

Group selection management in conifer forests: relationships between opening size and tree growth

Robert A. York, Robert C. Heald, John J. Battles, and Jennifer D. York

Abstract: Replicated circular openings ranging in size from 0.1 to 1 ha were cleared in 1996 at Blodgett Forest Research Station, California, and planted with seedlings of six native species. After 5 years of postharvest growth, heights were measured and analyzed according to species, opening size, and location within opening. The sequence of mean height from tallest to shortest, according to species, was as follows: giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz) > incense-cedar (*Calocedrus decurrens* (Torr.) Florin) > Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) ≈ ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) > sugar pine (*Pinus lambertiana* Dougl.) ≈ white fir (*Abies concolor* (Gord. & Glend.) Lindl.). To describe the influence of openings size on seedling height, we use an information-theoretic approach to select from competing models that predicted fifth-year height from group selection opening size. Asymptotic fits (modeled with Michaelis–Menton curves) were selected for giant sequoia, ponderosa pine, sugar pine, and incense-cedar. Quadratic fits were selected for white fir and Douglas-fir. Linear models predicting increasing growth with opening size were consistently ruled out for all species. Although a marked depression in seedling-height growth occurred along the edges within the openings, mean annual radial increment of the 90-year-old border trees surrounding the openings increased by 30%, compared with other canopy trees in the forested matrix between openings.

Résumé : Des ouvertures circulaires répétées dont la dimension variait de 0,1 à 1 ha ont été coupées à blanc en 1996 à la station de recherche forestière de Blodgett en Californie et plantées avec des semis de six espèces indigènes. Après 5 ans de croissance, la hauteur des semis a été mesurée et analysée en fonction de l'espèce, de la dimension de la trouée et de leur emplacement à l'intérieur de celle-ci. De l'espèce la plus haute à la plus basse en moyenne, on retrouve dans l'ordre : le séquoia géant (*Sequoiadendron giganteum* (Lindl.) Buchholz) > le cèdre à encens (*Calocedrus decurrens* (Torr.) Florin) > le douglas de Menzies typique (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) ≈ le pin ponderosa (*Pinus ponderosa* Dougl. ex Laws.) > le pin à sucre (*Pinus lambertiana* Dougl.) ≈ le sapin concolore (*Abies concolor* (Gord. & Glend.) Lindl.). Afin de décrire l'influence de la dimension de la trouée sur la hauteur des semis, nous avons utilisé une approche théorique à base d'information pour choisir parmi différents modèles qui prédisaient la hauteur à la cinquième année à partir de l'ensemble des dimensions des trouées. Des courbes asymptotiques (modélisées avec les courbes de Michaelis–Menton) ont été retenues pour le séquoia géant, le pin ponderosa, le pin à sucre et le cèdre à encens. Des courbes quadratiques ont été retenues pour le sapin concolore et le douglas de Menzies. Les modèles linéaires qui prédisaient une augmentation de croissance en fonction de la dimension des trouées ont été systématiquement écartés pour toutes les espèces. Bien qu'une diminution importante de la croissance en hauteur des semis soit survenue en bordure des trouées, l'accroissement radial annuel moyen des arbres de 90 ans situés en bordure des trouées a augmenté de 30 % comparativement aux arbres dominants ailleurs dans la forêt entre les trouées.

[Traduit par la Rédaction]

Introduction

Today the forests of North America are expected to provide economic, ecological, and recreational services to local,

national, and global communities. Consequently, the public considers forests as highly valued financial and conservation assets. Indeed, the health of the national forests is a pressing concern in the United States (e.g., Healthy Forest Initiative). However, as Kimmins (2002) noted, the rate of change in society's expectation of forestry outpaces the scientific foundation for implementing these new demands. For example, in the American west, social, political, and ecological worries about single-cohort silvicultural systems have motivated demands for multicohort systems that more closely approximate natural forest dynamics (O'Hara 2001) before methods for sound implementation of such systems have been developed or their effects have been assessed.

Group selection silviculture, a practice involving artificial creation of canopy gaps to promote regeneration, is an example of a multicohort system that may help landowners

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meet the multiple expectations of forest management. In theory, group selection mimics the structural and compositional diversity caused by fine-scale natural disturbances resulting in canopy gaps (Smith et al. 1997). In practice, it is a compromise approach for landowners aiming to avoid perceived environmental degradation associated with clearcuts and to avoid the limited productivity associated with single-tree selection (Bliss 2000). Performance evaluations to date suggest that among the variety of silvicultural systems implemented in a management regime, group selection may provide qualitatively distinct combinations of relatively high species diversity and low exotic species abundance, similar to those found in nonharvested stands (Battles et al. 2001). In California's Sierran mixed-conifer forests, experimental trials of group selection have been studied as a method for converting homogeneous forest structures into more heterogeneous arrangements (McDonald and Abbot 1994) and as a method for promoting the process of tree regeneration (Stephens et al. 1999). In other forest types, management practices incorporating group selection have been proposed as a means for restoring ecosystems (Storer et al. 2001), maintaining species diversity (Lahde et al. 1999; Schutz 1999; Hamer et al. 2003), and managing endangered species habitat (USDA Forest Service 1995).

Given its potential as a solution for meeting diverse objectives, group selection has recently been included in proposals for managing forests across regional scales (e.g., Herger-Feinstein Quincy Library Group 1998; USDA Forest Service 2002, 2003). However, managers embracing this development are faced with the challenge of supplying a significant yield of wood products from forests while attempting to stay within operational bounds established by the local disturbance regime. Moreover, scientific information to support these management decisions is often limited.

A major source of uncertainty rests with the details of implementing a group selection regime (Webster and Lorimer 2002). A primary concern is the cost in terms of growth productivity associated with the high edge/interior ratio of smaller openings (Leak and Filip 1977; Laacke and Fiske 1983; Bradshaw 1992; Dale et al. 1995). To address this concern, much of the research involving artificially created gaps has focused on the appropriate (often minimum) opening size that meets management objectives, particularly successful regeneration and growth of desired species within openings (Leak and Filip 1977; McDonald and Abbot 1994; Gray and Spies 1996; Van Der Meer et al. 1999; Coates 2000; Malcolm et al. 2001; McGuire et al. 2001). In more intensively managed forests, work has concentrated on quantifying the influence of opening size and within-opening position on the survival and growth of planted seedlings (Palik et al. 1997; Coates 2000; Gagnon et al. 2003; York et al. 2003). Still, the question of what is the "best" opening size, one that fulfills the multiple promises of group selection silviculture, remains largely unanswered for even well-studied forest ecosystems.

In this study, we addressed the question of the optimal opening size in terms of timber production for group selection silviculture in a Sierran mixed-conifer forest. Our experimental design included a range of opening sizes (0.1–1.0 ha), distributed and replicated across two adjacent management units. We took a standwise perspective in that we

evaluated the influence of opening size on both seedling and adult tree performance. Typically, the impact of openings on the remaining border trees is ignored, yet there is the potential for increased production as a result of release from competition. We used an information-theoretic approach to determine the nature of seedling response to increasing group size. Specifically, we examined whether the relationship between seedling growth (measured using the mean height of 5-year-old seedlings) and group size was best described by a linear, quadratic, or asymptotic function. Each alternative has a fundamentally different implication for forest management in the Sierra Nevada of California. In addition, the explicit integration of a controlled long-term experiment with analyses designed to weigh the strength of competing hypotheses provides an example of how to inform forest management decisions without excessive reliance on significance testing (Perry 1998; Anderson et al. 2000).

Materials and methods

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 of 1220–1310 m above sea level. 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; snowfall typically occurs between December and March. The soil develops from granodioritic parent material and is highly productive for the region. Heights of codominant canopy trees typically reach 27–34 m in 50–60 years (BFRS 2002). Olson and Helms (1996) provided a detailed description of BFRS and its management and trends in forest growth and yield.

Vegetation at BFRS is dominated by mixed-conifer forest composed of five coniferous tree species in various proportions and one hardwood tree species (Tappeiner 1980; Laacke and Fiske 1983). 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 (Beesley 1996), the study area was clearfell harvested for timber extraction in the early 1900s and allowed to regenerate naturally. The young-growth stands at BFRS have developed a mixed-species canopy, averaging 35 m in height and 83 m²/ha in basal area (BFRS 2002). There are six native overstory tree species at the site: white fir (*Abies concolor* (Gord. & Glend.) Lindl.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and California black oak (*Quercus kelloggii* Newb.). In harvested openings, BFRS also plants giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz), a species that is currently not present but in the past had an expanded range encompassing BFRS (Harvey 1985).

Experimental design

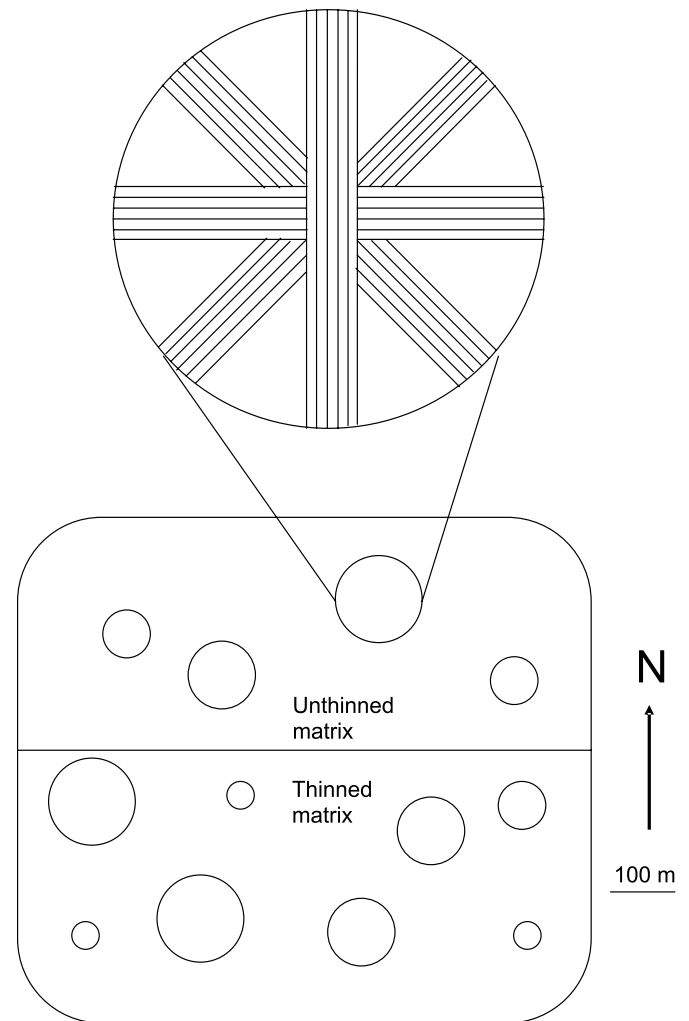
Group selection silviculture includes a regeneration harvest involving the removal of trees in distinct groups, typi-

cally 0.1–1.0 ha in area. Landowners may artificially plant the openings or rely on natural seed fall or advanced regeneration. The forest surrounding the regenerating openings (the matrix) may or may not be managed to influence structure and composition. 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 openings were harvested during the summer of 1996, when 15% of the 34-ha study area was converted to group selection openings. Four opening sizes (0.1, 0.3, 0.6, and 1.0 ha) were replicated three times (12 openings total). The ratios of opening diameter to surrounding canopy height for these opening sizes were 1, 1.8, 2.6, and 3.2. Aerial photography and ground searches were used to locate the group selection openings in areas with >80% canopy cover of about 80-year-old conifers. Opening sizes were then randomly assigned to the 1.0-, 0.6-, and 0.3-ha openings within selected stand areas that appeared large enough to accommodate the gaps within a similar-sized uncut buffer. The 0.1-ha openings were then distributed in the remaining selected area wherever they could fit and still have an associated buffer. In all cases, we attempted to ensure that the areas cut and the surrounding buffers were in similar stands.

Although forest managers are not likely to create openings that are circular because of local topography and considerations for logical harvesting units, our openings were cut as close to circular as possible so that (i) only the opening size and not the shape changed between treatments and (ii) the only spatial difference between edges at different locations within the same opening was the orientation relative to the center of the opening and the forested matrix (i.e., within-opening positions were comparable with respect to edge proximity). 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 nonmerchantable trees and piling slash for burning on site. After site preparation, the openings were mostly bare ground, with substantial cover of litter and small woody debris. During the spring of 1997, the openings were planted in a wagon-wheel design (Fig. 1). In all openings, six species (Douglas-fir, incense-cedar, white fir, ponderosa pine, sugar pine, and giant sequoia) were planted in rows (one species per row) extending from the center toward the edge in all cardinal and intercardinal directions. Douglas-fir, incense-cedar, white fir, and ponderosa pine were planted from bare-root stock. Sugar pine and giant sequoia were from container stock. Planting spots were double-planted (two seedlings within 0.5 m of each other) 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 cardinal and intercardinal rows with planted seedlings, which served as reserves for replacing dead seedlings. Competing non-tree vegetation was controlled with hand tools through the first three growing seasons. At the end of the third growing season (1999), when seedlings were well established, the less vigorous individual of the double-planted pair was removed. Planting spots with both trees dead (5% of all planting spots) were replanted with a nearby reserve seedling of the same species.

Fig. 1. Study area and planting design at Blodgett Forest Research Station, California. The circles in the lower diagram of the study area are scaled to represent the opening sizes (0.1, 0.3, 0.6, and 1.0 ha). The wagon-wheel planting design is illustrated above. Each line represents a row of the same species planted along cardinal and intercardinal directions (six species: Douglas-fir, giant sequoia, incense-cedar, ponderosa pine, and white fir).



Half of the study area (Fig. 1) was treated with a stand-thinning from below in 1985, when basal area was reduced by 6.2 m²/ha. The thinning was designed to allow retained overstory trees to fully occupy the site within 10 years. Group selection opening harvests were delayed until 1996, when regenerating seedlings were surrounded by a closed-canopy forest throughout the study area. In the analysis of border and matrix trees, the potential effect of stand density on postharvest growth response is incorporated as a categorical variable, with trees being from the thinned ($n = 120$) or the nonthinned ($n = 79$) portion of the study area.

Measurements

Five years after planting, we measured the heights of all planted seedlings ($N = 4340$) and basal diameters from a sample of seedlings ($n = 1653$). To measure the growth of border trees, we measured radial increments on cores collected at breast height from a systematic sample of trees sur-

Table 1. A priori model alternatives and their implications for the relationship between mean seedling height and group selection opening size.

Model alternative	No. of parameters (<i>K</i>)	Biological implication	Management implication
1. Linear	2	Seedling height increases with opening size across the size range 0.1–1.0 ha	Seedling height is maximized in the largest opening size
2. Quadratic	3	Seedling height increases with opening size and then decreases in the larger opening sizes	Larger opening sizes can have a negative effect on seedling height
3. Asymptotic (Michaelis–Menton)	2	Seedling height increases with opening size and then levels off above a certain opening size	Above a threshold, increases in opening size return comparatively little in increasing seedling height

rounding all openings. Starting at due north of center, we collected cores from trees at 40° intervals until we had covered the entire perimeter. Cores were collected from the side of the boles perpendicular to the edge (i.e., facing neither the opening center nor the matrix). Trees were cored to a depth of at least 10 years of growth, to encompass the period both 5 years before and 5 years after the harvest. Border trees were at least 15 cm diameter at breast height (DBH) and had at least 50% of their crowns exposed to the interiors of the openings. We collected cores from 125 border trees, the distributions among the species representing the mix of species in the surrounding canopy (Douglas-fir, $n = 50$; incense-cedar, $n = 24$; ponderosa pine, $n = 16$; white fir, $n = 35$). Although sugar pine and black oak are constituents of the Sierran mixed-conifer canopy, they were not measured because of scarcity in the local canopy.

The matrix trees between the openings formed the reference sample with which border-tree growth was compared. Matrix trees had to be at least 15 cm in diameter and have a canopy status of codominant (receiving direct light from above) or dominant (receiving light from above and at least one side). Trees selected for coring ($n = 74$) were sampled from a 60 m × 60 m grid dispersed throughout the 34-ha study area. Cores were stored in paper straws, sanded with successively finer grade sand paper, and mounted on wood platforms. A sliding-stage micrometer and a dissecting microscope were used to measure ring widths to the nearest 0.01 mm.

Data analysis

Analytical approach

The analyses and results are divided into three sections, each with a separate level of inference. In the first, we analyze the factors of height growth within the openings, considering the individual planted seedling as the experimental unit and the entire area within the group openings as the area encompassing the inferential population. The purpose of this analysis is to characterize the variability and trends of height growth within our experimental conditions. Because basal diameter closely paralleled height, it has been dropped from the analysis. In the second section, we analyze the relationship between mean seedling height and opening size. To make inferences about the effect of opening size on mean seedling growth across the entire study area, we consider the openings as being the experimental units. We use an information-theoretic analysis designed to achieve parsimony and thus maximize the applicability of the results to

other comparable sites. In the third section, we compare the population of border trees surrounding the openings with the matrix trees between the openings. The effect of edge on individual border-tree growth is analyzed with respect to treatments of stand density, species, opening size, and placement around the openings. Specific statistical methods are described below.

Factors of height growth

The fifth-year-height data were analyzed at the experimental-unit scale of individuals to find the effect that opening size, species, and within-opening position had on the growth of planted seedlings. Because we measured the entire population ($N = 4340$ trees), we had the power to resolve small height differences, which may or may not be meaningful from an ecological or management perspective. Therefore, our analysis was geared more toward measuring the magnitudes and precision of the effects of group size, species, and position on height means, rather than toward strict hypothesis testing.

Functional height response

We used an information-theoretic approach to choose from among three a priori hypotheses, each implying different relationships between mean seedling height and opening size. The alternatives represent simple models for explaining three different biological patterns (Table 1). The first alternative is a linear relationship, implying a monotonic increase in mean seedling height across the range of opening sizes. The second alternative is a quadratic relationship, with mean seedling height increasing with opening size and then decreasing, implying an emerging negative environmental effect on height growth in larger openings. The third alternative is an asymptotic relationship, most simply modeled with a Michaelis–Menton curve:

$$[1] \quad \text{Mean seedling height} = \frac{A \times \text{group size}}{B + \text{group size}}$$

where A is the asymptote (maximum height) and B is the slope of the lower portion of the curve. Mean seedling height is given in centimetres, and group size is given in hectares. The Michaelis–Menton curve was used because it uses few parameters (two) to describe a nonlinear relationship. It is typically used to describe kinetic relationships of chemical reactions but has more recently been used to describe ecological relationships (e.g., Coates 2000). The asymptotic relationship implies an increase in mean height among the smaller size openings, followed by a leveling off

above a certain opening size. The results of interest are the model selections, not the individual model parameters. To select from the model alternatives, we used Akaike's information criterion (AIC), a method of ranking alternatives according to goodness of fit while penalizing each model for extra parameters (model complexity). We used a modified AIC equation derived by Sugiura (1978) and described by Anderson et al. (2000) to account for small sample/parameter ratios among the alternatives (ratio is 12:2 for asymptotic and linear equations; ratio is 12:3 for quadratic equations).

$$[2] \quad AIC_i = n \log \left(\frac{RSS}{n} \right) + 2K + \frac{2K(K+1)}{n-K-1}$$

where AIC is the bias-corrected criterion for model alternative i ; RSS is the residual sum of squares of the model's regression; n is the sample size; and K is the number of parameters. Thus, as model fit (quantified by RSS) increases AIC decreases, and as the number of parameters increases, AIC also increases (i.e., the model with the lowest AIC value is the selected model). The AIC criteria for the three alternatives were transformed to Akaike weights, which give the likelihood that within the limits of the data and the set of alternatives, the given model is the most appropriate choice. Inference in the selection of the most suitable model is guided by the ratios of AIC weights. Ratios of ≥ 5 were interpreted as being strong evidence for model primacy. We followed the suggestions of Anderson et al. (2001) for reporting the results.

When developing these functions, we removed two statistical outliers from the analysis — one white fir datum and one Douglas-fir datum. The outlier for white fir was a 108-cm mean-height value from a 0.1-ha opening, and the outlier for Douglas-fir was a 158-cm mean-height value from a 0.1-ha opening. On the basis of Cook's D statistic (Cook 1977), both exerted undue leverage. Their residuals were >2 SE greater than their predicted values. Including the outliers does not change the model-selection results. However, the fit of the relationships is less variable without them.

Border-tree growth response

To determine the effect of edge on border-tree growth, we used radial mean annual increment as a measure of growth. Because we were interested in measuring the growth response to the conditions created by the harvest (i.e., release), the response variable was expressed as percent change in postharvest growth relative to preharvest growth. The postharvest period (1997–2001) covered the five full growing seasons following the harvest, and the preharvest period (1992–1996) covered the five growing seasons preceding the harvest. We did not include DBH as a covariate to control for the effect of tree size on growth, because the relative-growth-response variable already controlled for tree size to the degree that tree size was related to growth for the 5 years preceding the harvest. In other words, the 10 years of growth incorporated by the response variable would have also been included in the independent variable of diameter, leading to an overestimate of correlation. Further, the border and matrix trees had similar mean diameters (border-tree mean DBH = 61.6 cm, SE = 1.6 cm; matrix-tree mean DBH =

61.8 cm, SE = 2.1 cm) and were hence comparable with respect to tree size.

We relied on a general linear model to assess the uncertainty in our data. The model was used primarily to detect a difference in growth response between border and matrix trees while controlling for categorical variables of species and the difference in density between the two stands due to management history. The dependent variable, percent growth response, was transformed (cube root) to meet the normality assumption of the model. To determine the importance of opening size and within-opening orientation (i.e., placement around the opening) on border-tree growth, we performed a post hoc analysis of border-tree growth. The model included the significant effects from the primary model (species and management history as covariates), with opening size and within-opening orientation as the key variables to be tested. Orientation around the opening was expressed as a continuous variable, with values of "northness" calculated by taking the cosine of the azimuth from the opening centers toward each tree. Trees due north of center, therefore, had a northness value of 1, and trees due south of center had a northness value of -1 .

Results

Factors of seedling-height growth

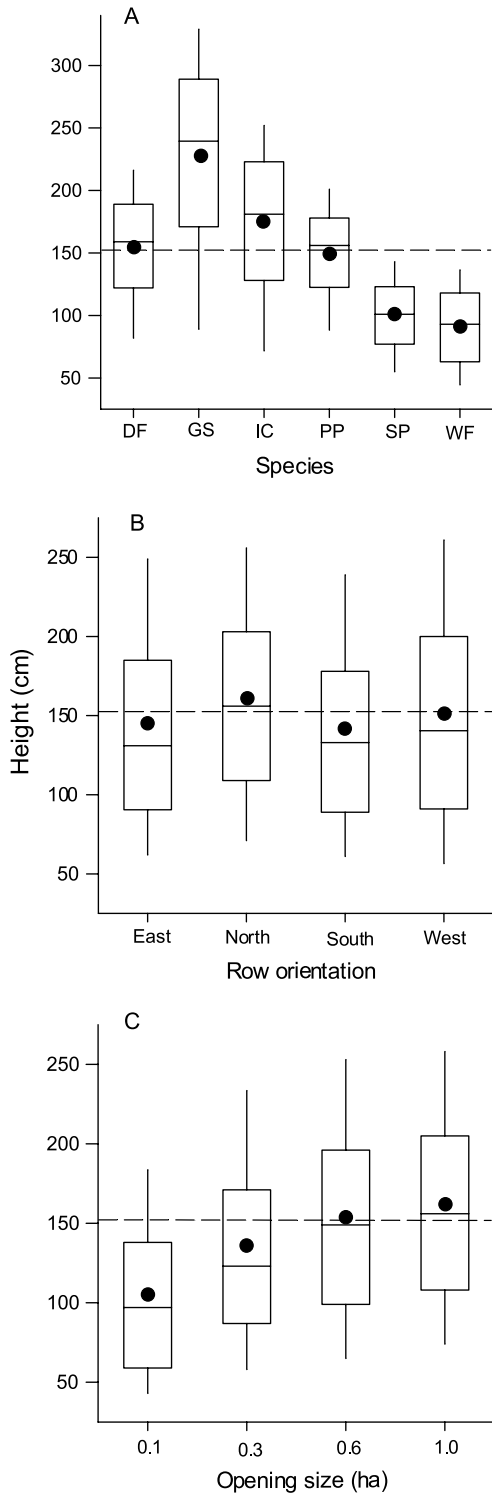
The overall mean fifth-year height was 151 cm (SD = 72 cm). The shortest seedling was a 9-cm sugar pine, and the tallest one was a 441-cm giant sequoia. Although heights overlapped considerably among all of the species, there was a distinct effect of species on the central tendencies of heights within all openings combined (Fig. 2A). The sequence from tallest to shortest was as follows: giant sequoia (mean = 227 cm, SD = 87 cm) > incense-cedar (mean = 174 cm, SD = 66 cm) > Douglas-fir (mean = 155 cm, SD = 50 cm) > ponderosa pine (mean = 150 cm, SD = 44 cm) > sugar pine (mean = 100 cm, SD = 34 cm) > white fir (mean = 91 cm, SD = 35 cm). For all opening sizes, giant sequoia was consistently the tallest species and both sugar pine and white fir were consistently shorter than average. Row orientation (Fig. 2B) did not result in as much departure from the overall average height as species did. Mean height was greatest in the north rows (mean = 161 cm, SD = 71 cm) and smallest in the south rows (mean = 141 cm, SD = 69 cm). Mean tree height increased with opening size (Fig. 2C). Consistent height suppression occurred in the 0.1-ha openings relative to the overall average. The 10-fold increase in opening size, from 0.1 ha to 1.0 ha, resulted in a 54% increase in mean height. The sequences of mean basal diameters according to species, opening size, and row orientation reflected those found for seedling heights.

The growth of all species was negatively influenced by proximity to edge (Fig. 3). Giant sequoia was the most sensitive to the edge environment, whereas sugar pine and white fir were fairly insensitive. For all species, trees along the south edges were shorter than those along the north edges (data not shown).

Functional height response

Of the three alternative models, mean fifth-year heights were best fit with either asymptotic or quadratic curves

Fig. 2. Fifth-year height data from planted group selection openings among species (A), row orientation (B), and opening size (C) at Blodgett Forest Research Station, California. The horizontal lines inside the bars represent the medians; dark circles, the means; vertical bars, the interquartile ranges of the data points around the means; whiskers, the 10th (bottoms) and 90th (tops) percentiles of the data points around the means. DF, Douglas-fir; GS, giant sequoia; IC, incense-cedar; PP, ponderosa pine; SP, sugar pine; WF, white fir.



(Fig. 4). The models of height response were ranked according to their AIC_i value (Table 2), and then the ratios of Akaike weights (w_i/w_j) were used to measure the relative strength of evidence among the alternatives. For all species, at least one of the three a priori models could be ruled out as a plausible alternative, given the data. The strength of evidence for an asymptotic model as the best fit for giant sequoia and incense-cedar was strong (ratios of ranks >5). Sugar pine and ponderosa pine were also best fit with asymptotic curves, but the importance of a quadratic model could not be ruled out (ratios of ranks <2). There was strong evidence for a quadratic model for Douglas-fir over the second-ranked linear model, with weak evidence for an asymptotic model. White fir was best fit with a quadratic model, and only a linear model could be ruled out. For all species combined, an asymptotic model was selected over a quadratic model, with a linear model having weak evidence.

Border-tree growth response

The main effect of interest (border location versus matrix location), as well as the contributing effects of species and management history (stand-density differences), was important ($p < 0.05$) in explaining variation in postharvest growth response. The sample of trees representing the entire population of border trees grew on average 41% more ($CI_{95} = 27.4\%–55.3\%$) than the sample of matrix trees. Border trees of all four species studied had a more positive growth response than matrix trees did (Fig. 5). The year-to-year magnitude and trend of radial growth were similar before the harvest for white fir, Douglas-fir, and incense-cedar (Fig. 6). Border and matrix white fir and Douglas-fir showed clear separations in growth response the year immediately following the harvest, whereas the growth responses of border and matrix incense-cedar did not diverge until 2 years after the harvest. Ponderosa pine border trees were growing less than matrix trees before the harvest and then released relative to matrix trees beginning 2 years after the harvest.

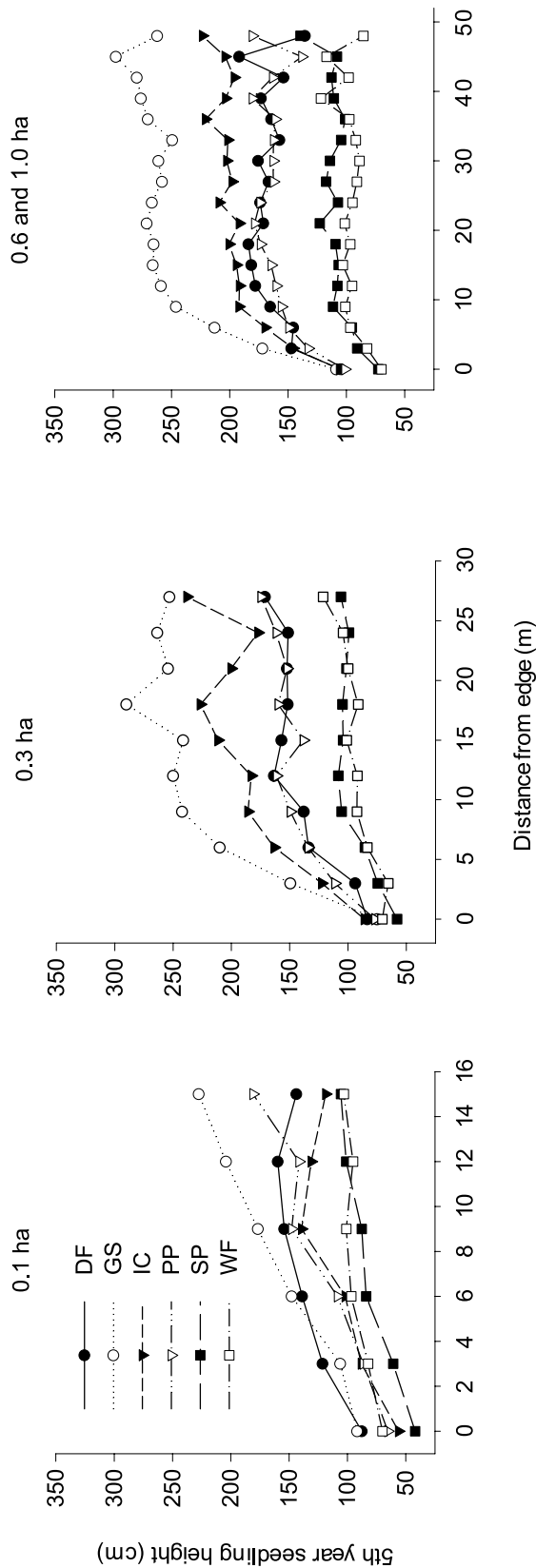
Neither opening-size nor northness covariates explained a significant proportion of variation in the growth of border trees. Management history remained important, as trees in the unthinned section of the study area had a larger growth release (mean = 68.7%, SE = 10%) than those in the thinned section (mean = 41.3%, SE = 7.1%).

Discussion

Factors of seedling-height growth

The increase in seedling growth with harvested opening size that we found is a commonly observed relationship across multiple forest types (Minkler and Woerhide 1965; Gray and Spies 1996; Van Der Meer et al. 1999; Coates 2000). For these studies to be applicable for management, the range of opening sizes considered must be large enough to capture potential changes in the rate of increase. In this study, the change in height growth associated with increasing opening size from 0.1 to 0.6 ha was a 97.4-centimetre increase per hectare increase, whereas increasing opening size from 0.6 to 1.0 ha resulted in an increase of only 19.3 centimetres per hectare increase (all species combined). In two nearby 8-ha plantations on similar sites at BFRS that

Fig. 3. Fifth-year mean seedling height profiles from group selection opening edges to centers at Blodgett Forest Research Station, California. DF, Douglas-fir; GS, giant sequoia; IC, incense-cedar; PP, ponderosa pine; SP, sugar pine; WF, white fir. Separate graphs are shown for the 0.1-, 0.3-, and 0.6- plus 1.0-ha openings.

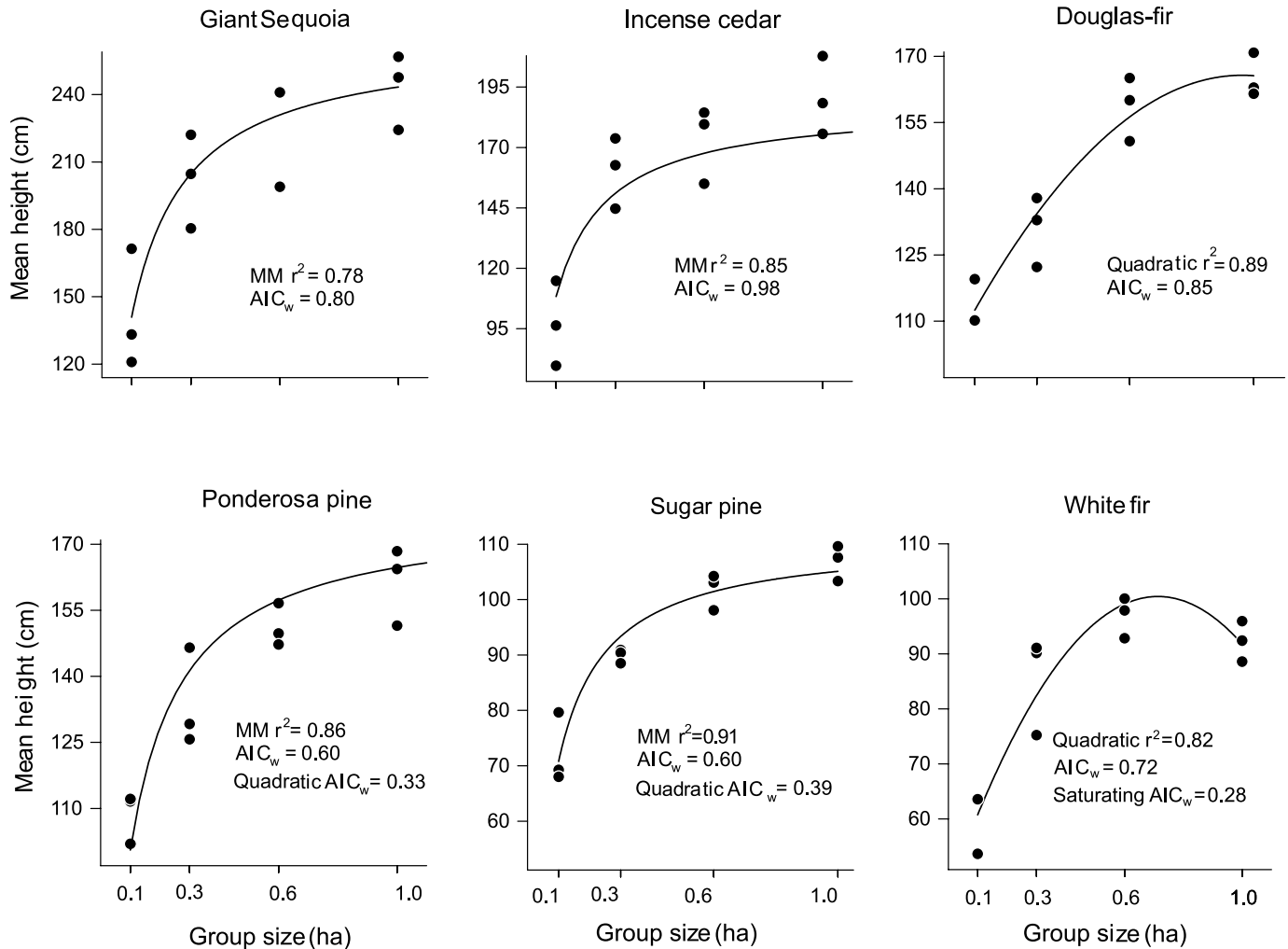


were also planted with an equal distribution of the same six species and controlled for competing vegetation, mean fifth-year height was 176.8 cm, an added height growth of only 2.2 centimetres per hectare increase in opening size >1.0 ha. The range of opening sizes that we considered was therefore clearly relevant to capturing the change in the rate of increase for seedling-height growth.

When grouped by row orientation (Fig. 2B), the height patterns do not clearly reflect the steep light and water gradients often associated with north-south transects within gaps (Canham et al. 1990; York et al. 2003). Because these rows incorporate seedlings near both the edges and the centers of the openings, they do not capture the fine-scale change in seedling height across the edge environment (Fig. 3). Nonetheless, the slight difference in mean height between the south and north rows is likely a consequence of the reduced light available along the southern edges (York et al. 2003).

The trees in this study were intentionally measured at a late enough age that between-species height differences originating from size and vigor at the time of planting could be assumed to be secondary to differences caused by species growth potential and opening characteristics. The fifth-year measurement also occurred before intertree competition at 3-m spacing could influence the height-opening-size relationships. Additionally, measurements were made at a practical time when cultural treatments, such as precommercial thinning, might be applied and therefore affect future composition. However, the influence of species, opening size, and within-opening location are likely to change over time. The ranks of height performance among the species changed slightly between the third and fifth years after planting. After the third year (data reported in York et al. 2003), sugar pine ranked last, but now it is ranked ahead of white fir. Giant sequoia continued to outgrow the other species (Fig. 2A), despite its marked sensitivity to edge environment (Fig. 3). The colimitation on the growth of giant sequoia by light and soil-moisture availability after 3 years (York et al. 2003) likely remains in force near the edges. Although fifth-year mean heights for ponderosa pine and sugar pine were below the overall mean, these species had the highest relative height increment between the third and fifth growing seasons. Both these species are known to exhibit a growth strategy of preferential root growth, instead of shoot expansion, during the seedling stage (Larson 1963; Pharris 1967; Lopushinsky and Beebe 1976). In this case, a shift in resource allocation to shoot growth appears to be occurring between years 3 and 5. This difference between the ranks of overall height growth and those of recent relative height growth illustrates the importance of timing in comparing growth performance among species. We expect both ponderosa pine and sugar pine height to rank relatively higher in the future. Future patterns of height growth will also depend on treatments that change the amounts of resources available. Even without any treatment, resource gradients within the openings are likely to change as the seedlings grow into trees and approach the height of the surrounding canopy. Although these fifth-year results can guide current management decisions, the dynamic interaction of these seedlings with each other and the surrounding trees over time will in-

Fig. 4. Mean height–opening size regression curves for the selected model of each species. Akaike information criterion weights (AIC_w) are given for the selected model and for the second-ranked model if the ratio of ranks between the first and second models is <5 . Adjusted coefficients of variation (r^2) are reported only for the selected model. Note that some y axes have different scales. MM, asymptotic (Michalis–Menton).



fluence future results and have implications for management.

Functional height response

Because of site-to-site variation and because many factors besides tree growth are considered in the choice and design of a silvicultural system, there is no “ideal” group selection opening size to use or species to select. However, clear patterns of height growth among opening sizes can be expected according to species autecologies and the gradients of resources that are created within openings and among opening sizes. The result common to all of the species in this study was that the linear model could be ruled out as a plausible best fit, given the data and the alternative models considered. The linear model would have implied a constantly increasing growth benefit from larger interior areas and (or) a mitigation of the negative edge effect with larger opening sizes.

The management implication for the species best fit with the asymptotic model (giant sequoia, ponderosa pine, sugar pine, and incense-cedar) is that above a minimum opening

size (0.3–0.6 ha) fifth-year seedling height increases only marginally, compared with smaller opening sizes, where the cost of small opening size is a pronounced seedling-height suppression. For giant sequoia and incense-cedar seedlings, however, fits do not reach an asymptote before 1.0 ha, and there is a lack of support for a quadratic model, suggesting that mean height is still maximized in the largest opening size.

Although Douglas-fir was best fit with a quadratic model, the maximum predicted height occurred at the largest opening size. Therefore, no negative effect of larger opening size was detected below 1.0 ha. Beyond 1.0 ha, mean height is predicted to decrease. In fact, mean Douglas-fir height in two nearby 8.0-ha plantations is slightly less than within the 1.0-ha openings (156 cm in 8.0 ha versus 165 cm in 1.0 ha), but controlled opening sizes larger than 1.0 ha are needed for finding the point of either saturation or decline in Douglas-fir seedling-height growth, especially considering the species’ characteristically high seedling-growth variability (York et al. 2003).

Table 2. Model selections using Akaike information criterion (AIC).

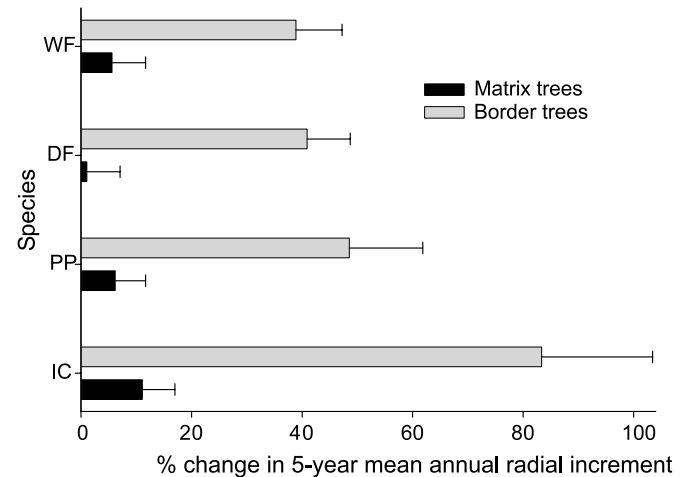
Model ranks	K_i	AIC _{<i>i</i>}	Δ_i	w_i	Ratio of ranks, w_1/w_i
Douglas-fir					
1. Quadratic	3	53.1	0	0.86	
2. Linear	2	56.8	3.7	0.13	6.6
3. MM	2	61.8	8.7	0.01	86
Giant sequoia					
1. MM	2	79.5	0	0.80	
2. Quadratic	3	83.0	3.5	0.14	5.7
3. Linear	2	84.5	5.1	0.06	13.3
Incense-cedar					
1. MM	2	68.8	0	0.98	
2. Quadratic	3	76.8	8	0.02	49
3. Linear	2	83.7	15.0	0.00 ^a	1748.9
Ponderosa pine					
1. MM	2	55.6	0	0.60	
2. Quadratic	3	56.9	1.2	0.33	1.8
3. Linear	2	59.9	4.2	0.07	8.6
Sugar pine					
1. MM	2	41.5	0	0.60	
2. Quadratic	3	42.3	0.9	0.39	1.5
3. Linear	2	53.3	11.8	0.01	60
White fir					
1. Quadratic	3	50.0	0	0.72	
2. MM	2	51.9	1.9	0.28	2.6
3. Linear	2	63.0	13.0	0.00 ^a	670.5

Note: Models for each species are ranked according to Akaike weights (w_i) and AIC_{*i*} differences (Δ_i). The ratios of the selected model's weight (w_1) to the other models' weights are used to determine strength of evidence for model selection. K_i , number of parameters (complexity) in the given model; MM, asymptotic (Michalis–Menton).

^aGreater than zero but less than 0.01.

White fir was the only species that had an actual decrease in mean height with any incremental increase in opening size. Mean height is predicted to decrease above an opening size of about 0.7 ha, but an asymptotic model could not be ruled out. The implication is that fifth-year height growth in 0.7-ha openings is either maximized or at least similar to that of larger openings.

If the primary objective is to maximize seedling growth, the relevant result is that the largest openings in our study consistently resulted in taller seedlings (except for white fir). However, the likely objective of management concerning opening size is to create openings large enough to avoid severe seedling-height suppression but small enough to maintain the ecological and social benefits of smaller openings (e.g., erosion potential and aesthetic quality). For all species, increasing opening size from 0.1 to 0.3 ha resulted in a steep increase in seedling height. Using an opening size of <0.3 ha would require considerable leverage from small-size benefits to counter the negative impacts on seedling height. With the asymptotic models, increases in opening size beyond 0.6 ha resulted in relatively small increases in seedling height. The benefits of smaller opening sizes would therefore hold more

Fig. 5. Percent postharvest growth response relative to preharvest growth at Blodgett Forest Research Station, California. Mean annual increment is calculated for the 5 years after the harvest (1997–2001) and compared with that for the 5 years before the harvest (1992–1996). WF, white fir; DF, Douglas-fir; PP, ponderosa pine; IC, incense-cedar.

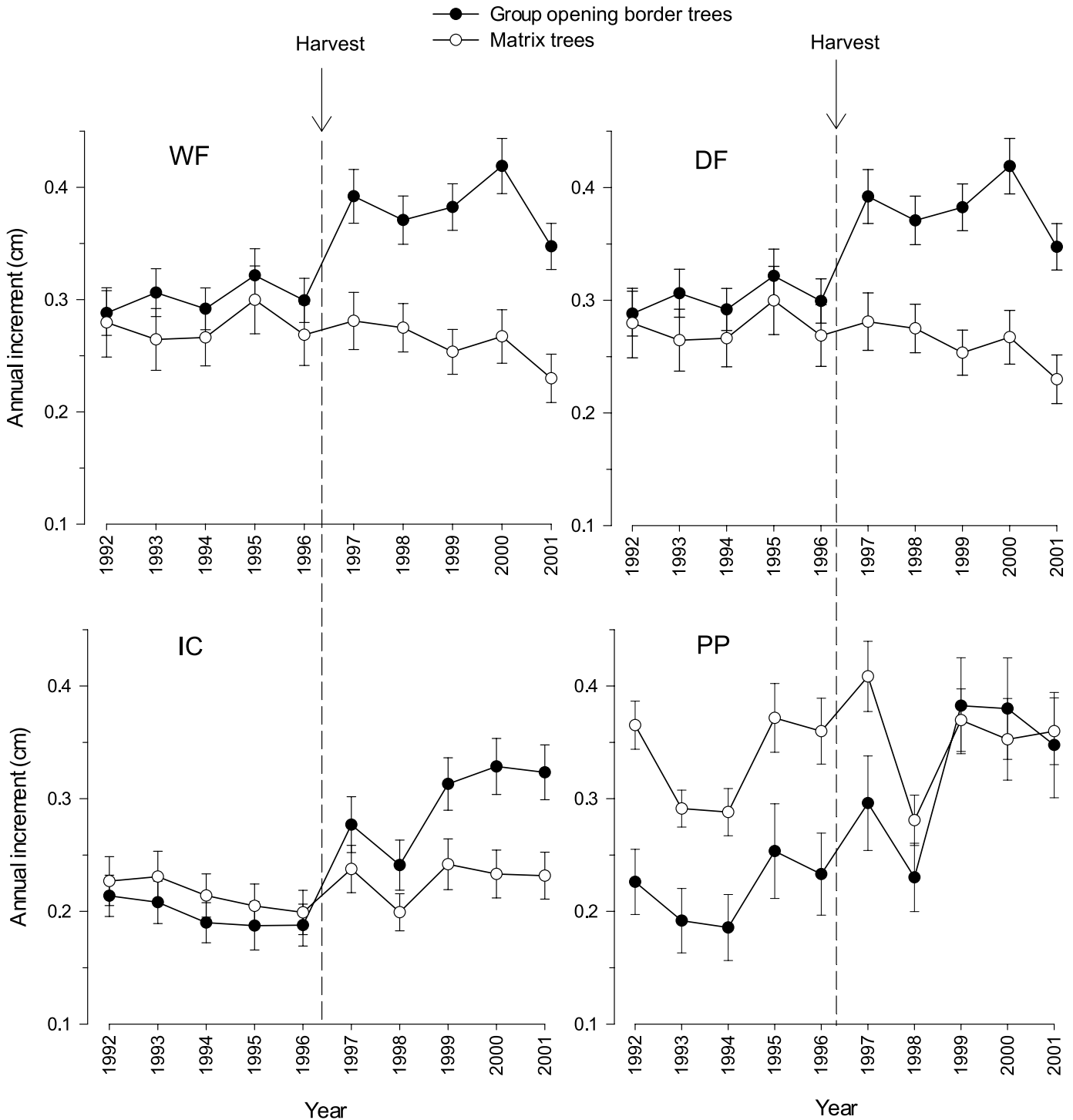
weight within this opening-size range and perhaps influence managers to select sizes close to the opening size at which height returns diminish (0.6 ha, in this case). One of the potential benefits of smaller groups that should be considered is the growth of the border trees, discussed below.

Border-tree growth

In an apparent trade-off in growth between seedlings and overstory trees along the opening edges, border trees in this study responded dramatically (Fig. 5) and quickly (Fig. 6) to the harvest, showing increased radial growth relative to matrix trees. This competitive overstory–understory relationship underlies the results of applied studies on the effects of variable overstory densities on seedling regeneration and growth that guide managers' decisions about intensity of overstory thinning (Zeide 1985; Oliver and Dolph 1992; Page et al. 2001). The same relationship applies in group selection openings and has implications for designing the size and density of openings. A key factor for decision-making and growth-optimization models involving group selection regimes would be the amount of edge area created by each regeneration harvest and its effect on overall stand growth over time.

Positive growth effects on trees surrounding natural gaps in northern hardwood forests have been observed in sugar maple (*Acer saccharum*) (DiGregorio et al. 1999), although no effect of edge was detected for American beech (*Fagus grandifolia*) trees surrounding similarly sized gaps (Poage and Peart 1993). Different magnitudes or even directions of growth response among mixed-conifer species surrounding group selection openings may also be expected because of differences in the physiological adjustments needed to acquire increased resources. All four species in this study have been noted to respond with rapid growth to thinning as seedlings or young trees (Burns and Honkala 1990). Our expectation for the larger trees was that they would respond in accordance with their relative shade tolerances (i.e., tolerant

Fig. 6. Interyear variation in radial growth for matrix and group selection opening-border trees at Blodgett Forest Research Station, California. Circles represent mean radial growth, and the whiskers represent standard errors of the means. The postharvest growth period is to the right of the dashed line. WF, white fir; DF, Douglas-fir; IC, incense-cedar; PP, ponderosa pine.



trees would release more than intolerant ones; *sensu* Daniel et al. 1979). However, no clear pattern according to shade tolerance was detected. Also notable was the lack of relationship with border-tree growth and orientation around the openings (northness). Although the suppression of seedling growth along the edges of the openings changes discernibly with species and within-opening position (especially north

versus south), similar distinctions for growth release of border trees are absent.

The magnitude of border-tree release for all species combined was influenced by preharvest stand density, as the thinned area did not respond as much as the unthinned area. Had the matrix been thinned concurrently with the harvest of the group selection openings (as is often the practice in in-

tensive management), the border-tree growth response would likely have been less pronounced. Likewise, a concurrent matrix-thinning may also have resulted in less height depression of seedlings along group edges, where competition from border trees reduces light and water availability (York et al. 2003). Thus, the influence of management history and cultural treatments that coincide with opening harvests must also be considered in the design of openings.

An interesting and applicable result of the border-tree analysis was the lack of relationship between opening size and percent growth response. The result is compatible with the selection of asymptotic curves for modeling mean seedling height, as an asymptotic curve of interior area against group size results when the depth of the edge influence remains constant as group size changes. Given a constant edge depth, smaller opening sizes have a relatively large area covered by the edge environment. The resulting negative consequences on seedling height in smaller openings occur at the same time as a relatively positive effect on border-tree growth. A collective of smaller groups with the same area as one large group has more edge per unit area and hence more potential border-tree growth. If the lack of relationship between opening size and growth release is true, the cost of smaller opening sizes in terms of seedling growth could be made up for to some degree by the increased border-tree growth. For example, had the entire 15% of the land area harvested for this study all been harvested in 0.1-ha openings, 21.3 border trees would have been created per hectare, representing 19% of all mature trees in the 34-ha study area. Had the same area been harvested with 1.0-ha openings, 6.8 border trees would have been created per hectare, representing 6% of all mature trees. Border trees are defined here as only those trees that are at least 50% exposed to the opening. The positive effect on trees adjacent to the openings could extend into the matrix, increasing the positive effect of edge on overall stand growth.

Conclusions

As managers seek to “catch up” to the social demands of forestry, ongoing studies and adaptive management will be needed to guide silvicultural decisions (Kimmins 2002). Our study demonstrates a method for describing simple patterns of seedling growth that have clear implications for management. Further, we demonstrate that the trade-off in growth between the understory and overstory cannot be neglected when considering overall stand growth. The asymptotic functions we found for the relationship between fifth-year height and opening size in this forest suggest that above about 0.6 ha (diameter is 2.6 times the canopy height), severe height suppressions associated with small group selection opening size are avoided. Conversely, smaller openings result in more border-tree growth per unit area. Although it may be possible to hone in on a group selection opening size that optimizes growth, it is not the intention of this study to find one “ideal” group size that maximizes timber yield. In reality, managers will factor in much more than tree growth when determining the size of opening to harvest (e.g., local regulations, erosion potential, logging damage, and topography). Managers can use specific information, such as we present here, about ecological factors that affect their objec-

tives and continue to rely on long-term studies to guide decisions in the future.

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