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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 (*Pseudotsuga 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.

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

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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40 2001). Group selection is one uneven-aged alternative
41 that addresses many of the concerns associated with
42 even-aged plantations, but still retains some of the
43 administrative and silvicultural benefits. Group selec-
44 tion management involves the periodic harvest of
45 small groups of trees coupled with some form of
46 stand density control in the matrix of larger trees
47 surrounding the openings. The subsequent openings
48 may be designed to resemble gaps in the canopy that
49 would be caused by natural agents (e.g. fire, insect,
50 disease). Over the long term, a shifting mosaic of
51 small patches develops across forests with group
52 selection management regimes. The most common
53 attribute that silviculturalists associate with the group
54 selection regime is the ability to regenerate a wide
55 variety of commercial species (Daniel et al., 1979;
56 Laacke and Fiske, 1983; Smith, 1986). In California's
57 Sierran mixed conifer forests, group selection has
58 been used as a method for converting homogeneous
59 forest structures into more heterogeneous arrange-
60 ments (McDonald and Abbot, 1994) and as a method
61 for promoting tree regeneration by mimicking natural
62 disturbances (Stephens et al., 1999). In other forest
63 types, the management regime has been proposed as a
64 means for ecological restoration (Storer et al., 2001),
65 maintaining high species diversity (Lahde et al., 1999;
66 Schutz, 1999), and for managing endangered species
67 habitat (USDA, 1995). The most common goal of
68 research involving artificially created gaps has been to
69 find the appropriate opening size that meets manage-
70 ment objectives, particularly successful regeneration
71 and growth of desired species (Coates, 2000; Gray and
72 Spies, 1996; Leak and Filip, 1977; Malcolm et al.,
73 2001; McDonald and Abbot, 1994; Van Der Meer
74 et al., 1999). Indeed, much of the hesitation on the part
75 of forest managers in implementing the group selec-
76 tion management regime comes from the lack of
77 knowledge about the loss of growing space associated
78 with small-sized openings.

79 The potential loss of productive growing space for
80 regenerating seedlings occurs because of the edge
81 effects in force near the perimeters of openings. In
82 the context of group selection silviculture, the edge
83 refers to the boundary between the opening created by
84 harvesting a group of trees and the matrix of intact
85 forest. Edge effects are defined as the ecological
86 phenomena associated with the environmental gradi-
87 ents that develop across the boundary and extend into

the adjacent communities (*sensu* Chen et al., 1992). 88
Often edge effects have been investigated with an 89
emphasis on the influence of openings (e.g. clearcuts, 90
agricultural fields) on the surrounding matrix forest. 91
Openings have been shown to influence interior for- 92
ests' wildlife composition (Berry, 2001; Hargis et al., 93
1999; King et al., 1996), vegetation structure (Chen 94
et al., 1992; Hughes and Bechtel, 1997), microclimate 95
(Chen et al., 1995; Raynor, 1971), and nutrient 96
exchange (Weathers et al., 1997). Exceptions where 97
edge effects on both openings and intact forests were 98
studied include Cadenasso et al. (1997), who found 99
that mature forest vegetation in the northeastern Uni- 100
ted States can create temperature and light gradients 101
that extend 15–20 m into adjacent fields. Studies that 102
have explored the impacts of forest edges on canopy 103
gap environments have focused on issues related to 104
species diversity or regeneration dynamics in the 105
context of gaps as a natural disturbance (e.g. Sipe 106
and Bazzaz, 1994; Brown, 1996; Gray and Spies, 107
1996). While results from these gap studies have 108
helped forest managers design silviculture methods 109
that imitate natural disturbances, they provide little 110
insight for predicting the effect of edges on the growth 111
and yield of trees within artificially created openings 112
resulting from group selection harvests. 113

A management scheme where group selection 114
openings are intermixed across a forested landscape 115
would generate a significant fraction of planting areas 116
in edge environments (Gustafson and Crow, 1996). 117
For the smaller openings, edge environments are 118
particularly important because of the high edge-to- 119
interior ratio (Forman and Gordon, 1986). Bradshaw 120
(1992) emphasized the importance of recognizing 121
edge effects when making management decisions and 122
suggests quantifying edge effects as a dominant 123
means for choosing among uneven- and even-aged 124
silvicultural options. In California, forest practice 125
regulations define minimum and maximum group 126
opening sizes, but foresters have flexibility in deter- 127
mining the size and number of openings, as well as the 128
regeneration method to use. In cases like the mixed 129
conifer forest where there is more than one potential 130
timber species to be regenerated, the size and strength 131
of the effect of the edge on performance will likely 132
vary between species. 133

Given the potential widespread implementation of 134
group selection silviculture in the Sierra Nevada, a 135

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

151 2. Methods

152 2.1. Study site

153 Blodgett Forest Research Station (BFRS) is located
154 on the western slope of the Sierra Nevada mountain
155 range in California (38°52'N; 120°40'W). The study
156 area lies within BFRS at an elevation between 1220
157 and 1310 m. The climate is Mediterranean with dry,
158 warm summers (14–17 °C) and mild winters (0–9 °C).
159 Annual precipitation averages 166 cm, most of it
160 coming from rainfall during fall and spring months,
161 while snowfall typically occurs between December
162 and March. The soil is from granodiorite parent
163 material and is highly productive for the region.
164 Heights of canopy trees typically reach 27–34 m in
165 50–60 years (BFRS data). Olson and Helms (1996)
166 provide a detailed description of Blodgett Forest, its
167 management, and trends in forest growth and yield.

168 Vegetation at BFRS is dominated by the mixed
169 conifer forest type, composed of variable proportions
170 of five coniferous and one hardwood tree species
171 (Laacke and Fiske, 1983; Tappeiner, 1980). Research
172 sites were all located on the same, north-facing slope
173 (10–25%). Like much of the mixed conifer forests in
174 the Sierra Nevada range, the study area was clearcut in
175 the early 1900s and allowed to regenerate naturally.
176 The forest has developed to form a mixed species
177 canopy, averaging 30 m in height (BFRS data). There
178 are six native dominant tree species including white fir
179 (*Abies concolor*), incense cedar (*Calocedrus decur-*

rens), coast Douglas-fir (*Pseudotsuga menziesii* var. 180
menziesii), sugar pine (*Pinus lambertiana*), ponderosa 181
pine (*Pinus ponderosa*), and California black oak 182
(*Quercus kelloggii*). In addition, BFRS plants giant 183
sequoia (*Sequoiadendron giganteum*), a species that is 184
currently non-native, but in the past had an expanded 185
range that encompassed BFRS (Harvey, 1985). 186

2.2. Experimental design 187

Group selection silviculture in California involves 188
removing trees in distinct groups, which have opening 189
sizes legislatively mandated to be between 0.1 and 190
1.0 ha. (California Department of Forestry, 2002). 191
California forest regulations give landowners the 192
option of artificially planting the openings, or relying 193
on natural seed fall or advanced regeneration. The 194
harvesting and site preparation methods we used in 195
this experiment (described below) are typical of those 196
used by a forest landowner whose main objective is 197
timber production. 198

The groups were harvested during the summer of 199
1996. Four opening sizes representing the range of 200
allowable sizes (0.1, 0.3, 0.6, and 1.0 ha) were repli- 201
cated three times (12 openings total). Although forest 202
managers are likely to deviate from opening shapes of 203
perfect circles because of local topography and con- 204
siderations for logical harvesting units, our openings 205
were cut as close to circular as possible. They are 206
round so that: (1) the total edge-to-interior ratio is 207
minimized, and (2) the only spatial difference between 208
edges at different locations within the same opening is 209
the orientation relative to the center of the opening and 210
the forested matrix. All trees within the groups were 211
cut with chainsaws and yarded with a rubber-tired 212
skidder. During the same year, site-preparation was 213
done by cutting non-merchantable trees and by piling 214
slash for burning on site. After site preparation, the 215
openings were mostly bare ground with some cover of 216
litter and woody debris. During the Spring of 1997 the 217
openings were planted in a “wagon wheel” design 218
(Fig. 1). In all openings, each of six species (Douglas- 219
fir, incense cedar, white fir, ponderosa pine, sugar pine, 220
and giant sequoia) were planted in rows extending 221
from the center towards the edge in all cardinal and 222
inter-cardinal directions. Douglas-fir, incense cedar, 223
white fir, and ponderosa pine were planted from bare- 224
root stock. Sugar pine and giant sequoia were from 225

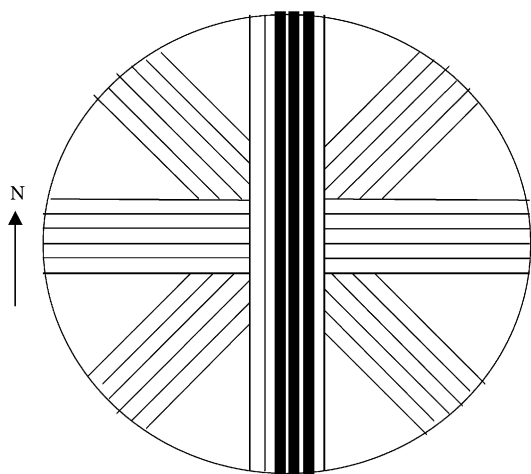


Fig. 1. Overhead view of the “wagon wheel” planting design in openings created at Blodgett Forest Research Station, California. Each line represents a row of the same species planted along cardinal and inter-cardinal directions (six species: Douglas-fir, giant sequoia, incense cedar, ponderosa pine,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

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

240 2.3. Study tree measurements

241 2.3.1. Species and sample locations

242 In July 2000 (i.e. during the fourth growing season),
 243 we quantified the gradients in light and water avail-
 244 ability and their relationship to height growth by
 245 measuring three variables on a subset of study trees:
 246 water potential, light availability, and current year’s
 247 height extension. We limited the study trees to
 248 three species: Douglas-fir, ponderosa pine, and giant
 249 sequoia. Not only are these species likely to be planted

250 on a commercial scale by landowners, but they also
 251 represent a range of tolerance to shade. Subjective
 252 rankings of these species according to their relative
 253 shade tolerances have classified Douglas-fir as mid-
 254 tolerant and ponderosa pine and giant sequoia as
 255 intolerant (Baker, 1950; Minore, 1979; Weatherspoon,
 256 1990). These rankings have generally held true in
 257 studies of survival and growth response to shade stress
 258 (Emmingham and Waring, 1973; Minore, 1979; Oliver
 259 and Dolph, 1992; Stark, 1968). In each opening, nine
 260 study trees of each species were measured (27 total
 261 per opening). We examined influences of light and
 262 water availability on height extension from three
 263 within-opening locations: north edges, south edges,
 264 and centers. The north and south edge samples
 265 included the three closest trees to the edge (0, 3,
 266 and 6 m away from the drip line). The center trees
 267 sample was comprised of the tree closest to the center
 268 of the opening plus the two trees spaced 6 m north
 269 and south of the center tree. Trees along the north
 270 and south rows were chosen because these positions likely
 271 represent the widest range of abiotic differences
 272 within the opening. For example, Canham et al.
 273 (1990) found the steepest gradients in incident radi-
 274 ation along north–south axes of gaps, and Heinemann
 275 et al. (2000) found highest within-gap moisture avail-
 276 ability along northern edges for gaps in a southern
 277 hemisphere temperate forest.

278 2.3.2. Light availability

279 Hemispherical photography was used to estimate
 280 light availability. Photographs were taken looking
 281 upward just above the terminal leader of each study
 282 tree using a fish-eye lens (Nikon 8 mm f/2.8) that
 283 provides a 180° view of the canopy. Color slides were
 284 taken early or late in the day when the sun was low in
 285 the sky. Slides were converted to digital images
 286 (900 dpi) using a Nikon CoolScan slide scanner. By
 287 restricting photo acquisition to near-isotropic sky
 288 conditions, we minimized the need for digital image
 289 enhancement.

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

297 (Battles, 1999; Canham et al., 1990). Specifically,
 298 %TT estimates the percentage of incident photo-
 299 synthetically active radiation (PAR) transmitted to a
 300 point in the understory during the growing season.
 301 Values range from 0% for a completely closed canopy
 302 to 100% for a completely open site. Incident PAR was
 303 calculated from standard equations of solar geometry
 304 and a site-specific atmospheric transmission coeffi-
 305 cient (K_T). We computed the growing season K_T from
 306 daily solar flux data collected above the canopy of a
 307 nearby stand. Note that %TT is a theoretical estimate
 308 of PAR based on canopy architecture measured via
 309 fisheye photography and modeled inputs of above-
 310 canopy solar radiation. We calculated precision from a
 311 subset of randomly chosen photos (>5% of the total).
 312 Relative root mean square error of the %TT estimate
 313 was 2%.

314 2.3.3. Water availability

315 We used a pressure chamber (Pressure Measure-
 316 ment Systems) to estimate relative degrees of moisture
 317 stress due to above and below ground factors. Pre-
 318 dawn measurements were taken during July 1999
 319 when the soils at Blodgett Forest were no longer
 320 saturated from spring snow melt but had not yet
 321 reached late-summer drought status (J. Battles, unpub-
 322 lished data). This seasonal trend in soil moisture status
 323 is typical of the Sierra Nevada (Ziemer, 1964; Arkley,
 324 1981; Anderson et al., 1995; Royce and Barbour,
 325 2001). By sampling in July, we maximized our ability
 326 to detect any within-opening gradients in water poten-
 327 tial.

328 For each opening we measured all of the study trees
 329 in one morning (pre-dawn). We sampled twigs from
 330 giant sequoia and Douglas-fir, and fascicle from pon-
 331 derosa pine. For specific methods of collecting and
 332 measuring samples, we followed recommendations of
 333 Ritchie and Hinckley (1975). Samples were collected
 334 from the current year's growth near the middle of the
 335 plant's crown. We used a hand-shear to cut the twig
 336 samples and pulled fascicle samples off by hand. All
 337 samples were immediately measured for xylem water
 338 potential (MPa) after collection. We randomly remea-
 339 sured 30% of the sample trees to calculate precision
 340 error, which was $\pm 15\%$ of the mean. Such a high
 341 precision error is partially attributable to the fact that
 342 the remeasurements were not actually precision
 343 checks since during the first measurement, the sample

344 used in the pressure chamber was destroyed. The
 345 second sample from a precision check tree was col-
 346 lected within about 10 min after measuring the first
 347 sample from approximately the same location on the
 348 tree (mid-crown). Variability in water potential read-
 349 ings, therefore, resulted from differences arising from
 350 time between readings as well as locations on the
 351 plant.

2.4. Data analysis 352

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

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

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

3. Results 382

3.1. Patterns in third year height 383

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

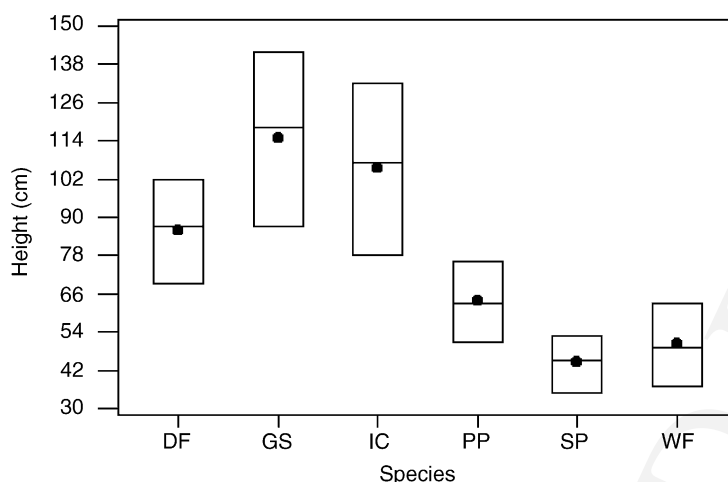


Fig. 2. Third year height data for each species from a complete census ($n = 4342$; approximately even mix of species) of trees with group selection openings at Blodgett Forest Research Station, California. The horizontal lines inside the bars represent the medians; the dark circles represent the means; 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.

386 ing size (Fig. 3, $F_{3,4326} = 77.9$, $P < 0.001$) and by row
 387 orientation (Fig. 4., $F_{7,4326} = 14.1$, $P < 0.0001$). The
 388 sequence from tallest to shortest based on species
 389 was: giant sequoia > incense cedar > Douglas-fir >
 390 ponderosa pine > white fir > sugar pine (Fig. 2). This

391 sequence was the same for each of the 0.3, 0.6, and
 392 1.0 ha opening sizes. For the 0.1 ha opening size
 393 the sequence was: giant sequoia > Douglas-fir >
 394 incense cedar > ponderosa pine > white fir > sugar
 395 pine. Mean tree height increased with opening size. A

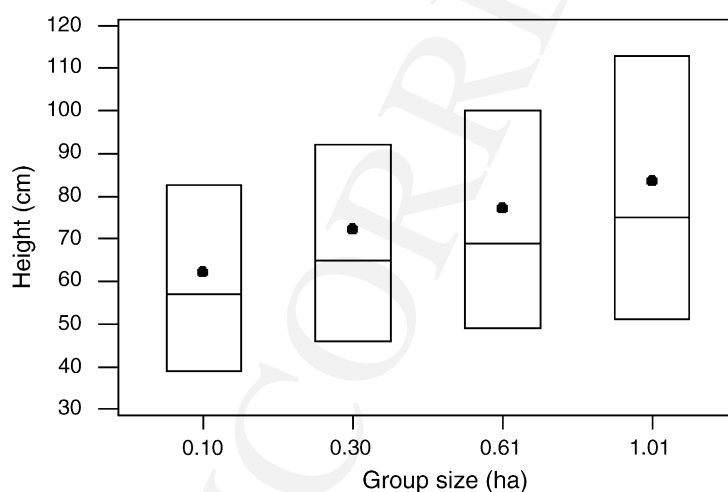


Fig. 3. Third year height data for each opening size with all species combined ($n = 4342$; approximately even mix of species) from group selection openings at Blodgett Forest Research Station, California. The horizontal lines inside the bars represent the medians; the dark circles represent the means; 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.

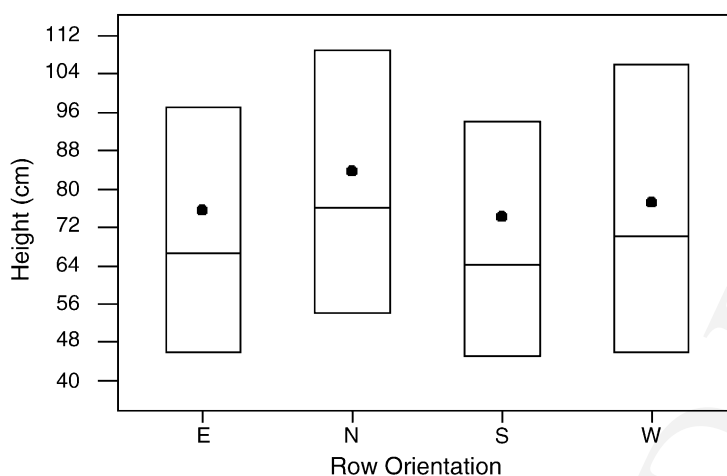


Fig. 4. Third year height data according to the direction of planted rows from center towards edge with all species and opening sizes combined ($n = 4342$; approximately even mix of species) at Blodgett Forest Research Center, California. The horizontal lines inside the bars represent the medians; the 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.

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

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

3.2. Resource gradients

424

Light availability as measured by %TT varied by 425
 within-opening location ($F_{2,118} = 48.9$, $P < 0.001$) 426

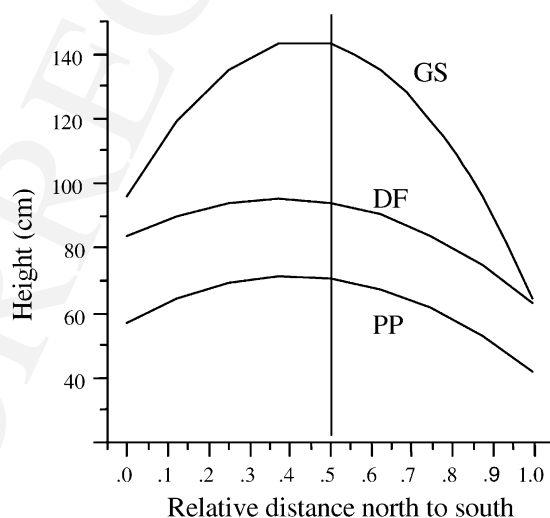


Fig. 5. Heights of trees for all group selection opening sizes combined at Blodgett Forest Research Center, California regressed against relative distance across north–south transects. The vertical line represents the center of the opening. Coefficient of variations (r^2)/sample sizes are Douglas-fir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

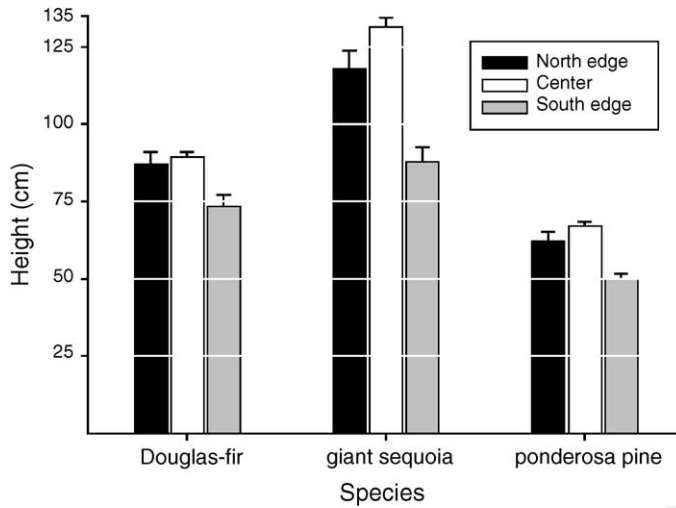


Fig. 6. Mean third year heights of study trees by species (Douglas-fir, giant sequoia, ponderosa pine) and within opening location at Blodgett Forest Research Center, California. Error bar = S.E.M.

427 and opening size ($F_{3,118} = 10.0$, $P < 0.001$, Fig. 7).
 428 Mean light availability within opening sizes ranged
 429 from 78% (S.E. = 2.4) in the 1.0 ha opening to 54%
 430 (S.E. = 3.5) in the 0.1 ha opening. Not only was there

a greater fraction of incident light available near the 431
 center of openings (81%, S.E. = 1.6) compared to 432
 edges (58%, S.E. = 2.4) but also the north edge trees 433
 received more %TT than trees in the south edge (Fig. 7, 434

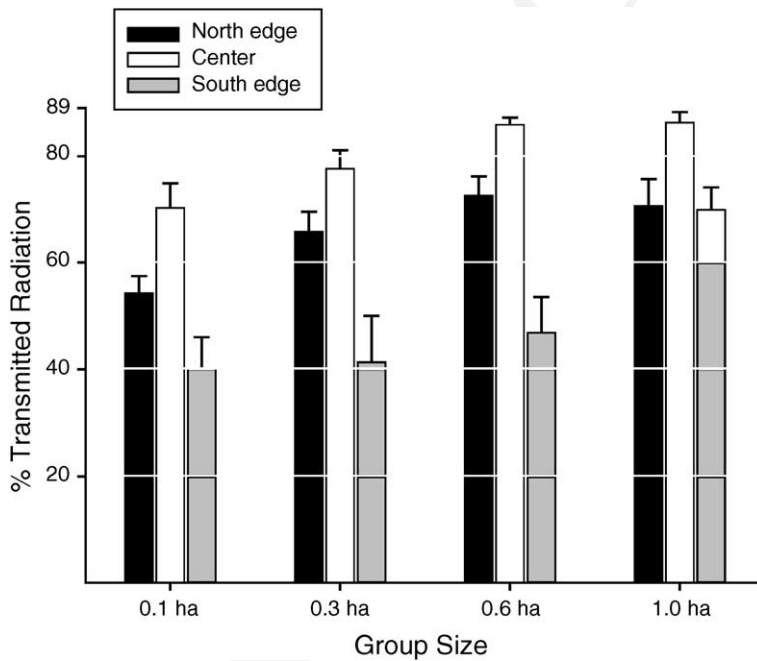


Fig. 7. Mean percent transmitted radiation available to study trees by opening size and within opening location at Blodgett Forest Research Center, California. Error bar = S.E.M. %TT is the same for each species (Douglas-fir, giant sequoia, ponderosa pine).

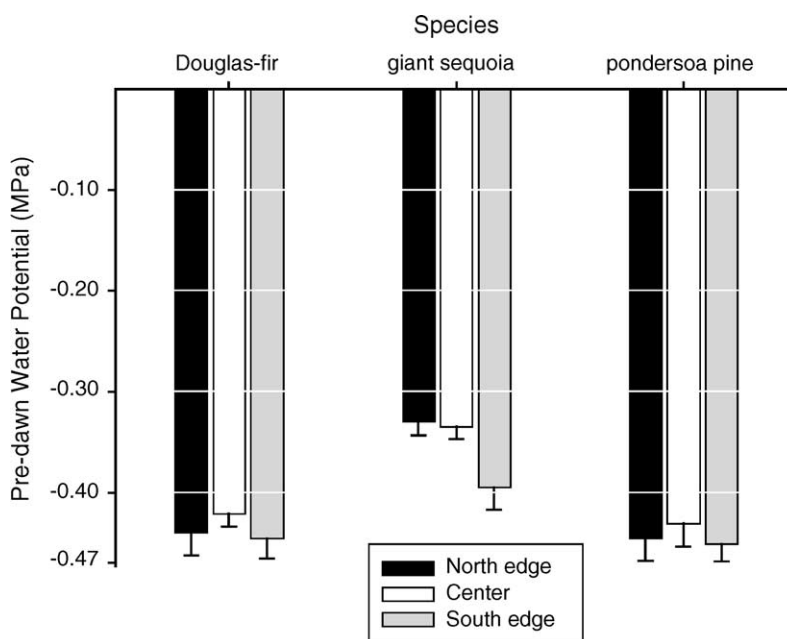


Fig. 8. Mean pre-dawn water potential of study trees by species (Douglas-fir, giant sequoia, ponderosa pine) and within opening location at Blodgett Forest Research Center, California. Error bar = S.E.M.

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

444 Pre-dawn water potential varied by species
 445 ($F_{2,333} = 31.05$, $P < 0.001$), opening size ($F_{3,333} =$
 446 4.44 , $P = 0.004$), and location ($F_{2,333} = 4.35$, $P =$
 447 0.014) with none of the interaction terms important.
 448 For this analysis, it was necessary to transform the
 449 response variable by the natural log; means are
 450 reported as the back-transformed value with the appro-
 451 priate units. Water potentials measured for giant
 452 sequoia trees were less negative (-0.34 MPa) than
 453 for the other two species (-0.42 MPa, Tukey's test,
 454 $P < 0.001$, Fig. 8). In terms of opening size, the major
 455 difference was that mean water potential in the smal-
 456 lest openings was less negative (-0.36 MPa) than in
 457 the larger sizes (-0.40 to -0.41 MPa, Tukey's test,
 458 $P < 0.05$ for all three comparisons). For within spe-

459 cies comparisons, water potential tended to be more
 460 negative for trees near the edges compared to the
 461 center (Fig. 8), but only the giant sequoia trees along
 462 the south edge had water potentials that were consis-
 463 tently more negative than trees growing in the center
 464 (Tukey's test, $P < 0.01$).

465 3.3. Multiple regression

466 The coefficient of variation (r^2) obtained from the
 467 multiple regression models (response variable was
 468 natural log transformed) was used to judge the extent
 469 of the variation in height extension that could be
 470 explained by %TT and water potential combined
 471 (Table 1). Leverage plots and associated partial F -
 472 tests were used to compare %TT and water potential
 473 as contributors to height extension variability. In all
 474 cases the model explained a significant ($P < 0.05$)
 475 amount of the variation. Giant sequoia had the high-
 476 est r^2 value, followed by ponderosa pine, then
 477 Douglas-fir. %TT was an important ($P < 0.05$) con-
 478 tributor in the model for all three species. Water
 479 potential contributed significantly to the Douglas-
 480 fir (at $P < 0.1$) and giant sequoia (at $P < 0.05$)

Table 1
Results of multiple regressions¹ for three species growing in group selection openings at Blodgett Forest Research Station, California

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

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

models, but was not a 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.

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

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

Opening size (ha)	Percent area influenced by the edge ^a			
	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.

740 edge zone of influence may then become the surround-
741 ing trees that influence the new opening.

742 5. Conclusions

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

751 These results have implications for silviculturalists
752 developing planting designs for group selections. If
753 forest managers implementing group selection silvicult-
754 ure desire to maximize yield while planting a variety of
755 species in even mixes, specific areas within the open-
756 ings with different light and water environments can be
757 reserved for the most suitable species. If the three
758 species studied here are used, we recommend planting
759 designs that favor giant sequoia in the centers. Ponder-
760 osa pine can be specifically reserved for the north edges,
761 and Douglas-fir can be planted throughout the openings
762 or near edges where microsites appear favorable.

763 Uncited references

764 [Trappe \(1962\)](#) and [Trappe \(1977\)](#).

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