggests that they will furnish only minor future competition to the tree seedlings. This cutting system offers good potential as an indirect vegetation management technique. A major goal of future research will be to find that opening size where the tree seedlings grow well and the shrubs do not.

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