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Edge effects in mixed conifer group selection openings: tree height response to resource gradients

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Abstract

Replicated circular openings ranging in size from 0.1 to 1 ha were cleared on a Sierran mixed conifer forest in 1996 at the Blodgett Forest Research Station, California and planted with seedlings of six native species. After 3 years of growth, heights of all trees were measured and analyzed according to species, opening size, and location within the opening. To determine the cause of the edge influence on height, we measured differences along north–south transects in extension growth, pre-dawn water potential, and light availability for three species of trees: giant sequoia (Sequoiadendron giganteum), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Ptseudotsuga menziesii* var. *menziesii*). The sequence of mean height from tallest to shortest based on species was: giant sequoia > incense cedar > Douglas-fir > ponderosa pine > white fir > sugar pine. For all species combined, a ten-fold increase in the area of the opening corresponded to a 34% increase in mean height. Trees were tallest on average in the north rows and shortest in the south rows. There was no difference in height between trees in the east and west rows. As expected, resource availability was greatest near the center and least near the edges with north edges receiving significantly more light than southern edges. In general, observed edge effects on sapling height growth were correlated with light and water supply. However there were important differences between species in the nature of the co-limitation. Giant sequoia growth was most sensitive to light and water availability. Together they explained more than 47% of the observed variation in giant sequoia height. In contrast, only light was a significant predictor of ponderosa pine performance. Douglas-fir heights were significantly related to both light and water but there was more unexplained variability in the Douglas-fir model compared to the other species. These highly controlled experimental group openings provide a standard reference for silviculturalists using the group selection method of regeneration.

Keywords: Silvicultural systems; Edge effect; Blodgett forest research station; Group selection

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1. Introduction

Social, political, and ecological concerns with even-aged forest management have motivated the development of uneven-aged methods that more closely approximate natural forest dynamics (O'Hara,

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2001). Group selection is one uneven-aged alternative that addresses many of the concerns associated with even-aged plantations, but still retains some of the administrative and silvicultural benefits. Group selection management involves the periodic harvest of small groups of trees coupled with some form of stand density control in the matrix of larger trees surrounding the openings. The subsequent openings may be designed to resemble gaps in the canopy that would be caused by natural agents (e.g. fire, insect, disease). Over the long term, a shifting mosaic of small patches develops across forests with group selection management regimes. The most common attribute that silviculturalists associate with the group selection regime is the ability to regenerate a wide variety of commercial species (Daniel et al., 1979; Laacke and Fiske, 1983; Smith, 1986). In California's Sierran mixed conifer forests, group selection has been used as a method for converting homogeneous forest structures into more heterogeneous arrangements (McDonald and Abbot, 1994) and as a method for promoting tree regeneration by mimicking natural disturbances (Stephens et al., 1999). In other forest types, the management regime has been proposed as a means for ecological restoration (Storer et al., 2001), maintaining high species diversity (Lahde et al., 1999; Schutz, 1999), and for managing endangered species habitat (USDA, 1995). The most common goal of research involving artificially created gaps has been to find the appropriate opening size that meets management objectives, particularly successful regeneration and growth of desired species (Coates, 2000; Gray and Spies, 1996; Leak and Filip, 1977; Malcolm et al., 2001; McDonald and Abbot, 1994; Van Der Meer et al., 1999). Indeed, much of the hesitation on the part of forest managers in implementing the group selection management regime comes from the lack of knowledge about the loss of growing space associated with small-sized openings.

The potential loss of productive growing space for regenerating seedlings occurs because of the edge effects in force near the perimeters of openings. In the context of group selection silviculture, the edge refers to the boundary between the opening created by harvesting a group of trees and the matrix of intact forest. Edge effects are defined as the ecological phenomena associated with the environmental gradients that develop across the boundary and extend into the adjacent communities (*sensu* Chen et al., 1992). Often edge effects have been investigated with an emphasis on the influence of openings (e.g. clearcuts, agricultural fields) on the surrounding matrix forest. Openings have been shown to influence interior forests' wildlife composition (Berry, 2001; Hargis et al., 1999; King et al., 1996), vegetation structure (Chen et al., 1992; Hughes and Bechtel, 1997), microclimate (Chen et al., 1995; Raynor, 1971), and nutrient exchange (Weathers et al., 1997). Exceptions where edge effects on both openings and intact forests were studied include Cadenasso et al. (1997), who found that mature forest vegetation in the northeastern United States can create temperature and light gradients that extend 15–20 m into adjacent fields. Studies that have explored the impacts of forest edges on canopy gap environments have focused on issues related to species diversity or regeneration dynamics in the context of gaps as a natural disturbance (e.g. Sipe and Bazzaz, 1994; Brown, 1996; Gray and Spies, 1996). While results from these gap studies have helped forest managers design silviculture methods that imitate natural disturbances, they provide little insight for predicting the effect of edges on the growth and yield of trees within artificially created openings resulting from group selection harvests.

A management scheme where group selection openings are intermixed across a forested landscape would generate a significant fraction of planting areas in edge environments (Gustafson and Crow, 1996). For the smaller openings, edge environments are particularly important because of the high edge-to-interior ratio (Forman and Gordon, 1986). Bradshaw (1992) emphasized the importance of recognizing edge effects when making management decisions and suggests quantifying edge effects as a dominant means for choosing among uneven- and even-aged silvicultural options. In California, forest practice regulations define minimum and maximum group opening sizes, but foresters have flexibility in determining the size and number of openings, as well as the regeneration method to use. In cases like the mixed conifer forest where there is more than one potential timber species to be regenerated, the size and strength of the effect of the edge on performance will likely vary between species.

Given the potential widespread implementation of group selection silviculture in the Sierra Nevada, a long-term project was established at Blodgett Forest Research Station (Georgetown, California) to evaluate the performance of this management regime. The goal of this paper is to quantify the extent of edge effects on seedling height across a typical range of group selection opening sizes. We focused on the initial patterns in growth that developed by the end of the third growing season. In addition, we asked how the gradients in light and water availability that develop across the forest-opening boundary influence species-specific height responses. Our hope is to gain a better understanding of which aspects of the edge environment were limiting the potential growth of planted seedlings in group selection management systems.

2. Methods

2.1. Study site

Blodgett Forest Research Station (BFRS) is located on the western slope of the Sierra Nevada mountain range in California (38°52′N; 120°40′W). The study area lies within BFRS at an elevation between 1220 and 1310 m. The climate is Mediterranean with dry, warm summers (14–17 °C) and mild winters (0–9 °C). Annual precipitation averages 166 cm, most of it coming from rainfall during fall and spring months, while snowfall typically occurs between December and March. The soil is from granodiorite parent material and is highly productive for the region. Heights of canopy trees typically reach 27–34 m in 50–60 years (BFRS data). Olson and Helms (1996) provide a detailed description of Blodgett Forest, its management, and trends in forest growth and yield.

Vegetation at BFRS is dominated by the mixed conifer forest type, composed of variable proportions of five coniferous and one hardwood tree species (Laacke and Fiske, 1983; Tappeiner, 1980). Research sites were all located on the same, north-facing slope (10–25%). Like much of the mixed conifer forests in the Sierra Nevada range, the study area was clearcut in the early 1900s and allowed to regenerate naturally. The forest has developed to form a mixed species canopy, averaging 30 m in height (BFRS data). There are six native dominant tree species including white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii)*, sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa)*, and California black oak (*Quercus kelloggii*). In addition, BFRS plants giant sequoia (*Sequoiadendron giganteum*), a species that is currently non-native, but in the past had an expanded range that encompassed BFRS (Harvey, 1985).

2.2. Experimental design

Group selection silviculture in California involves removing trees in distinct groups, which have opening sizes legislatively mandated to be between 0.1 and 1.0 ha. (California Department of Forestry, 2002). California forest regulations give landowners the option of artificially planting the openings, or relying on natural seed fall or advanced regeneration. The harvesting and site preparation methods we used in this experiment (described below) are typical of those used by a forest landowner whose main objective is timber production.

The groups were harvested during the summer of 1996. Four opening sizes representing the range of allowable sizes (0.1, 0.3, 0.6, and 1.0 ha) were replicated three times (12 openings total). Although forest managers are likely to deviate from opening shapes of perfect circles because of local topography and considerations for logical harvesting units, our openings were cut as close to circular as possible. They are round so that: (1) the total edge-to-interior ratio is minimized, and (2) the only spatial difference between edges at different locations within the same opening is the orientation relative to the center of the opening and the forested matrix. All trees within the groups were cut with chainsaws and yarded with a rubber-tired skidder. During the same year, site-preparation was done by cutting non-merchantable trees and by piling slash for burning on site. After site preparation, the openings were mostly bare ground with some cover of litter and woody debris. During the Spring of 1997 the openings were planted in a ‘‘wagon wheel’’ design (Fig. 1). In all openings, each of six species (Douglas-fir, incense cedar, white fir, ponderosa pine, sugar pine, and giant sequoia) were planted in rows extending from the center towards the edge in all cardinal and inter-cardinal directions. Douglas-fir, incense cedar, white fir, and ponderosa pine were planted from bare-root stock. Sugar pine and giant sequoia were from

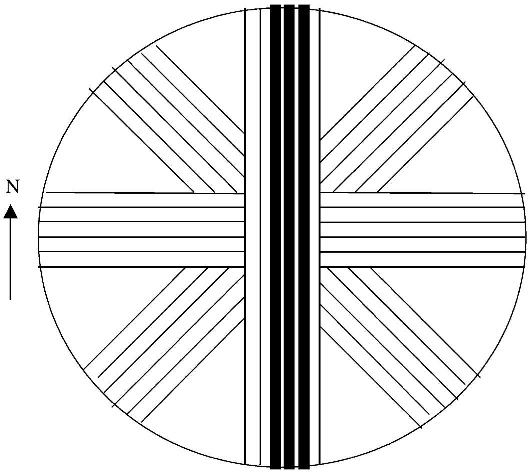

Fig. 1. Overhead view of the "wagon wheel" planting design in openings created at Blodgett Forest Research Station, California. Each line represents a row of the same species planted along cardinal and inter-cardinal directions (six species: Douglas-fir, giant sequoia, incense cedar, ponderosa pine, sugar pine, and white fir). Study trees were sampled along the lines in bold.

container stock. Planting spots were double-planted at every 3 m along the rows, ending at the drip-line of the surrounding forest edge. Rows were spaced 3 m apart, and equal 3 m × 3 m spacing around each planting spot was ensured by filling in gaps between rows with planted trees not included in the study. Competing non-tree vegetation was controlled with both hand-tools and herbicides. At the end of the third growing season (1999), the less-vigorous individual of the double-planted pair was removed and the heights of the remaining trees were measured ($n = 4323$). These third-year height data were used to detect any patterns in growth among species or across opening sizes and to delineate the extent of edge zone influence.

2.3. Study tree measurements

2.3.1. Species and sample locations

In July 2000 (i.e. during the fourth growing season), we quantified the gradients in light and water availability and their relationship to height growth by measuring three variables on a subset of study trees: water potential, light availability, and current year's height extension. We limited the study trees to three species: Douglas-fir, ponderosa pine, and giant sequoia. Not only are these species likely to be planted on a commercial scale by landowners, but they also represent a range of tolerance to shade. Subjective rankings of these species according to their relative shade tolerances have classified Douglas-fir as mid-tolerant and ponderosa pine and giant sequoia as intolerant (Baker, 1950; Minore, 1979; Weatherspoon, 1990). These rankings have generally held true in studies of survival and growth response to shade stress (Emmingham and Waring, 1973; Minore, 1979; Oliver and Dolph, 1992; Stark, 1968). In each opening, nine study trees of each species were measured (27 total per opening). We examined influences of light and water availability on height extension from three within-opening locations: north edges, south edges, and centers. The north and south edge samples included the three closest trees to the edge (0, 3, and 6 m away from the drip line). The center trees sample was comprised of the tree closest to the center of the opening plus the two trees spaced 6 m north and south of the center tree. Trees along the north and south rows were chosen because these positions likely represent the widest range of abiotic differences within the opening. For example, Canham et al. (1990) found the steepest gradients in incident radiation along north–south axes of gaps, and Heinemann et al. (2000) found highest within-gap moisture availability along northern edges for gaps in a southern hemisphere temperate forest.

2.3.2. Light availability

Hemispherical photography was used to estimate light availability. Photographs were taken looking upward just above the terminal leader of each study tree using a fish-eye lens (Nikkon 8 mm f/2.8) that provides a 180° view of the canopy. Color slides were taken early or late in the day when the sun was low in the sky. Slides were converted to digital images (900 dpi) using a Nikon CoolScan slide scanner. By restricting photo acquisition to near-isotropic sky conditions, we minimized the need for digital image enhancement.

We analyzed the digital images using the Gap Light Analyzer (version 2.0.4) image processing software (Frazer et al., 2000) to calculate the percent of total transmitted radiation (%TT). The %TT measurement provides a robust estimate of long-term average light levels as well as precise information about the geometry of light penetration through the forest openings

(Battles, 1999; Canham et al., 1990). Specifically, %TT estimates the percentage of incident photosynthetically active radiation (PAR) transmitted to a point in the understory during the growing season. Values range from 0% for a completely closed canopy to 100% for a completely open site. Incident PAR was calculated from standard equations of solar geometry and a site-specific atmospheric transmission coefficient (K_T). We computed the growing season K_T from daily solar flux data collected above the canopy of a nearby stand. Note that %TT is a theoretical estimate of PAR based on canopy architecture measured via fisheye photography and modeled inputs of above-canopy solar radiation. We calculated precision from a subset of randomly chosen photos (>5% of the total). Relative root mean square error of the %TT estimate was 2%.

2.3.3. Water availability

We used a pressure chamber (Pressure Measurement Systems) to estimate relative degrees of moisture stress due to above and below ground factors. Pre-dawn measurements were taken during July 1999 when the soils at Blodgett Forest were no longer saturated from spring snow melt but had not yet reached late-summer drought status (J. Battles, unpublished data). This seasonal trend in soil moisture status is typical of the Sierra Nevada (Ziemer, 1964; Arkley, 1981; Anderson et al., 1995; Royce and Barbour, 2001). By sampling in July, we maximized our ability to detect any within-opening gradients in water potential.

For each opening we measured all of the study trees in one morning (pre-dawn). We sampled twigs from giant sequoia and Douglas-fir, and fascicles from ponderosa pine. For specific methods of collecting and measuring samples, we followed recommendations of Ritchie and Hinckley (1975). Samples were collected from the current year's growth near the middle of the plant's crown. We used a hand-shear to cut the twig samples and pulled fascicle samples off by hand. All samples were immediately measured for xylem water potential (MPa) after collection. We randomly remeasured 30% of the sample trees to calculate precision error, which was ±15% of the mean. Such a high precision error is partially attributable to the fact that the remeasurements were not actually precision checks since during the first measurement, the sample used in the pressure chamber was destroyed. The second sample from a precision check tree was collected within about 10 min after measuring the first sample from approximately the same location on the tree (mid-crown). Variability in water potential readings, therefore, resulted from differences arising from time between readings as well as locations on the plant.

2.4. Data analysis

Our data analysis had two main objectives: (1) estimate the magnitude of effect that different factors have on tree height growth and (2) model height growth as a function of environmental gradients. Therefore, our statistical approach was geared more toward measuring the uncertainty in our estimates rather than strict hypothesis testing. With sample sizes in some instances exceeding 4000 trees, we had the power to resolve very small height differences, which may or may not be meaningful from an ecological or management perspective.

We primarily relied on general linear models to assess the uncertainty in our data. We note in the text when it was necessary to transform the response variables to meet the assumptions of the model. In most cases the extent of our analyses was to determine whether an independent variable could explain a significant fraction of the observed variation in the data. When we did perform post-hoc comparisons, we used Tukey's simultaneous tests.

We used ordinary least squares to construct explanatory models to our data. The north–south trend in tree height was fit to a quadratic function of relative distance from the north edge. To examine the amount of variance in extension height growth explained by edge to center gradients in the light and water regime, we ran a multiple regression for each species with height growth as the response variable and %TT and pre-dawn water potential as the predictor variables.

3. Results

3.1. Patterns in third year height

Mean third-year height of all trees differed by species (Fig. 2, $F_{5,4326} = 855.6$, $P < 0.001$), by opening size

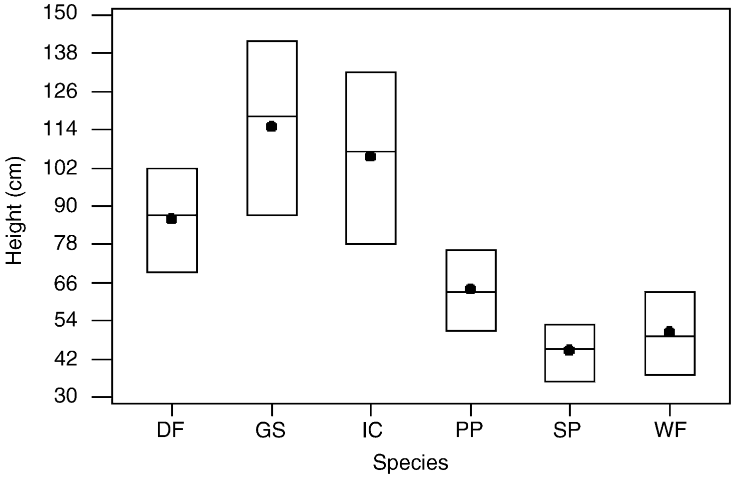

Fig. 2. Third year height data for each species from a complete census ($n = 4342$; approximately even mix of species) of trees with group selection openings at Blodgett Forest Research Station, California. The horizontal lines inside the bars represent the medians; the dark circles represent the means; the vertical bars represent the interquartile ranges of the data points around the medians; DF = Douglas-fir, GS = giant sequoia, IC = incense cedar, PP = ponderosa pine, SP = sugar pine, WF = white fir.

(Fig. 3, $F_{3,4326} = 77.9$, $P < 0.001$) and by row orientation (Fig. 4., $F_{7,4326} = 14.1$, $P < 0.0001$). The sequence from tallest to shortest based on species was: giant sequoia > incense cedar > Douglas-fir > ponderosa pine > white fir > sugar pine (Fig. 2). This sequence was the same for each of the 0.3, 0.6, and 1.0 ha opening sizes. For the 0.1 ha opening size the sequence was: giant sequoia > Douglas-fir > incense cedar > ponderosa pine > white fir > sugar pine. Mean tree height increased with opening size. A

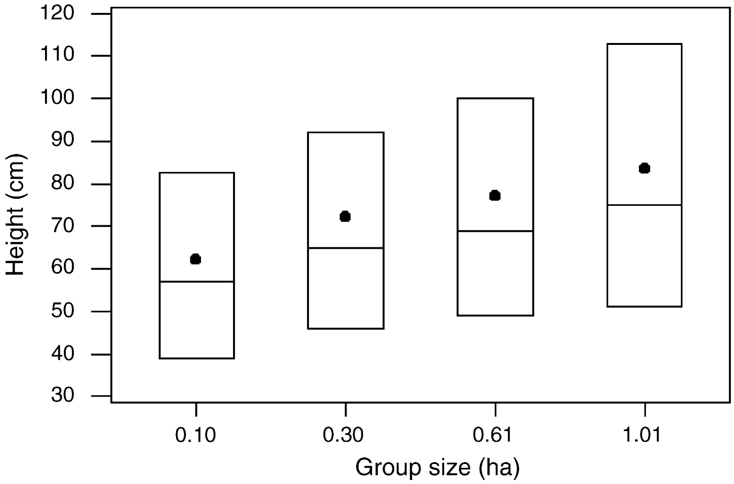

Fig. 3. Third year height data for each opening size with all species combined ($n = 4342$; approximately even mix of species) from group selection openings at Blodgett Forest Research Station, California. The horizontal lines inside the bars represent the medians; the dark circles represent the means; the vertical bars represent the interquartile ranges of the data points around the medians. Species include Douglas-fir, giant sequoia, incense cedar, ponderosa pine, sugar pine, and white fir.

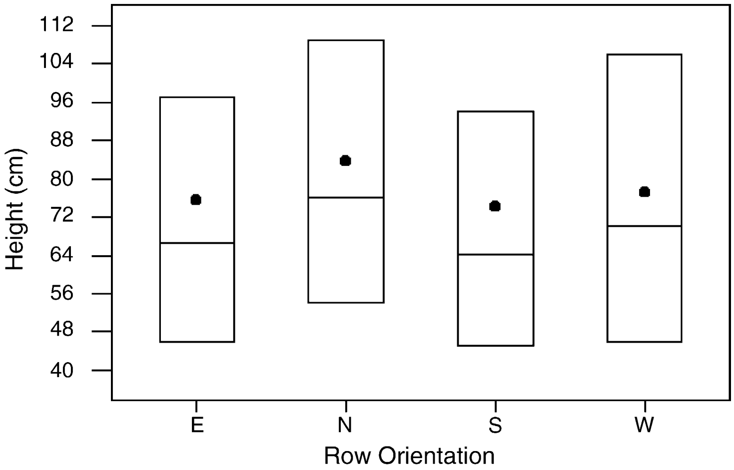

Fig. 4. Third year height data according to the direction of planted rows from center towards edge with all species and opening sizes combined ($n = 4342$; approximately even mix of species) at Blodgett Forest Research Center, California. The horizontal lines inside the bars represent the medians; the dark circles represent the means; the vertical bars represent the interquartile ranges of the data points around the medians. Species include Douglas-fir, giant sequoia, incense cedar, ponderosa pine, sugar pine, and white fir.

ten-fold increase in the area of the opening corresponded to a 34% increase in mean height (Fig. 3). Trees were tallest on average in the north rows (mean = 83.8 cm, S.E. = 1.4 cm) and shortest in the south rows (mean = 74.2 cm, S.E. = 1.9 cm). There was no difference in height between trees in the east and west rows (Fig. 4).

Trends in height along the north–south transects followed a unimodal pattern for all three study species, with quadratic functions providing reasonable fits to the data (Fig. 5). Maximum height for all three species was north of center and minimum height was at the south edges of openings. Giant sequoia trees had an especially large difference in height between center and edge locations. In particular, there was a sharp reduction in height of giant sequoia trees near the south edges of openings. Ponderosa pine and Douglas-fir heights changed along the transects like giant sequoia, but did not show the same degree of sensitivity to edge proximity. Heights grouped into center, south edge, and north edge zones had similar within group patterns (Fig. 6), where mean height for each species was tallest in the center, and shortest in the south edge zone. Based on the results of Tukey's post hoc comparisons, the probability of observing these patterns due to chance was less than 0.05 in all cases except for the difference between Douglas-fir trees in center and north edge zones.

3.2. Resource gradients

Light availability as measured by %TT varied by within-opening location ($F_{2,118} = 48.9$, $P < 0.001$)

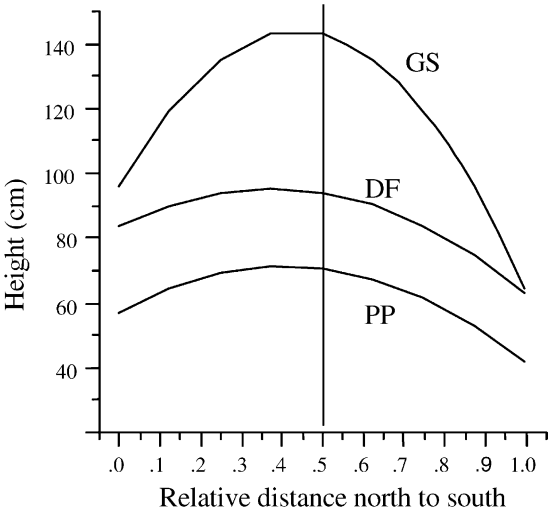

Fig. 5. Heights of trees for all group selection opening sizes combined at Blodgett Forest Research Center, California regressed against relative distance across north–south transects. The vertical line represents the center of the opening. Coefficient of variations (r^2)/sample sizes are Douglas-fir (DF) = 0.31/278; giant sequoia (GS) = 0.39/281; ponderosa pine (PP) = 0.26/282. All fits are significant ($P < 0.001$).

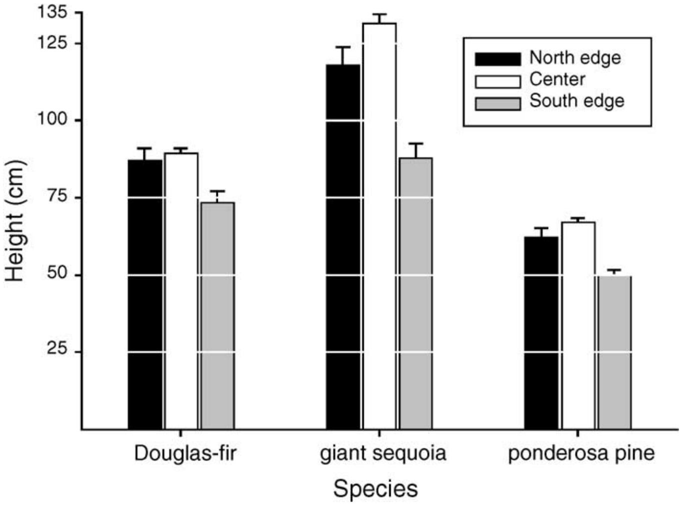

Fig. 6. Mean third year heights of study trees by species (Douglas-fir, giant sequoia, ponderosa pine) and within opening location at Blodgett Forest Research Center, California. Error bar = S.E.M.

and opening size ($F_{3,118} = 10.0$, $P < 0.001$, Fig. 7). Mean light availability within opening sizes ranged from 78% (S.E. = 2.4) in the 1.0 ha opening to 54% (S.E. = 3.5) in the 0.1 ha opening. Not only was there a greater fraction of incident light available near the center of openings (81%, S.E. = 1.6) compared to edges (58%, S.E. = 2.4) but also the north edge trees received more %TT than trees in the south edge (Fig. 7,

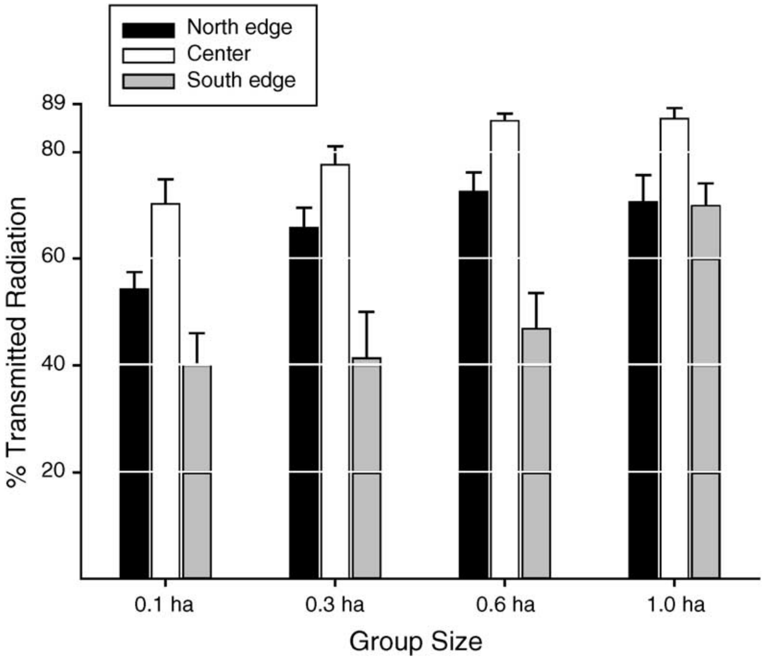

Fig. 7. Mean percent transmitted radiation available to study trees by opening size and within opening location at Blodgett Forest Research Center, California. Error bar = S.E.M. %TT is the same for each species (Douglas-fir, giant sequoia, ponderosa pine).

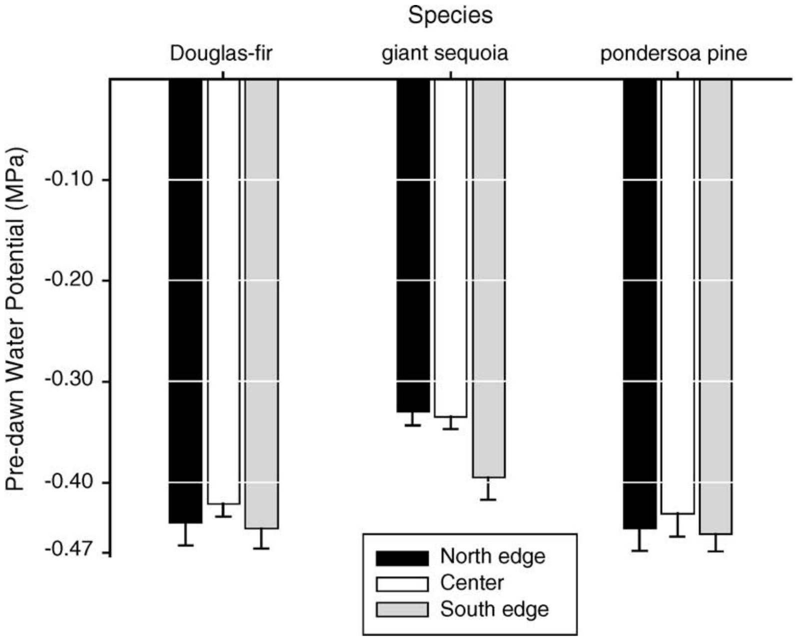

Fig. 8. Mean pre-dawn water potential of study trees by species (Douglas-fir, giant sequoia, ponderosa pine) and within opening location at Blodgett Forest Research Center, California. Error bar = S.E.M.

Tukey's simultaneous test, $P < 0.001$ for all pairwise comparisons). On average, trees on the south edge received only 60% of the light available at the center while trees on the north edge received more than 80% of the light available at the center. Note that %TT is the same for all species since at each sample location where the photographs were taken, all three species were planted at the same distance from the surrounding canopy.

Pre-dawn water potential varied by species ($F_{2,333} = 31.05$, $P < 0.001$), opening size ($F_{3,333} = 4.44$, $P = 0.004$,) and location ($F_{2,333} = 4.35$, $P = 0.014$) with none of the interaction terms important. For this analysis, it was necessary to transform the response variable by the natural log; means are reported as the back-transformed value with the appropriate units. Water potentials measured for giant sequoia trees were less negative (−0.34 MPa) than for the other two species (−0.42 MPa, Tukey's test, $P < 0.001$, Fig. 8). In terms of opening size, the major difference was that mean water potential in the smallest openings was less negative (−0.36 MPa) than in the larger sizes (−0.40 to −0.41 MPa, Tukey's test, $P < 0.05$ for all three comparisons). For within species comparisons, water potential tended to be more negative for trees near the edges compared to the center (Fig. 8), but only the giant sequoia trees along the south edge had water potentials that were consistently more negative than trees growing in the center (Tukey's test, $P < 0.01$).

3.3. Multiple regression

The coefficient of variation (r^2) obtained from the multiple regression models (response variable was natural log transformed) was used to judge the extent of the variation in height extension that could be explained by %TT and water potential combined (Table 1). Leverage plots and associated partial F-tests were used to compare %TT and water potential as contributors to height extension variability. In all cases the model explained a significant ($P < 0.05$) amount of the variation. Giant sequoia had the highest r^2 value, followed by ponderosa pine, then Douglas-fir. %TT was an important ($P < 0.05$) contributor in the model for all three species. Water potential contributed significantly to the Douglas-fir (at $P < 0.1$) and giant sequoia (at $P < 0.05$) models, but was not a

Table 1
Results of multiple regressions[a] for three species growing in group selection openings at Blodgett Forest Research Station, California

Species	*n*	r^2	Partial *F*-test for %TT	Partial *F*-test for water potential
Douglas-fir	64	0.13	$P = 0.04$	$P = 0.09$
Giant sequoia	66	0.47	$P < 0.001$	$P < 0.001$
Ponderosa pine	72	0.20	$P < 0.001$	$P = 0.30$

[a] Fourth year height extension (cm) is the response variable (natural log transformed); light (%TT) and water potential (MPa) are the predictor variables.

significant contributor for the ponderosa pine model (Table 1).

4. Discussion

There are no other studies of planted seedling performance under a Sierran mixed conifer group selection management regime. This study is also unique in that the experimental design purposely followed the silvicultural practices (site preparation, planting, vegetation control) that a typical landowner uses. It is within this management context that we evaluate the effects of group selection silviculture on seedling growth and quantify the influence of the edge environment.

The observed increase in mean seedling height with opening size (Fig. 2) is consistent with studies in other forest types involving artificial gaps (Coates, 2000; Gray and Spies, 1996; Minkler and Woerhide, 1965; Van Der Meer et al., 1999), as well as with many other studies using natural gaps (e.g. Brokaw, 1985). The artificial gaps that we created are larger than those created in the studies mentioned above, but they represent the range of sizes that can legally be used under the group selection regime for Sierran mixed conifer forests. Unlike Coates (2000), who also used both artificial openings and planted seedlings to study the effect of gap size on fifth-year height in a northern temperate forest, we did not find a leveling-off point in growth that was associated with a maximum opening size. Instead, mean height for all species combined increased by 34% between 0.1 and 1.0 ha opening sizes. One similarity with Coates (2000) was the marked difference between species in growth response to opening size. Between 0.1 and 1.0 ha sizes, mean height for giant sequoia increased by 54%, compared to a 28% increase for ponderosa pine, and a 15% increase for Douglas-fir. The fact that non-tree vegetation was suppressed in this study may explain some differences between results of this and other studies. McDonald et al. (1997) studied 4-year old seedlings that regenerated naturally without vegetation control, but did not find a significant opening size effect on seedling height. They suggested the potential for an optimum opening size that limits competition from brush species, while still fostering tree growth. Such an interaction between opening size and level of non-tree competition would be absent in the experimental openings of this study. Monitoring species-specific and opening size-specific patterns of growth over time will be important for assessing long-term performance for the group selection regime.

Like the relationship of opening size with tree height, within opening location had consistent effects on each species, although the strength of the influence varied between the species. The pattern of height rankings according to location (center > north edge > south edge) has been observed in studies of seedling growth in tree-fall gaps (Demetry, 1995; Denslow et al., 1990; Palik et al., 1997). The particular sensitivity of giant sequoia to south edge environments, however, has not been reported. Mean height of giant sequoia seedlings measured from 0 to 6 m away from south edges was 53% less than mean height of giant sequoias measured in center locations. Both Douglas-fir (31%) and ponderosa pine (34%) had obvious height reductions near the south edges, but they were not as extreme as the reductions were with giant sequoia. Heights for the three study species peaked just north of center in the openings (Fig. 5). This pattern of heights is similar to the pattern of light availability which was measured in a different study across north–south transects within the same group selection openings that were used in this study (J. Battles, unpublished data). Although maximum daily temperature is likely to be highest, and relative humidity is likely to be lowest in areas north of center, the increased availabilities of light and soil moisture appear to be benefiting height growth more than the negative influence of any increased vapor pressure deficits.

The change in resource availability typically found in gaps (Canham et al., 1990; Denslow et al., 1990) is thought to have profound ecological consequences

(Ricklefs, 1977). For example, resource gradients can cause differential establishment and survival between species that leads to a predictable spatial distribution of species within a gap, organized by environmental tolerances. Microsite variability in factors important for seedling establishment such as seedbed type, competing vegetation, and woody debris, further explain within opening patterns of species composition and growth (Gray and Spies, 1996; Battles and Fahey, 2000). The within-gap environments of the experimental gaps in this study are undoubtedly more homogeneous than natural tree fall gaps as well as artificial gaps created to mimic natural disturbances. The piling and burning of woody debris with tractors, a common site preparation treatment, created a relatively homogenous substrate and micro-topography across much of the openings. Planting healthy seedlings and controlling competing vegetation (also common cultural practices) made microenvironmental obstacles to seed germination and establishment irrelevant. The reduction of microsite heterogeneity allows us to make a more direct cause-effect relationship between resource gradients and seedling height growth.

Co-limitation along the edges of the openings by light and water resources appears to be occurring in giant sequoia. While other variables contributing to microclimate and genetic differences are likely present, light and water together are sufficient explanations for variation in height growth (Table 1). Giant sequoia seedlings near the south edges had significantly more negative water potentials than the north edge seedlings (Fig. 8). Two potential reasons for the higher moisture stress are large aboveground vapor pressure deficits and strong competition for soil moisture from large root densities. Daily vapor pressure deficits are likely to be higher near the north edges of openings because of higher radiation input (Fig. 7). If there is a difference in matrix tree root densities, it is also most likely to be higher near the north edge, where matrix trees have crowns exposed to sunlight. It is therefore unlikely that high vapor pressure deficits or root competition is causing the more negative water potentials along the south edges. Instead, the low light environment may be limiting root growth and access to soil moisture that is available at lower depths. The dependency of giant sequoia seedlings on adequate soil moisture has been well documented (Harvey and Shellhammer, 1991; Harvey et al., 1980; Schubert, 1962; Stephenson, 1994). Stark (1968), found that planted giant sequoia seedlings growing under low light and high soil moisture environments had relatively high survival rates, but their growth was severely curtailed. Seedlings along the south edges of the openings may be especially challenged to develop the species' drought adaptive two-tiered rooting system (Stark, 1968) because of low light availability and hence may be experiencing greater moisture stress because of limited root growth.

In other studies, Douglas-fir seedling growth has responded to increasing levels of light (Minore, 1988; Oliver and Dolph, 1992). Moreover, its ability to survive drought in mixed conifer forests (Waring and Major, 1964; White, 1987) justifies its typical drought tolerance classifications of moderate to high (Minore, 1979). In this study, light availability and water potential (at $\alpha < 0.1$) were both important in limiting Douglas-fir height extension, but compared to the other species, variation was not well accounted for by these two resources alone (Table 1). As with giant sequoia, Douglas-fir total height growth was limited by the edge environment, with the south edge having the strongest influence, but height extension did not correspond as well as with other species to light and water availability. Other factors adding to growth variation may include herbivory, temperature, microsite differences, and colonizing mycorrhizae from surrounding trees that were not harvested.

Ponderosa pine's physiological adaptations to drought (e.g. Stone and Jenkinson, 1970; Wambolt, 1973)) and intolerance of shade (e.g. McDonald, 1976; Oliver and Dolph, 1992; Oliver and Ryker, 1990) have been well documented. In this study, ponderosa pine was the only species where water potential was not important in explaining variability in height extension. Light availability alone was a good predictor of height growth (Table 1), and thus is likely the dominant influence in limiting ponderosa pine height. The height depressions along the south edges correspond with lower levels of light availability (Fig. 7), but tree heights in the opening centers were not as tall as expected. The relatively large amount of light in the centers of these openings was still not enough for ponderosa pine to achieve dominant heights compared to associated species, as is commonly seen in clearcut and seed tree regeneration harvests (McDonald, 1976). Third-year height for ponderosa pine ranked fourth out of the six species planted and last among the three study species (Fig. 2). However, fourth year height extension ranked second behind giant sequoia (data not presented), indicating a possible delayed surge in growth by ponderosa pine. Soil penetration through preferential root growth instead of shoot expansion is a common strategy of drought tolerant species (Kramer and Kozlowski, 1979) and has been observed in ponderosa pine seedlings (Larson, 1963; Lopushinsky and Beebe, 1976). As more resources are allocated to shoot expansion in the future, we expect ponderosa pine height to rank higher in at least the largest size openings.

Quantifying the area that is influenced by edge effect is arbitrary since it depends on the type of influence under consideration. One method that seems relevant to forest managers interested in growth and yield is to first define the influence to be the sum of edge effect environments that limit seedling height, and then delineate the edge effect boundary at the distance from the edge where height is no longer meaningfully suppressed. Because there is no abrupt increase in height with distance from the edge, the boundary is determined by the amount of growth reduction considered significant. As an example of this method, we used the three study species to find the percent of the opening area influenced by the edge (Table 2). Beginning with trees planted at the drip-line, we compared mean heights between all trees planted at 0 m from the edge to trees planted >0 m from the edge. If there was more than a 25% reduction between the two groups, all drip-line trees were considered to be in the edge environment and the next set of trees closer to the center were included in the next comparison (i.e. trees <3 m away compared to trees >3 m away). This iterative process was repeated until the difference between center and edge trees was less than 25%. Growth reductions of 25% were considered to be meaningful in this case, but other values could be used. Corresponding with its sensitivity to resource gradients, giant sequoia had the highest amount of edge effect area for all three opening sizes (Table 2). Percent edge for ponderosa pine changed the most dramatically from small to large openings. Variability in percent edge for Douglas-fir paralleled the species' height variability. Because the study site was on a north-facing aspect, the edge's influence is likely magnified on the south sides. The influence of aspect and slope on seedling performance in group selection openings has not been quantified.

Table 2
Percent of area influenced by the edge environment within group selection openings for three species at Blodgett Forest Research Station, California

	Percent area influenced by the edge[a]			
Opening size (ha)	0.1	0.3	0.6	1.0
Douglas-fir	16	27	5	1
Giant sequoia	84	68	44	27
Ponderosa pine	79	29	22	1

[a] An area is considered influenced by the edge if the area's mean third year tree height is 25% less than the mean height of trees closer to the center of the opening.

The appropriate opening size for meeting management objectives will change depending on forest type, growing conditions, and management constraints. Fairbairn (1963) recommended a range of 0.13–0.4 ha, while others have expressed the appropriate size in terms of the surrounding forest height. Olson and Helms (1996) suggested a minimum of 1–2 surrounding tree heights for opening diameters in western mixed conifer forests, while Fischer (1980) suggested a minimum of 4–6 tree heights for adequate regeneration of shade-intolerant species. Roach and Gingrich (1968) put forth the idea that there is "no silvicultural reason for limiting maximum size." Forest managers will realize the limitations in the use of this study for recommending appropriate opening sizes. The effect of species, opening size, and within opening position on height found in this study may change by the time thinning treatments or final harvests are implemented. These same variables may change the rankings of species performances by influencing inter-tree competition as resource spaces are occupied through growth. Plans for fifth year measurements will include examinations of mortality and biomass to make a more comprehensive evaluation of performance. The continuation of this study will be important, as the effect of edge is tracked over time. Trees along the edge will approach the stature of the surrounding trees, but the time it takes for edge zone trees to catch up to either center trees or surrounding matrix trees has important management implications. Depending on the rotation age or other harvest intentions of the land owner, the matrix forest surrounding the edge may be harvested, and hence the negative effect of the edge removed. Those trees that were in the edge zone of influence may then become the surrounding trees that influence the new opening.

5. Conclusions

These highly controlled experimental group openings provide a standard reference for silviculturalists using the group selection method of regeneration. It is unlikely that circular openings like these, planted with wagon-wheel designs and even species distributions, will be created in managed forests. However, deviations in shape and species composition from our design can be guided by these results.

These results have implications for silviculturalists developing planting designs for group selections. If forest managers implementing group selection silviculture desire to maximize yield while planting a variety of species in even mixes, specific areas within the openings with different light and water environments can be reserved for the most suitable species. If the three species studied here are used, we recommend planting designs that favor giant sequoia in the centers. Ponderosa pine can be specifically reserved for the north edges, and Douglas-fir can be planted throughout the openings or near edges where microsites appear favorable.

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