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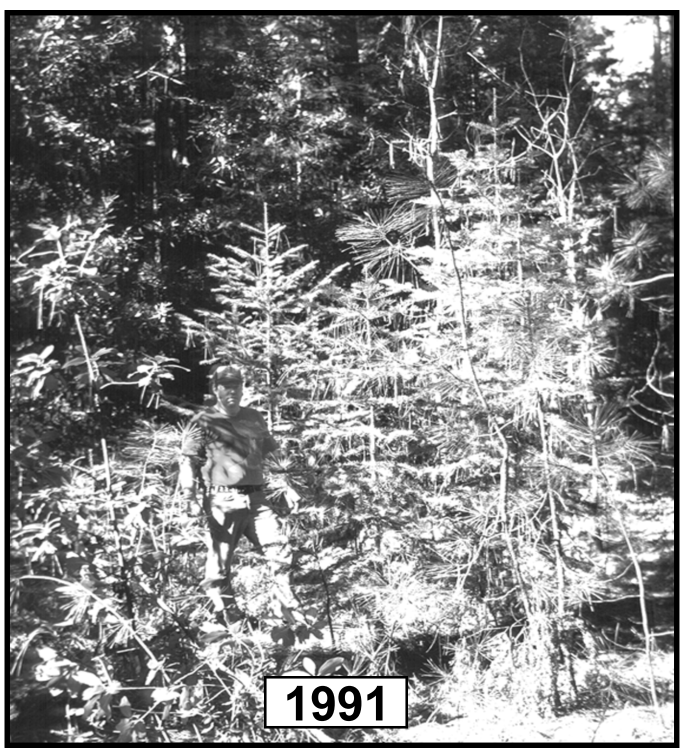
PSW-RP-241

Plant Community Development After 28 Years in Small Group-Selection Openings

Philip M. McDonald **Phillip E. Reynolds**



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Abstract

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Thirty openings, 9, 18, and 27 meters in diameter, were created by group-selection harvest on a high quality site in northern California in 1963. In 1991, or 28 years after site preparation, the plant community in the openings had stabilized at 55 species. A major shift was from annuals to perennials. New seedlings of ponderosa and sugar pine were able to become established for the first 15 years and those of Douglas-fir and California white fir for the first 25 years. Density and development of conifer and hardwood saplings, shrubs, forbs, graminoids, and ferns were examined for differences in openings size and aspect. In general, plants in almost all classes of vegetation were more numerous and developed better in the larger openings and on the south aspect. Tanoak was an exception, with significantly more seedlings in the smallest opening size and on the north aspect. After 28 years, conifer and hardwood saplings averaged more than 25,230 per hectare, and shrubs, forbs, graminoids, and ferns averaged more than 220,700 per hectare. Conifer and hardwood species grew two to four times faster in height the last 18 years than during the first 10 years. The tallest saplings were 9 to 12 meters in height after 28 years.

Retrieval Terms: group selection, mixed-conifers, plant community dynamics, regeneration, Sierra Nevada, silviculture

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Metric-English Conversions

From	To	Operation
Centimeter (cm)	Inch	x 0.39
Hectare (ha)	Acre	x 2.47
Kilometer (km)	Mile	x 0.62
Meter (m)	Foot	x 3.28
Millimeter (mm)	Inch	x 0.039
Square meter per hectare (m^2/ha)	Square foot per acre	x 4.36

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In Brief...

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The trend toward forest management methods that are perceived as more gentle on the land, its vegetation, and its creatures continues to grow. Sustaining ecosystems and maintaining ecosystem components are key to modern forest practice. The group-selection cutting method, which involves the removal of trees in small aggregations, promotes a landscape that has the appearance of continuous forest cover with small openings. Such openings can resemble those created when wildfire creeps through a stand and flares through tree crowns in areas of heavy fuels. Because it has this natural counterpart, limits the harvest to a small fraction of the trees in a stand at any one time, and promotes many age classes, the group-selection method is regarded as both gentle on the land and one that promotes a complex stand, resilient to major damage.

The group-selection cutting method is perhaps the least used and poorest understood of all the silviculture regeneration harvesting methods. Consequently, some knowledge gaps exist, and one of the most serious is a lack of long-term information on plant species composition, succession, and development within the small openings inherent to the method.

In 1963, 48 small openings, 9, 18, and 27 meters in diameter, were created by timber harvest on the Challenge Experimental Forest in northern California. The dominant overstory species in the study area was ponderosa pine. A gentle scraping with a bulldozer bared the soil and created a seedbed that was receptive to colonization by tree, shrub, and herbaceous species. All vegetation had to become established and develop in an environment characterized by openings that were impacted by roots and crowns of adjacent trees.

In 1991, 30 openings (10 of each diameter) were remeasured. Conifer and hardwood saplings, shrubs, forbs, graminoids, and bracken fern were sampled in each opening for density and height. Root-collar diameter was recorded for conifers and hardwoods, and all plant species in the openings were listed.

Results from this study showed that the number of plant species increased from 40 in 1973 to 55 in 1977 and remained at 55 in 1991. The plant community in 1991 consisted of 5 conifers, 5 hardwoods, 16 shrubs, 24 forbs, 4 graminoids, and 1 fern. Almost all were perennials.

Unlike even-aged silvicultural regeneration methods where the first few seedcrops stock the land, many seedcrops are effective for establishing regeneration in group-selection openings. Ponderosa pine and sugar pine seedcrops were effective for the first 15 years after site preparation; Douglas-fir and California white fir seedcrops provided new seedlings for an additional 10 years.

In 1974 the total number of conifer and hardwood seedlings was almost 27,800 per hectare with stand composition of 71 percent ponderosa pine, 16 percent tolerant conifers, and 13 percent hardwoods. In 1991 the total number of conifer and hardwood saplings was more than 25,230 per hectare with stand composition of 22 percent ponderosa pine, 37 percent tolerant conifers, and 41 percent hardwoods. Thus, the composition of the stand has shifted toward the more tolerant conifers and hardwoods at the expense of ponderosa pine. Comparative height values support this trend. Among the five conifer species and the combined hardwoods, ponderosa pine ranked no better than fourth in average sapling height in 1973 and 1991 and for tallest trees in 1991. However, in spite of the large decrease in ponderosa pine numbers, this species will continue to be a significant component of the stand, particularly near centers of larger openings.

Size of opening and aspect had a major influence on plant density and development. In general, almost all statistically significant differences for all classes of vegetation were between the largest opening sizes and the smallest and between the north and south aspect. Plainly, more plants, and plants that developed better, occurred in the larger openings and on south aspects. Tanoak was a partial exception, having significantly more plants in the smallest opening size and on a north aspect, but developing better in both mean height and root-collar diameter on south aspects.

Several shrub species that develop rapidly and reach large size in more sunlit environments did not grow well in group-selection openings. This finding suggests that vegetation managers can use the environment, especially components like shade and organic material, to control undesirable vegetation; thus, *indirect* methods can be added to their repertoire of vegetation control techniques. We also found that because the entire 9-m opening probably was impacted by shade and roots from adjacent trees, and conifer and hardwood sapling growth was poorest in 9-m openings, this size of opening probably is too small for operational application in group-selection cutting.

Finally, the density and development data for the conifer and hardwood saplings, plus the finding that their growth rate was two to four times faster the second 18 years than the first 10 years, suggest that this application of group-selection cutting will produce a spatially distinct age class. Furthermore, it shows promise as a way to convert from essentially a ponderosa pine stand to a mixed conifer-hardwood stand.

The Forest Service, U.S. Department of Agriculture, is responsible for Federal Leadership in forestry. It carries out this role through four main activities:

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- Cooperation with State and local governments, forest industries, and private landowners to help protect and manage non-Federal forest and associated range and watershed lands;
- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas; and
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

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Introduction

Forest land managers are currently experiencing a dilemma: on the one hand, the human population is expanding and the wildland base is shrinking; on the other hand, the need for wood products is increasing. Furthermore, society is demanding that the inherent productivity of the land be maintained and that it be productive in terms of "yields." These yields take many forms and range from the commodities of wood and water to the amenities of pleasing scenery and viewing wildlife. Society also is advocating timber harvesting methods that are perceived as more gentle on the land and that do not materially affect ecosystem processes. Within the framework of sustaining ecosystem processes is a need for information on silvicultural practices and their effect on species composition, structure, and function over time (Aune and others 1993).

The silvicultural regeneration cutting system that has been suggested for major implementation on Federal forest land in California is group selection. Ecologically, it has special appeal because it creates scattered small openings like those that develop when wildfires creep through the forest and occasionally flare through groups of trees.

Fiske and others (1992) reported the broad effects of a group-selection strategy for the Sierra Nevada mixed conifer forest type. However, information on the density and development of conifer and hardwood seedlings, shrubs, and herbaceous vegetation in group-selection openings is lacking (McDonald and Fiddler 1991), and no information on plant species diversity or longer-term successional trends is available. Concomitantly, Libby (1992) noted: "If we are going to manage gaps [openings] to recruit vigorous sugar pines into the overstory, we need to learn a lot more about the size and nature of the gaps that will release sugar pine and not suppress it" (p. 216). Critical questions are whether the desired species become established and develop satisfactorily in group-selection openings (Guldin 1991) and how this development compares to that achieved with other cutting methods.

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 0.01 to 0.8 hectares (ha). The upper size limit of openings is governed primarily by their environment. Openings should not be large enough to lose the site protection of the surrounding trees (Daniel and others 1979). Thus, slope, aspect, and height of surrounding trees influence opening size. Several of these openings, scattered throughout a stand, usually are harvested together on a cyclic basis. The cycle is often 10 to 20 years. In this paper, the cycle was longer than 20 years, but the results are still pertinent because second-cycle openings are often widely dispersed and usually have little influence on previous openings.

Traditionally, in group selection there is no rotation and cutting continues in perpetuity, usually removing clusters of mature trees. Initial and early entries into the stand, however, often have a large element of "improvement" in them, whereby trees of younger ages are removed (Hawley 1946). This provides the 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.

Earlier studies (McDonald 1966, 1976) presented seedfall and regeneration data for small openings cut to group-selection standards in northern California. McDonald and Abbott (1994) reported seed crops for five conifer and three hardwood species, quantified seedfall for four conifer species, and discussed survival and density of conifer and hardwood seedlings during the 1965-1974 period. Seedling height was presented for trees and selected shrubs through 1973.

McDonald and Abbott (1994) found that each seedcrop contributed to seedling numbers to the point that density in the small openings became very high—more than 24,215 conifer and 3,580 hardwood seedlings per ha, at least 4 years old, in each opening. Height of seedlings after 9 years ranged from 0.2 meter (m) for ponderosa pine in 9-m diameter openings to 0.9 m for hardwoods in 27-m openings. Ponderosa pine seedlings were significantly taller in 27-m openings (0.4 m) than in 9-m openings (0.2 m), and hardwoods in 18- and 27-m openings (0.8 and 0.9 m) were significantly taller than counterparts in 9-m openings (0.5 m). Plants of all species were generally taller in the largest openings because of better development near the center. Shrubs, however, were tall and thin, with a much different form than when growing in sunlit environments.

This paper reports information after group-selection cutting in northern California in which the plant community in 1991 is compared to surveys in 1973 and 1977; density and development of 10 conifer and hardwood species are quantified and related to opening size and aspect; and average density, foliar cover, and height of shrubs, forbs, graminoids, and bracken fern are also quantified after 28 years.

Methods

Species and Site

The study was located on the Challenge Experimental Forest in northern California (latitude 39° 30'; longitude 121° 13'). Here, site quality is high, and the dominant species, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), will average about 34 m in height in 50 years (Powers and Oliver 1978). Other tree species scattered over the Forest are coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), sugar pine (*Pinus lambertiana* Dougl.), California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), and incense-cedar (*Libocedrus decurrens* Torr.). Scientific and common names of trees are from Little (1979) and scientific and common names of all other species are from Hickman (1993). 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. Less common hardwoods are bigleaf maple (*Acer macrophyllum* Pursh) and Pacific dogwood (*Cornus nuttallii* Audubon). These tree species correspond to the montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges (Rundel and others 1977).

Altogether, trees larger than 8.9 cm in diameter at breast height (d.b.h.) number more than 613 per ha and contain about 62 m^2/ha of basal area. Dominant trees were about 100 years old and 42 m tall when the study began. Trees in the dominant and codominant crown classes averaged about 77 per ha, 70 percent of which were ponderosa pines. Dormant but viable seeds of whiteleaf manzanita (*Arctostaphylos viscida* Parry), deerbrush (*Ceanothus integerrimus* H. & A.), and several other shrub species are abundant in the soil on the Experimental Forest. Apparently, these species were widespread in the past in many areas where not a trace above ground remains today.

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 32°C; the midwinter minimum is -1°C. The growing season is about 200 days. Precipitation averages 1,727 mm 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.

Treatments, Measurements, and Analysis

Groups of large and small trees in the natural stand were harvested in the fall of 1963 to create openings of 9, 18, and 27 m in diameter (crown drip-line to crown drip-line). Each opening size was replicated 16 times, and all openings were located within 1.6 km 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 60 m 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 logging 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 virtually no competing vegetation (*fig. 1*).

All openings were visited in summer 1991 and their condition noted. A number of openings were no longer representative of group selection because the environment had been modified by logging in nearby compartments, edge trees had fallen, or introduced blackberries had become extensive. Consequently, the 1991 sample was comprised of 10 openings of each size. Twelve openings occurred on north aspects and 18 openings on south aspects:

Opening size (m)	*Aspect*	*Number*
9	N	6
	S	4
18	N	3
	S	7
27	N	3
	S	7

All conifer and hardwood seedlings and saplings (referred to as saplings) were sampled in 1-m wide transects that extended from the opening center to the border. The transects were centered on the four cardinal directions (north, south, east, and west) and varied in length with the radius of the three opening sizes. This design allowed for a more intensive sample in the center of the openings. All saplings in each transect were measured for height and diameter at the root crown. To sample shrubs, forbs, and grasses, a 4-m^2 subplot was randomly

Figure 1
After site preparation, each opening was free of slash and vegetation and constituted an ideal medium for future colonization.

located near the center and in each quadrant of each opening. Density and height were quantified.

Another sample took place in 1992. This was a destructive sample whereby a total of 1,533 ponderosa pine, sugar pine, Douglas-fir, and California white fir saplings were severed at groundline and aged to determine year of origin. Sampling was similar to the 1991 sample, with random selection of seedlings near the center and in each quadrant of each opening. The age of many saplings was checked by small, colored (for species), and coded (for seed crop) plastic sticks placed at the base of each seedling during the regeneration surveys of 1965-1974 (*fig. 2*).

The plant community in the small openings was that which invaded either from seed or from below-ground structures. No root crowns of hardwood trees or shrubs remained. All plant species were recorded in 1973, 1977, and 1991.

The experimental design was completely randomized. Statistical techniques were analysis of variance (ANOVA) and multiple comparison tests. In general, Tukey's (HSD) equal N test was used for opening sizes, and the Spjotvoll-Stoline analysis was applied for aspect and elsewhere where the sample size was unequal. Significance in all tests was at $\alpha = 0.1$.

Results

Plant Community Dynamics

In 1974 or 11 growing seasons after site preparation, the plant community in the group-selection openings consisted of 40 species, including 10 trees, 9 shrubs, 16 forbs, 4 graminoids (grasses and sedges), and 1 species of fern (*fig. 3*; *table 1*). Fourteen years after site preparation, the community had increased to 55 species, with 1 additional shrub, 12 more species of forbs, and 2 more graminoids (*table 1*). After 28 years, the plant community consisted of 55 species and included 10 species of trees, 16 shrubs, 24 forbs, 4 graminoids, and the ubiquitous bracken fern (*table 1*). New additions to the shrubs included two introduced but naturalized species of blackberries: Himalayan (*Rubus discolor*) and cut-leaved (*R. laciniatus*) (*table 2*). Birds and other animals apparently disseminated seeds of these species into the openings. Losses to the shrub category were a species of *Arctostaphylos* and one of *Baccharis*.

Several successional trends were evident based on different numbers of species present the 11th and 28th year. Number of species of conifer and hardwood seedlings remained constant, shrub species doubled, forbs increased

Figure 2
Ten seasons after site preparation, this small plot contained many conifer seedlings including ponderosa pine (white sticks) and taller Douglas-fir (upper left) and sugar pine (upper right).

by 50 percent, and grass species increased and then leveled off at 11th-year levels. The only annual species present were forbs. These increased slightly the 14th year but then decreased to 5 species after 28 years. Perennial forb species increased 90 percent during this timespan.

Age Distribution of Conifer Seedlings

In the group-selection openings, the seedlings originated from many seedcrops to the point that sapling density became excessive (McDonald and Abbott 1994). But which seedcrops were effective? On the basis of the destructive sample of 1992, and for all openings taken together, most ponderosa and sugar pine seedlings became established on both north and south aspects during the first 15 years after site preparation. Very few found the environment of the openings to be conducive to survival after that. However, Douglas-fir and California white

Table 1—*Plant species in small group-selection openings various years after site preparation, Challenge Experimental Forest, 1974-1991*

Vegetation component	Years after site preparation		
	11	**14**	**28**
	---------------- Number of species		--------------
Trees			
Conifer	5	5	5
Hardwood	5	5	5
Shrubs	9	10	16
Forbs			
Annual	6	8	5
Perennial	10	20	19
Graminoids	4	6	4
Ferns	1	1	1
Total	**40**	**55**	**55**

Figure 3
Eleven seasons after site preparation, this typical 27-m opening contained numerous conifer seedlings, graminoids, shrubs, and forbs.

Table 2—*Plant species in small group-selection openings, Challenge Experimental Forest, 1991*

Scientific name	Common name
Trees	
Abies concolor var. *lowiana*	California white fir
Acer macrophyllum	Bigleaf maple
Arbutus menziesii	Pacific madrone
Cornus nuttallii	Pacific dogwood
Libocedrus decurrens	Incense-cedar
Lithocarpus densiflorus	Tanoak
Pinus lambertiana	Sugar pine
Pinus ponderosa	Ponderosa pine
Pseudotsuga menziesii	Coast Douglas-fir
Quercus kelloggii	California black oak
Shrubs	
Arctostaphylos viscida	Whiteleaf manzanita
Ceanothus integerrimus	Deerbrush
Ceanothus lemmonii	Lemon ceanothus
Ceanothus prostratus	Squawcarpet
Chamaebatia foliolosa	Bearclover
Lonicera hispidula	Hairy honeysuckle
Prunus virginiana var. *demissa*	Western choke-cherry
Symphoricarpos mollis	Creeping snowberry
Rhamnus rubra	Sierra coffeeberry
Ribes roezlii	Sierra gooseberry
Rosa gymnocarpa	Wood rose
Rubus discolor	Himalayan blackberry
Rubus laciniatus	Cut-leaved blackberry
Rubus leucodermis	Blackcap raspberry
Rubus parviflorus	Thimbleberry
Toxicodendron diversilobum	Western poison oak
Forbs	
Adenocaulon bicolor	Trail plant
Aster radulinus	
Apocynum androsaemifolium	Dogbane
Campanula prenanthoides	California harebell
Chimaphila umbellata	Prince's pine
Clarkia rhomboidea	
Collomia heterophylla	
Dichelostemma capitatum	Blue dicks
Fragaria vesca	Wood strawberry
Galium bolanderi	Bedstraw
Goodyera oblongifolia	Rattlesnake plantain
Hieracium albiflorum	White-flower hawkweed
Horkelia tridentata	Three-tooth horkelia
Hypericum concinnum	Gold-wire
Iris hartwegii	
Lupinus sp.	
Madia gracilis	
Osmorhiza chilensis	
Polygala cornuta	Milkwort
Sidalcea malvaeflora	
Solanum americanum	
Trientalis latifolia	Western starflower
Vicia americana	
Viola lobata	
Graminoids	
Bromus sp.	
Carex sp.	
Elymus glaucus	Blue wildrye
Juncus sp.	
Ferns	
Pteridium aquilinum var. *pubescens*	Bracken fern

fir seedlings continued to become established for an additional 10 years, also on both aspects. Apparently, adjacent trees and vegetation in the openings ameliorated the environment on south aspects so that the shade-tolerant Douglas-fir and California white fir seedlings could become established.

Conifer and Hardwood Saplings

Density

After 28 years, density of all conifer and hardwood saplings within all openings combined ranged from 24,230 per ha in 9-m diameter openings to 26,580 per ha in 18-m openings (*table 3*). Total density for conifers after 28 years was 10,710 per ha in 9-m diameter openings, 18,750 per ha in 18-m openings, and 15,060 per ha in 27-m openings. Total hardwood densities for similar opening sizes were 13,520, 7,830, and 9,840 per ha, respectively. Neither total conifers or total hardwoods or the total of both differed significantly among opening sizes.

Because the analysis of conifer ages indicated differences between aspects, all conifer and hardwood saplings present in all openings in 1991 were quantified by north and south aspects. The total number of saplings per ha (hardwoods and conifers combined) on north aspects was slightly more than 31,000; on south aspects more than 21,000—a statistically significant difference (*table 4).* The total number of hardwoods was significantly larger on north slopes than on south slopes, but the total number of conifers did not differ significantly among aspects.

When analyses were expanded to include individual species in each of the three opening sizes, saplings of Douglas-fir and California white fir were the most numerous conifers in 9-m openings with 3,820 and 2,260 saplings per ha, respectively; tanoak saplings were the most numerous of the hardwoods (11,200 per ha) in 9-m openings (*table 3*). In 18-m openings, ponderosa pine saplings were the most numerous (7,050 per ha), followed by California white fir (5,540 per ha) and Douglas-fir (2,560 per ha). Tanoak, with 4,250 saplings per ha, remained the most numerous of the hardwoods in this opening size. In 27-m openings, ponderosa pine saplings (7,450 per ha) were most numerous followed by Douglas-fir (3,960 per ha). Tanoak (5,040 per ha) continued to be the most

Table 3—*Density of conifer and hardwood species on all aspects in three sizes of group-selection openings, Challenge Experimental Forest, 1991*

	Opening size (m)			
Species	**9**	**18**	**27**	**SE**[1]
	Density (no./ha)			
Conifers				
Ponderosa pine	2,210 a[2]	7,050 b	7,450 b	1,020
Sugar pine	1,400 a	1,290 a	740 a	1,370
Douglas-fir	3,820 a	2,560 a	3,960 a	1,110
California white fir	2,260 a	5,540 a	2,390 a	760
Incense-cedar	1,020 a	2,310 a	520 a	1,300
Total	**10,710**	**18,750**	**15,060**	
Hardwoods				
Tanoak	11,200 a	4,250 b	5,040 b	510
California black oak	590 a	1,160 a	1,150 a	1,210
Pacific madrone	810 a	1,860 a	1,210 a	880
Bigleaf maple	270 a	0 a	1,290 a	780
Pacific dogwood	650 a	540 a	1,150 a	1,290
Total	**13,520**	**7,830**	**9,840**	

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Table 4—*Density of conifer and hardwood species for all opening sizes on north and south aspects, group-selection cutting, Challenge Experimental Forest, 1991*

Species	Aspect		
	North	South	SE[1]
	Density (no./ha)		
Conifers			
Ponderosa pine	3,410 a[2]	7,010 b	1,040
Sugar pine	1,860 a	660 b	240
Douglas-fir	4,400 a	2,810 b	420
California white fir	5,780 a	1,810 b	730
Incense-cedar	690 a	1,680 a	640
Total	**16,140**	**13,970**	
Hardwoods			
Tanoak	11,870 a	3,470 b	1,180
California black oak	500 a	1,280 b	190
Pacific madrone	1,120 a	1,410 a	250
Bigleaf maple	220 a	720 a	310
Pacific dogwood	1,180 a	510 a	220
Total	**14,890**	**7,390**	

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

numerous hardwood. Statistical differences were limited to ponderosa pine and tanoak. Ponderosa pine saplings were significantly more numerous in 18- and 27-m openings than in 9-m openings. Tanoak saplings were significantly more numerous in 9-m openings than in larger openings.

When individual species were analyzed by aspect, several significant differences were noted. Ponderosa pine and California black oak saplings were significantly more numerous on south aspects. Ponderosa pine saplings numbered 7,010 per ha on the south aspect versus 3,410 saplings per ha on the north. Sapling density for California black oak was 1,280 per ha on the south aspect and 500 per ha on the north (*table 4*). Three additional conifer and one hardwood species were significantly more numerous on the north aspect. These were sugar pine (1,860 saplings per ha on the north versus 660 on the south), Douglas-fir (4,400 versus 2,810), California white fir (5,780 versus 1,810), and tanoak (11,870 versus 3,470).

Development

When analyzed by opening size, ponderosa pines were significantly taller in 27-m openings (215 cm) than in 9-m openings (84 cm), and California white fir saplings were significantly taller in 18-m openings (256 cm) than in 9-m openings (104 cm) (*table 5*). For hardwoods, California black oak saplings were significantly taller in 18-m openings (214 cm) and 27-m openings (260 cm) than in 9-m openings (45 cm). Pacific madrone saplings were significantly taller in 27-m openings (470 cm) than in 9-m openings (209 cm), whereas saplings in 18-m openings (352 cm) were intermediate.

When analyzed by aspect, several conifer and hardwood species were taller on the south aspect than on the north (*table 6*). California black oak was the exception. Sugar pine (444 cm on south versus 107 cm on north), Douglas-fir (224 cm versus 75 cm), California white fir (214 cm versus 135 cm), and tanoak (242 cm versus 179 cm) were the only species that were significantly taller.

Analysis of root collar diameters by species showed that the smallest average diameter occurred in the 9-m openings without exception (*table 7*). For species

Table 5—*Average height of conifer and hardwood saplings on all aspects in three sizes of group-selection openings, Challenge Experimental Forest, 1991*

Species	Opening size (m)			
	9	18	27	SE[1]
	Height (cm)			
Conifers				
Ponderosa pine	84.1 a[2]	145.7 ab	214.9 b	22.3
Sugar pine	86.4 a	217.2 a	406.8 a	92.4
Douglas-fir	86.4 a	173.8 a	233.1 a	34.1
California white fir	103.9 a	255.9 b	173.5 ab	20.8
Incense-cedar	58.1 a	102.8 a	92.2 a	20.1
Hardwoods				
Tanoak	179.1 a	226.9 a	244.2 a	18.5
Californiablack oak	45.0 a	214.1 b	259.9 b	33.8
Pacific madrone	209.2 a	352.1 ab	469.6 b	40.5
Bigleaf maple	371.2 a	-	427.0 a	208.0
Pacific dogwood	118.1 a	399.0 a	115.5 a	56.8

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Table 6—*Average height of conifer and hardwood saplings for all opening sizes on north and south aspects, group-selection cutting, Challenge Experimental Forest, 1991*

Species	Aspect		
	North	South	SE[1]
	Height (cm)		
Conifers			
Ponderosa pine	107.0 a[2]	183.8 a	23.1
Sugar pine	106.7 a	444.1 b	85.2
Douglas-fir	74.7 a	224.3 b	32.6
California white fir	134.6 a	214.1 b	22.3
Incense-cedar	62.5 a	101.1 a	19.4
Hardwoods			
Tanoak	179.3 a	241.5 b	18.0
California black oak	227.3 a	181.3 a	37.2
Pacific madrone	303.2 a	409.7 a	43.9
Bigleaf maple	371.2 a	427.0 a	208.0
Pacific dogwood	147.0 a	265.8 a	63.8

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

with statistically significant differences in root collar diameter, that of ponderosa pine was largest in 27-m openings (23.3 mm) versus 9-m openings (8.4 mm); California white fir was largest in 18-m openings (33.1 mm) versus 9-m openings (15.8 mm); California black oak was largest in 18- and 27-m openings (21.0 and 25.5 mm respectively) versus 9-m openings (5.1 mm); and Pacific dogwood was largest in 18-m openings (41.3 mm) versus 9- and 27-m openings (10.7 and 12.9 mm, respectively).

When all openings sizes were combined and results presented by aspect, average root collar diameter was largest on the south aspect for almost all species of conifers and hardwoods (*table 8*). Ponderosa pine, sugar pine, Douglas-fir, California white fir, and tanoak all had statistically larger diameters when growing on a south aspect. No species had a statistically larger mean diameter on a north aspect.

Table 7—*Average root collar diameter of saplings on all aspects in three sizes of group-selection openings, Challenge Experimental Forest, 1991*

Species	Opening size (m)			
	9	18	27	SE[1]
	Diameter (mm)			
Conifers				
Ponderosa pine	8.4 a[2]	16.4 ab	23.3 b	2.5
Sugar pine	12.0 a	33.5 a	71.0 a	17.7
Douglas-fir	12.4 a	22.0 a	31.1 a	4.5
California white fir	15.8 a	33.1 b	23.4 ab	2.8
Incense-cedar	9.4 a	19.4 a	15.9 a	4.0
Hardwoods				
Tanoak	29.0 a	37.1 a	38.8 a	3.9
California black oak	5.1 a	21.0 b	25.5 b	2.8
Pacific madrone	25.0 a	46.1 ab	71.5 b	6.9
Bigleaf maple	28.2 a	-	37.0 a	18.3
Pacific dogwood	10.7 a	41.3 b	12.9 a	5.2

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Table 8—*Average root collar diameter of saplings for all opening sizes on north and south aspects, group-selection cutting, Challenge Experimental Forest, 1991*

Species	Aspect		
	North	South	SE[1]
	Diameter (mm)		
Conifers			
Ponderosa pine	10.4 a[2]	20.8 b	2.5
Sugar pine	14.6 a	77.2 b	16.4
Douglas-fir	9.2 a	30.3 b	4.2
California white fir	16.6 a	30.4 b	2.7
Incense-cedar	9.5 a	18.7 a	3.9
Hardwoods			
Tanoak	22.9 a	43.2 b	3.4
California black oak	19.8 a	19.0 a	3.2
Pacific madrone	38.9 a	60.4 a	7.5
Bigleaf maple	28.2 a	37.0 a	18.3
Pacific dogwood	16.1 a	27.3 a	6.1

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Shrubs, Forbs, Graminoids, and Ferns

Density

Twenty-eight years after site preparation, shrubs in the small openings were characterized by those that tolerate shade. The most abundant shrub was western poison oak (*Toxicodendron diversilobum* [Torrey and A. Gray] Greene) followed in decreasing order by honeysuckle (*Lonicera hispidula* Douglas var. *vacillans* A. Gray) and wood rose (*Rosa gymnocarpa* Nutt.). These and the other 13 shrub species numbered 15,750 per ha in 9-m openings, 37,250 in 18-m openings, and more than 37,800 per ha in 27-m openings (*table 9*). The two larger opening sizes had a significantly higher shrub density than that in the smallest opening size.

The three most abundant forbs, all perennials, were a species of iris (*Iris hartwegii* Baker), western starflower (*Trientalis latifolia* Hook.), and a milkwort (*Polygala cornuta* Kellogg). Total forb density was 122,480 per ha in 9-m openings, 115,310 in 18-m openings, and more than 161,000 in 27-m openings (*table 9*). Forb density did not differ statistically among opening sizes.

Graminoids, chiefly species of brome (*Bromus* spp.) and sedge (*Carex* spp.), had densities of 23,500 per ha in 9-m openings and over 15,000 per ha in 18- and 27-m openings (*table 9*). Graminoids did not differ statistically among opening sizes.

Bracken fern, which typically is found in more open environments on the Experimental Forest, increased steadily in density as opening size increased: 8,380 per ha in 9-m openings, 12,740 in 18-m openings, and 21,510 in 27-m openings (*table 9*). Fern density differed significantly between the 9- and 27-m opening, but not with the 18-m opening.

When shrubs, forbs, graminoids, and fern were analyzed by aspect, density was consistently greater on the south aspect. Statistical differences in number of plants per ha on north versus south aspects occurred for shrubs (20,990 versus 36,470), graminoids (3,670 versus 27,620), and bracken fern (9,120 versus 17,600) (*table 10*). Forbs numbered 106,620 per ha on north slopes and 150,490 on south slopes, but did not differ statistically.

Development

Height of shrubs, forbs, graminoids, and ferns on all aspects varied among opening sizes, but no trend was discernible (*table 11*). For those classes of vegetation where statistical differences occurred, shrubs were significantly taller in 18-m openings than in 9-m openings and intermediate in 27-m openings.

Table 9—*Average density of shrubs, forbs, graminoids, and ferns on all aspects in three sizes of group-selection openings, Challenge Experimental Forest, 1991*

Species	Opening size (m)			
	9	18	27	SE[1]
	Density (no./ha)			
Shrubs	15,750 a[2]	37,250 b	37,840 b	4,440
Forbs	122,480 a	115,310 a	161,050 a	16,440
Graminoids	23,500 a	15,020 a	15,600 a	5,320
Bracken fern	8,380 a	12,740 ab	21,510 b	2,270
Total	**170,110**	**180,320**	**236,000**	

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Table 10—*Density of shrubs, forbs, graminoids, and ferns over all opening sizes on north and south aspects, group-selection cutting, Challenge Experimental Forest, 1991*

Species	Aspect		
	North	South	SE[1]
	Density (no./ha)		
Shrubs	20,990 a[2]	36,470 b	4,560
Forbs	106,620 a	150,490 a	16,080
Graminoids	3,670 a	27,620 b	4,790
Bracken fern	9,120 a	17,600 b	2,320
Total	**140,400**	**232,180**	

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Bracken fern was significantly taller in 27-m openings than in 18-m openings, whereas 9-m openings were intermediate. Height of shrubs, forbs, graminoids, and bracken fern did not differ significantly between aspects (*table 12*).

Discussion and Conclusions

In this study on the Challenge Experimental Forest in northern California, 48 openings, 9-, 18-, and 27-m in diameter, were created in 1963. The openings were located such that groups of mostly mature trees were harvested along with many individuals of poor form, slow growth, and low development potential.

After site preparation, the mineral soil seedbed provided an excellent medium for seeds of conifers and hardwoods, shrubs, forbs, and graminoids to germinate, and for seedlings to become established. Twenty-four seedcrops of ponderosa pine, sugar pine, Douglas-fir, and California white fir were quantified from 1964 to 1973 (McDonald and Abbott 1994). An additional 13 crops occurred from 1974 to 1981 (McDonald 1992) with even more observed from 1982 through 1991. The large amount of seed, receptive seedbed, and sheltered environment led to the establishment of an excessive number of conifer and hardwood seedlings (27,795 per ha in 1973). Extensive age analysis of seedling stems indicated that most ponderosa and sugar pines became established during the first 15 years after site preparation, with the more tolerant California white fir and Douglas-fir contributing new seedlings to the recruitment pool for an additional 10 years. Of interest, was that tolerant conifer seedlings could become established for 25 years after site preparation in the group selection environment.

Table 11—*Average height of shrubs, forbs, graminoids, and ferns on all aspects in three sizes of group-selection openings, Challenge Experimental Forest, 1991*

	Opening size (m)			
Species	9	18	27	SE[1]
	Height (cm)			
Shrubs	38.7 a[2]	77.6 b	50.2 ab	7.5
Forbs	14.4 a	15.8 a	18.0 a	0.9
Graminoids	37.3 a	32.4 a	33.3 a	4.2
Bracken fern	47.0 ab	45.2 a	59.1 b	2.7

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Table 12—*Average height of shrubs, forbs, graminoids, and ferns over all opening sizes on north and south aspects, group-selection cutting, Challenge Experimental Forest, 1991*

	Aspect		
Species	North	South	SE[1]
	Height (cm)		
Shrubs	53.1 a[2]	57.1 a	8.0
Forbs	13.2 a	18.0 a	0.8
Graminoids	22.8 a	40.2 a	3.8
Bracken fern	52.1 a	51.3 a	3.0

[1]SE = Standard error.

[2]For each species, means followed by the same letter do not differ at the 0.1 level.

Although seeds were plentiful, quality seedbeds were scarce. We noted numerous month-old seedlings of all conifer species, especially ponderosa pine, after each seedcrop. Apparently, recruitment was difficult because favorable microsites already were occupied by established vegetation. At the end of the study in 1991, conifer and hardwood saplings averaged more than 25,230 per ha, and shrubs, forbs, graminoids, and ferns averaged more than 220,700 per ha.

Not only was the vegetation dense, it also was made up of many species. The number of species in the small shady openings increased in general for the first 14 years after site preparation and then leveled off at about 55 species for the rest of the study. Their origin reflected several classical regeneration strategies (Grime 1979). Most species originated from buried seeds in the soil, from seeds blown in by the wind, and from rhizomes beneath the soil surface. Together, they formed a community dominated by conifer and hardwood saplings with a large component of shrubs and mostly perennial forbs. Most of the shrubs were low in stature and tolerant of shade. Bracken fern and graminoids were present in almost all openings. Bracken fern tended to be more abundant in larger openings on south aspects, and the graminoids had more plants in the smallest openings on south aspects.

The environment in which the various plant species had to become established and survive was characterized in general by shade and the use of site resources by trees adjacent to the openings. High plant density within openings was another influence. Opening size and aspect, in general, also influenced plant species density and development. Larger openings apparently provided more area free of edge effects and hence more available site resources. Higher density and better development tended to occur in the central portion of the larger openings. Aspect seemed to correlate to the shade tolerance of some species. However, for many species, density and development did not differ among opening sizes or between aspects.

Development of almost all vegetation was poorest in the 9-m diameter openings. This opening size probably is too small to be considered for operational application. Roots of adjacent trees probably extend throughout openings of this size and deny site resources (soil moisture and light) to new conifer and hardwood seedlings (McDonald and Abbott 1994). Shade-tolerant plant species, however, especially those with no particular need to grow rapidly, found this environment quite suitable. Tanoak seedlings and seedling-sprouts (small seedlings that die back to the root crown and resprout again and again [McDonald 1978]) are a case in point. In this study, the 11,200 tanoaks per ha in the 9-m diameter openings were using a particular regeneration strategy called "seedling bank" (Grime 1979): the bank of tanoak persists; grows slowly, at least above ground; and awaits a major disturbance that will create a more favorable environment.

On the basis of the density and development information in this study, we can project the likely composition of the future plant community. In the short-term, most species are adapted to the environment of the small openings; thus, the number of species, which already has leveled off, probably will remain stable. The current high density of plants, especially the large number of perennial shrubs and forbs, probably will decline because of the ever-increasing size of the conifers and hardwoods, the shade they cast, and their increasing demand for site resources. However, the number of conifer and hardwood saplings also is excessive, and the shorter and weaker members will die. Ponderosa pine saplings, many of which are more than 25 years old and less than 1 meter tall, are particularly vulnerable (*fig. 4*). Their numbers have already declined significantly. In 1973 ponderosa pine amounted to 82 percent of total conifer reproduction; in 1991, it constituted 37 percent of the total.

Figure 4
Growing near the edge of a 27-m opening, this 27-year-old ponderosa pine seedling is less than 1 meter tall.

The relative growth rate of the saplings also is a major influence on the future plant community. In many of the 18- and 27-m diameter openings, saplings of both conifers and hardwoods are expressing dominance and increasing in growth rate. Average height in meters for conifer species and combined hardwoods after 10 years (1973) (McDonald and Abbott 1994) and 18 years later (1991) was:

Species	*1973*	*1991*
Ponderosa pine	0.32	2.15
Sugar pine	0.40	4.07
Douglas-fir	0.40	2.33
California white fir	0.45	1.74
Incense-cedar	0.27	0.92
Hardwoods	0.69	3.03

All species grew at least twice as fast in height the last 18 years as they did the first 10 years. Sugar pine grew more than five times as fast, followed by ponderosa pine and Douglas-fir, which grew more than three times as fast.

Because the development data are an average of a large number of saplings of many ages, they tend to mask individual species development. For example, the tallest tree, in meters, by species were:

Ponderosa pine	11.1
Sugar pine	15.7
Douglas-fir	15.1
California white fir	9.1
Bigleaf maple	11.5

Douglas-fir had by far the largest number of tall saplings. Although the other hardwoods had one or two tall members, most were much shorter. But regardless of species, all saplings had a tall slender form and less taper to the stem than counterparts in more sunlit environments (*fig. 5*).

Long-term, the tree component in the group-selection openings is converting from a primarily ponderosa pine stand to a mixed conifer and hardwood stand dominated by the more shade-tolerant species. Ponderosa pine will continue to be present but generally limited to the centers of the larger openings. Overall, the vegetative component of the small openings will continue to be robust. And the protection to the soil furnished by all the plants, plus the thick carpet of needles, leaves, and other organic material that is developing, suggest that the inherent productivity of the site will be maintained.

Earlier, McDonald and Fiddler (1993) suggested that the field of vegetation management be expanded to include *indirect* vegetation manipulation techniques. In indirect vegetation management, the environment manipulates vegetation, not human-caused treatments such as manual grubbing, grazing, or applying herbicides. Key natural elements in the environment that can be used by vegetation managers are organic matter and shade. In southeastern Arkansas, for example, Shelton (1995) found that increasing amounts of organic matter decreased both the number of natural loblolly pine (*Pinus taeda* L.) seedlings and the amount of competing vegetation. In the group-selection openings of this study, shade caused aggressive sunlight-adapted species in the genera *Arctostaphylos*, *Ceanothus* , and *Rhamnus* to develop poorly. More specifically, they grew tall and slender—unlike their traditional bushy form in areas with more sunlight. The weakened shrubs eventually die—a trend we noted in this study and one that intensified with time (McDonald and Abbott 1994). Thus, the normally aggressive shrub species were never really competitive, and the few that remained at the end of the study were moribund.

Figure 5
In 1991, or 28 years after site preparation, the openings are full of slender conifer and hardwood saplings such as California white fir and tanoak.

Although the opening sizes studied here are at the lower end of the size range associated with group selection, findings from them contribute to the application of this regeneration cutting method. Stands can be regenerated with a diversity of species while maintaining high forest cover; the reproduction, although still too numerous, should continue to grow and even accelerate in growth in the future—forming a spatially distinct age class.

Certainly, the plant community of the openings in this study is distinct from the plant community in the uncut forest surrounding them. This uncut area is characterized by conifers and an understory of tanoak and suppressed incense-cedar saplings and trees. The ground is covered with a thick carpet of leaves and needles and scattered tanoak seedlings and seedling-sprouts. A few incense-cedar and Douglas-fir seedlings also are present, but most are so suppressed that growth is limited and future mortality is virtually assured.

Silviculturists traditionally apply a controlled disturbance to a forested ecosystem to create a desired species composition, number of plants, and stand structure that will yield the amenities and commodities needed by society. Inherent in this disturbance is a goal to guide the course and rate of secondary plant succession toward a mature forest. This is accomplished by enhancing the environment for desired species and making it unsuitable for undesirable species. After 28 years the small openings in this study that were created by group-selection cutting provide the silviculturist with a method to naturally convert essentially a one-species stand to that of several desired species, and to naturally exclude undesirable species of aggressive shrubs.

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