Using light to predict fuels-reduction and group-selection effects on succession in Sierran mixed-conifer forest

Seth W. Bigelow, Malcolm P. North, and Carl F. Salk

Abstract: Many semi-arid coniferous forests in western North America have reached historically unprecedented densities over the past 150 years and are dominated by shade-tolerant trees. Silvicultural treatments generally open the canopy but may not restore shade-intolerant species. We determined crossover-point irradiance (CPI) (light at which the height growth rank of pairs of species changes) for seedlings in Sierra Nevada mixed-conifer forest and used these to interpret light environments produced by fuels-reduction thinning and group selection with reserved large trees. Nine of 21 species pairs had well-defined CPIs. The CPI of the most common shade-tolerant and intolerant species (white fir (*Abies concolor* (Gordon & Glendl.) Lindl. ex Hildebr.) and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson)) was 22.5 mol·m^{-2}·day^{-1} or 41% of full sun. Median understory irradiance increased from 9.2 mol·m^{-2}·day^{-1} (17% full sun) in pretreatment forest to 13 mol·m^{-2}·day^{-1} (24% full sun) in lightly and 15.5 mol·m^{-2}·day^{-1} (28% full sun) in moderately thinned stands and 37 mol·m^{-2}·day^{-1} (67% full sun) in group-selection openings. We estimate that 5%–20% of ground area in lightly to moderately thinned stands would have enough light to favor shade-intolerant over shade-tolerant growth compared with 89% of ground area in group-selection openings. The CPI provides a tool to assess regeneration implications of treatment modification such as increasing heterogeneity of thinning to enhance regeneration or reserving large trees in group-selection openings to maintain wildlife habitat.

Résumé : Plusieurs forêts résineuses semi-arides de l'ouest de l'Amérique du Nord ont atteint des densités historiquement sans précédents au cours des 150 dernières années et sont dominées par des espèces tolérantes à l'ombre. Les traitements sylvicoles ont généralement pour effet d'ouvrir le couvert sans nécessairement rétablir la présence d'espèces intolérantes à l'ombre. Nous avons déterminé le point de croisement pour l'irradiance (PCI) (le degré de lumière correspondant à une inversion du rang de deux espèces basé sur leur croissance en hauteur) de semis dans une forêt mélangée de conifères de la Sierra Nevada et nous l'avons utilisé pour interpréter l'environnement lumineux produit par une éclaircie visant à diminuer les combustibles et par une coupe de jardinage par groupes avec réserve de gros arbres. Neuf des 21 paires d'espèces avaient un PCI bien défini. Le PCI des espèces tolérante et intolérante à l'ombre les plus communes (sapin argenté(*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.) et pin ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson)) était de 22,5 mol·m^{-2}·jour^{-1} ou 41 % de la pleine lumière. L'irradiance médiane du sous-bois a augmenté de 9,2 mol·m^{-2}·jour^{-1} (17 % de la pleine lumière) dans la forêt non traitée à 13 mol·m^{-2}·jour^{-1} (24 % de la pleine lumière) dans l'éclaircie légère, 15,5 mol·m^{-2}·jour^{-1} (28 % de la pleine lumière) dans l'éclaircie modérée et 37 mol·m^{-2}·jour^{-1} (67 % de la pleine lumière) dans les ouvertures de la coupe de jardinage par groupes. Nous estimons que de 5 % à 20 % de la surface du sol des peuplements faiblement à modérément éclaircis auraient suffisamment de lumière pour favoriser la croissance d'une espèce intolérante à l'ombre plutôt que celle d'une espèce tolérante comparativement à 89 % de la surface du sol dans le cas des ouvertures de la coupe de jardinage par groupes. Le PCI peut être utilisé comme un outil pour estimer l'implication sur la régénération de la modification des traitements sylvicoles, comme l'augmentation de l'hétérogénéité de l'éclaircie dans le but d'améliorer la régénération ou la réserve de gros arbres dans les ouvertures de la coupe de jardinage par groupes dans le but de maintenir les habitats fauniques.

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Introduction

Tree canopy cover and density in many Sierra mixed-conifer forests are currently higher than before extensive logging and fire suppression by European-Americans during and after the gold rush era beginning in 1849 (Taylor 2004; Youngblood et al. 2004). Dense overstories favor recruitment of shade-tolerant trees, thereby driving tree species composition towards dominance by species that are also more fire sensitive (Stephens and Finney 2002). New management regimes, such as fuels-reduction thinning and group selection, are re-opening forest canopies (Blackwell and Troyer 2004) but it is unclear how well these practices will restore historic species composition and favor regeneration of more fire-tolerant species. Improved understanding of juvenile tree responses to light and the effects of management treatments on understory light may allow better planning of forestry treatments to achieve species restoration goals.

Light availability affects competitive relationships among regenerating tree species, and partitioning of the light environment is a major driver of local tree species composition in Sierran mixed-conifer forests (Oliver and Dolph 1992). Species such as white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) perform well in shaded environments, whereas Jeffrey pine (*Pinus jeffreyi* Balf.) and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) perform best in open, high-light environments (Gray et al. 2005). The differential performance of these species in varying light environments has been linked to growth efficiency, or biomass produced per unit of leaf area (Gersonde and O'Hara 2005). The minimum light level required to promote shade-intolerant over shade-tolerant species has not been quantified, although several studies suggest 40% of full sun as an approximation (Drever and Lertzman 2001; Gersonde et al. 2004; Bigelow et al. 2009). The light level at which the relative performance of a pair of species changes is referred to as the crossover-point irradiance (CPI) (Sack and Grubb 2001). Determining the CPI for pairs of species of contrasting shade tolerance may provide a guide to planning treatments with sufficient light for intolerants to outperform tolerants.

Opening the canopy increases understory light by increasing the area of ground that is directly irradiated by overhead sun and by increasing irradiance of tree crowns that transmit light (Landsberg and Gower 1997). The narrow conical shape of conifer crowns means that light penetrates directly to the forest floor when a tree is removed, unlike in deciduous forests where overlapping crowns are more common (Canham et al. 1999). As the size of an opening increases (e.g., when multiple trees are removed), the amount of light reaching the center of the gap increases as a function of the size of the opening and the height of the surrounding stand (Lieffers et al. 1999). In tall (>40 m tree height) Sierran mixed-conifer forest, gap sizes of 0.07–0.13 ha are predicted to provide significant areas with 40% above-canopy light (Gersonde et al. 2004). Species composition also affects light transmittance to the forest floor: the crowns of shade-tolerant trees tend to be denser than the crowns of shade-intolerants, hence transmitting less light (Canham et al. 1999). The amount of under-story light is therefore related to tree stem density, tree size distribution, and species composition.

Direct measurement of light requires equipment and techniques that are not readily accessible to forest managers, so it is important to know the ability of indirect measures to characterize understory light. Several studies show mean understory light as inversely and linearly correlated with canopy cover (proportion of forest floor covered by the vertical projection of tree crowns: Lhotka and Loewenstein 2006; Bigelow et al. 2009). Nevertheless, the ability to predict mean understory light levels is of limited help in assessing area available for regeneration of shade intolerants unless the form of the distribution of understory light is known (e.g., whether symmetrical). In contrast, spherical densiometers provide estimates of canopy closure (proportion of the sky hemisphere obscured by vegetation over a point: Jennings et al. 1999) at individual points. Such estimates are also linearly, although weakly, correlated with point estimates of light (Lhotka and Loewenstein 2006). Defining the strength and nature of the relationship between direct and indirect light estimates may increase the opportunity for practical application of light-based competition concepts such as CPI.

Thinning of small-diameter trees to reduce wildfire hazard is the dominant management on publicly held forests of western North America. However, it is recognized to be limited in its ability to enhance regeneration of shade-intolerant species (Reinhardt et al. 2008). For this reason, and also because of the limited monetary value of small trees, such treatments are sometimes deployed in conjunction with group selection, a treatment that removes all trees from areas generally <1 ha in size. The ability of shade-intolerant trees to grow rapidly in such openings is well documented (York et al. 2004). In US Forest Service lands in the Sierra Nevada, large trees >76 cm diameter at breast height (DBH) are reserved in group-selection openings due to their wildlife habitat value (Blackwell and Troyer 2004). In group selection, regeneration concerns center on whether large trees retained in relatively small openings may compete against and unduly suppress shade intolerants. Understanding the relative ability of these treatments to affect shade-intolerant recruitment via effects on understory light is of particular value because several of the shade-intolerant Sierra Nevada mixed conifer species are more resistant to fire than most co-occurring shade tolerants (Stephens and Finney 2002). Attention to treatments effects on regeneration may have long-term benefits for fire behavior in these landscapes.

This study examines crossover points in the growth–light relationship for seven common tree species of Sierran mixed-conifer forest and reports on light conditions created by different fuels-reduction and group-selection treatments in a manipulative experiment. Specific objectives were (*i*) to develop light-dependent height growth models for common tree species of Sierran mixed-conifer forest, (*ii*) to determine which pairs of species changed in height growth ranks across the light gradient, (*iii*) to document understory light conditions created by fuels-reduction thinning and group-selection treatments, and (*iv*) to use the concepts in *ii* to infer which species would be favored under the silvicultural treatments of *iii*.

Fig. 1. Location of seedling light-dependent growth study and fuels-reduction thinning and group-selection experiment in Plumas National Forest, northern California, USA. Symbols corresponding to the seedling legend show where individual naturally regenerated seedlings were sampled. Symbols for experimental treatments show GPSed plot outlines and therefore are irregularly shaped.
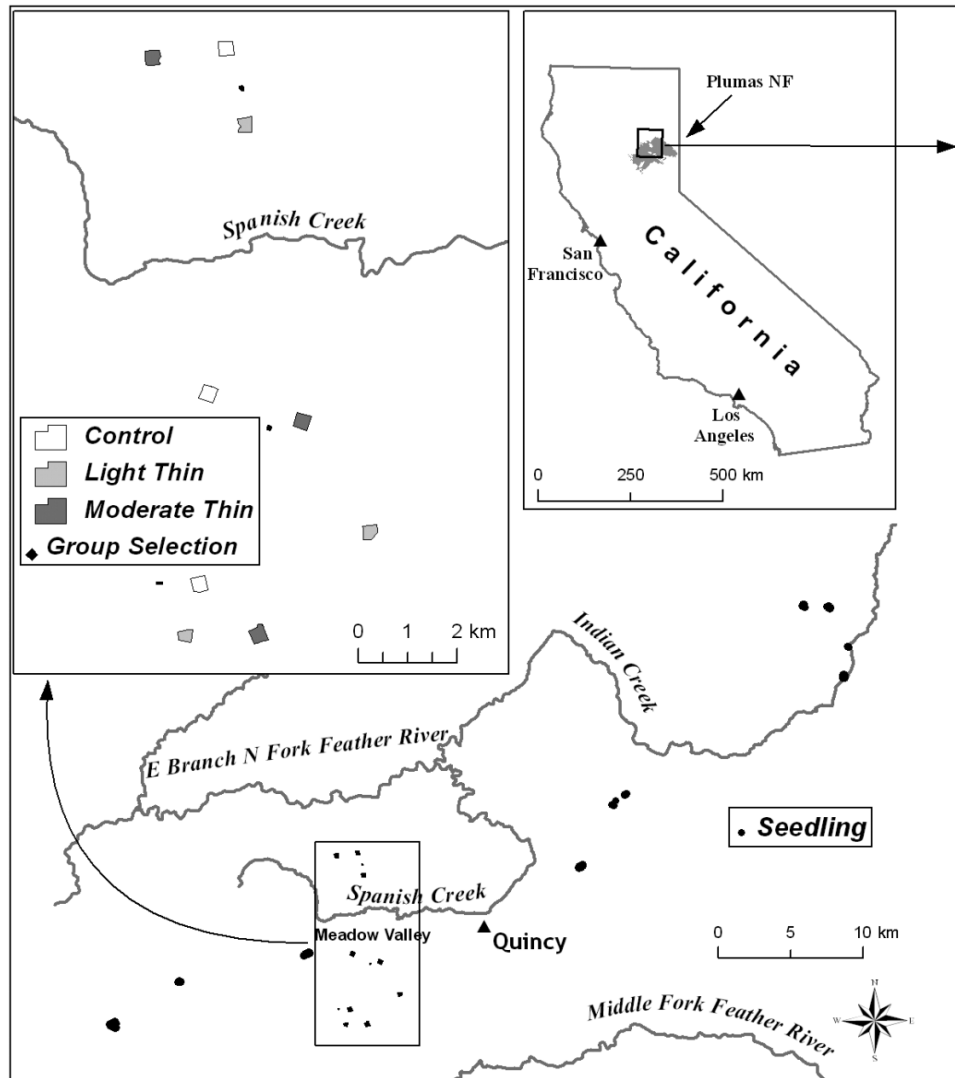
Methods

Study site

The study was located in lower montane mixed-conifer forest in Plumas County, California, within the Plumas National Forest (Fig. 1). The most abundant tree species are the shade-tolerant *A. concolor*, *P. menziesii* and incense cedar (*Calocedrus decurrens* (Torr.) Florin), the intermediate species sugar pine (*Pinus lambertiana* Douglas), and the shade-intolerant *P. ponderosa*, *P. jeffreyi*, and California black oak (*Quercus kelloggii* Newberry). Prior to the Euro-American era (beginning in 1849), the forest had a disturbance regime of low-severity ground fires with a return interval of 8–22 years (Moody et al. 2006). Understories are sparse in most areas; larger openings may contain shrubs such as greenleaf manzanita (*Arctostaphylos patula* Greene) and deerbrush (*Ceanothus integerrimus* Hook. & Arn.).

The seedling study was conducted along a 55 km east–west transect that straddled the main crest of the Sierra Nevada range (Fig. 1). Sampling elevations along the transect

varied from 1250 to 1900 m; bedrock geology varied from decomposed granite to slate, sandstone, and chert (Durrell 1988). The experimental forestry treatments took place in Meadow Valley (39°55′N, 121°04′E) (Fig. 1). The base of the valley (1150 m) is an ancient lake bed; the steep scarp of the Sierra Nevada range rises an additional 900 m to the west and smaller ridges rise 500 m to the north, south, and east.

Light-dependent height growth in seedlings

Between 50 and 75 naturally established seedlings (<0.5 m height) of each of the seven most abundant tree species were sought within walking distance of forest roads in forested areas where there was no sign of recent disturbance. Stand structures were highly variable but most contained scattered large old trees (e.g., >50 m in height) and higher densities of smaller, second-growth trees dominated by the shade-tolerant species *A. concolor*, *P. menziesii*, and *C. decurrens*. Sampling was clustered in roughly seven areas along the west-to-east transect (Fig. 1), and seedlings were selected to encom-

pass as wide a range of light environments as possible at each area. The transect was originally chosen to produce a precipitation gradient (wetter in the west, drier in the east) and to encompass variation in soil parent material, but an earlier study revealed no correlation between sapling growth and soil moisture, carbon isotope discrimination, mineralizable nitrogen, or soil pH along the gradient (Bigelow et al. 2009). Because of these previous results, environmental sampling in the present study was limited to light. Growing season light, also referred to as "irradiance", was estimated from a hemispherical lens photograph of the canopy taken at ~1.3 m height directly above each sapling (Appendix A). Canopy photographs were taken in 2004 and a randomly selected subset was repeated in 2006. Seedling height was measured in 2003 (2004 for *Q. kelloggii*) and continued annually through 2006.

Experimental thinning and group selection

An experimental application of common management treatments was carried out to assess their effects on understory light. The experimental stands initially had dense overstories (60%–84% canopy cover). Treatments were thinning to 50% or 30% canopy cover targets and group selection. There were three replicate blocks, each of which included a control stand. Plots were around Meadow Valley and comprised one block with predominantly south-facing slopes on the northern side of the valley, one block with northwest-facing slopes on the southeastern side, and one block with level to gently north-facing slopes on a plateau south of the valley. Elevation range was 1200–1650 m and maximum distance between sites was 11 km (Fig. 1). Plots for controls and experimental thinning treatments were established in 2003 and group selection sites were added in 2004. Criteria for selection of control and thinned plots involved finding approximately square, approximately 300 m × 300 m forested areas without maintained roads, large openings, or recent treatments. Stands for group selection were chosen from among ones that were close to the thinning and control plots and had been previously designated and marked for harvest by National Forest personnel. Light measurements took place in a 100 m × 100 m core (slightly smaller for the group-selection openings), leaving 100 m buffers on all sides of the measurement area. Buffers around thinned sites were treated and buffers around control and group selection sites were untreated.

Thinning prescriptions followed those concurrently in use elsewhere on the Plumas National Forest. Prescriptions prioritized the removal of the shade-tolerant species *A. concolor*, *C. decurrens*, and *P. menziesii* and preferentially removed unhealthy trees and those from suppressed, intermediate, and codominant classes. The size of removed trees ranged from a minimum height of 1 m up to a DBH of 75 cm. Thinning was applied with the goal of leaving approximately evenly spaced residual trees and evenly distributed canopy cover. Group-selection boundaries designated areas between 0.7 and 0.8 ha; trees ≥76 cm DBH were left uncut. Tree marking was done in the fall of 2005 and treatments were applied in May–June 2007. Designated trees in thinning and group-selection plots were cut by a feller-buncher, skidded to landings outside the plots, and cut to length and (or) chipped.

Trees were measured on all plots with a protocol based on the Forest Inventory and Analysis program (USDA 2005). All trees ≥12.7 cm DBH were measured in four circular 7.2 m radius subplots; one subplot was centered on the middle of the 1 ha measurement core and the three other subplots formed a triangle around the center subplot. Each subplot was ringed by a 17.8 m outer radius annular plot in which only trees with a DBH ≥61 cm were measured. Subplots and annular plots lay within a circular 1 ha plot, centered on the central subplot, in which any remaining trees ≥76 cm DBH were measured. The circular 1 ha plot largely overlapped the square 1 ha measurement core of the control and thinning plots. The group-selection openings were somewhat irregularly shaped and measured trees that fell outside the treatment boundaries were excluded from analysis. Trees were measured prior to treatment (2004) and 2 months posttreatment (2007).

Direct and indirect estimates of light in experimental plots

For hemispherical image analysis, 100 photographs were taken per stand prior to treatment (2003, control plots and thinning plots; 2004, group selection), 1 month after treatments (2007, all plots), and 3 years after treatment (2010, all plots). Photographs were taken on a 10 m square grid in the 100 m × 100 m measurement core. Some flags on the grid were disturbed during treatment, so not all post-treatment photographs were taken in precisely the same place as pre-treatment photographs. Data from photographs taken outside the group-selection treatment boundaries were not included in any analyses.

Canopy cover (i.e., the proportion of ground area covered by the vertical projection of tree crowns) was measured with a vertical sighting tube (Geographic Resource Solutions, Arcata, California) on a denser grid (5 m spacing) in the same area as the hemispherical photograph grid. In group-selection openings, only points that fell within the opening boundaries were included in the analysis. Canopy cover was measured at the same times as when hemispherical photographs were taken.

We collected data for a regression predicting photosynthetic photon flux density (in units of moles per square metre per day) from canopy closure estimates (the proportion of the sky hemisphere obscured by vegetation when viewed from a single point: Jennings et al. 1999) made with a spherical densiometer (model C; Forest Densiometers, Bartlesville, Oklahoma). A square grid comprising nine sampling stations 50 m apart (30 m in group-selection openings) was established in the center of each stand. Estimates of canopy closure after treatment in 2007 were made at the nine sampling stations. Photographs for hemispherical image analysis were taken within 1 week of densiometer readings at the same locations. Linear regression was used to assess the ability of the spherical densiometer to predict understory light measured at the same point. The coefficient of determination (r^2) was used as a measure of goodness of fit.

Analysis of seedlings' light-dependent height growth and CPI

The potential functional forms for expressing annual height growth as a function of light were linear ($a + bI$), saturating

(Michaelis–Menten, $aI/[(a/b) + I]$), and exponential (exp $(a − bI)$). Akaike's information criterion (AIC_c), corrected for small sample size, was used to select the best approximating model and associated parameters (Burnham and Anderson 2002). The error term was modeled using a normal distribution. Optimization of parameters was done with simulated annealing (Goffe et al. 1994) under the *bbmle* package (Bolker 2008) in the R statistical environment (R Development Core Team 2008).

Once a model was selected for each species, CPIs for pairs of species whose growth curves crossed within the observed range of irradiance were obtained by setting noninformative prior distributions for the model parameters and obtaining 10 000 samples from the joint posterior distribution. We found the intersection points for each of the posterior samples using a Newton–Raphson approach and used the mean of those intersection points as a CPI estimate and the 250th and the 9750th values of the ordered 10 000 intersection points as the 95% credible interval. Statistical programming was done via the R package *R2WinBUGS* (Sturtz et al. 2005).

Analysis of experimental thinning and group selection

Canopy cover data were analyzed with analysis of variance using the mixed procedure (SAS Institute Inc. 1999). The statistical model was canopy cover = block + year + treatment + year × treatment. An autoregressive covariance structure was specified for the repeated measurements that occurred on each plot. Specific contrasts were established to determine whether there was a difference in post-treatment canopy cover between the light- and moderate-thinning targets and to determine whether canopy cover changed from 2 months post-treatment to 3 years post-treatment. Irradiance was analyzed in the same way by taking the median of the 100 observations per plot (fewer for group-selection openings).

To understand the relationship between canopy cover and area available for regeneration of shade-tolerant versus shade-intolerant species, we made a linear regression of proportion of light observations >CPI against stand canopy cover in non-group-selection plots. The CPI used was that for the most common shade-intolerant (*P. ponderosa*) and shade-tolerant species (*A. concolor*). Group-selection openings were analyzed independently because of the different spatial configuration of canopy cover in these plots.

Results

Seedling light-dependent height growth and CPI

Shade-tolerant and shade-intolerant species had different maximum height growth rates (Fig. 2). Many individuals of the shade-intolerant species *P. ponderosa* and *P. jeffreyi* had growth rates exceeding 10 cm·year^{-1}. All such fast-growing individuals occurred in mean light >20 mol·m^{-2}·day^{-1} (36% of full sun based on an above-canopy light estimate of 55 mol·m^{-2}·day^{-1}). The shade-intolerant, broad-leaved deciduous tree *Q. kelloggii* had a mean rate of height growth that was indistinguishable from zero (likely due to deer browsing) and we did not include this species in further analyses. Most individuals of the shade-tolerant species *A. concolor*, *P. menziesii*, and *C. decurrens* and the intermediate-tolerant *P. lambertiana* grew <5 cm·year^{-1}. Some individuals had negative

height growth rates but we incorporated these data into the analysis rather than censoring the data at zero so that they would be reflective of actual field conditions.

There were several patterns of light-dependent height growth among seedling species (Fig. 2). The best models showed a linear (*A. concolor* and *P. lambertiana*) or exponential (*C. decurrens* and *P. ponderosa*) increase in height growth with light (Table 1). The mean model of no growth response to light was the best fit for *Q. kelloggii*, *P. menziesii*, and *P. jeffreyi*.

Nine of 21 possible species pairs had a crossover (Table 2). *Pinus ponderosa*, with its strong exponential height growth response to light, shared a CPI with all species except *Q. kelloggii*. Its CPI with *A. concolor*, the most common shade-tolerant species, was 22.5 mol·m^{-2}·day^{-1} (95% credible interval 14.6–28.9 mol·m^{-2}·day^{-1}), or 41% of full sun. This CPI was higher than *P. ponderosa*'s CPI with any of the other shade-tolerant species. CPIs for shade-tolerant species pairs tended to have extremely broad credible intervals (e.g., *A. concolor* and *P. menziesii* CPI credible interval 4.2–38.9 mol·m^{-2}·day^{-1}).

### Forest structure in response to experimental treatments

Canopy cover in the twelve 1 ha measurement grids ranged from 60% to 84% prior to treatment (Fig. 3). Small-diameter trees dominated stands: the average quadratic mean diameter in control plots was 31.4 cm (12.4 in.) (Table 3). Pretreatment basal area in the group-selection plots was considerably lower than in the other plots (43 versus 54–64 m^2·ha^{-1}), but canopy cover was comparable with that of other plots. The proportion of pine and *Q. kelloggii* stems compared with total number of stems varied from 0.09 in the controls to 0.32 in the plots slated for light thinning.

Mean post-treatment canopy cover was 57% in the lightly thinned plots and 49% in the moderately thinned plots; thus, the canopy cover targets of 50% and 30% were not attained. The lowest canopy cover in the moderate-thinning treatment was 40.3%. Mean canopy cover in group-selection openings was 12.5% due to residual large-diameter trees. Basal area in control plots increased by an average of 3.4 m^2·ha^{-1} over the 3 years that elapsed between the pre-treatment and post-treatment censuses. Post-treatment mean basal areas in the lightly and moderately thinned plots were similar: 49.3 and 49.0 m^2·ha^{-1}, respectively (Table 3). Residual basal area in the group selection plots was 7.8 m^2·ha^{-1}. Quadratic mean diameter increased by 1.6 cm in control plots and 5.1 and 6.3 cm, respectively, in lightly and heavily thinned plots. Trees in group-selection openings increased in quadratic mean diameter by 41.7 cm; the resulting quadratic mean diameter, 74.7 cm, was consistent with retention of only large-diameter trees. Pine and *Q. kelloggii* as a proportion of total stems increased from 0.32 to 0.38 in lightly thinned plots and from 0.17 to 0.19 in moderately thinned plots.

Understory light

The average plot-level median photosynthetic photon flux density in the 12 plots prior to treatment was 9.2 mol·m^{-2}·day^{-1} (SD = 1.9), or 17% of above-canopy light (Fig. 4). Treatment strongly increased understory light ($p < 0.0001$); after treatment, the mean of median light was 13.0 mol·m^{-2}·day^{-1} in lightly thinned plots, 15.5 mol·m^{-2}·day^{-1} in moderately thinned plots, and 38.3 mol·m^{-2}·day^{-1} in group selections

Fig. 2. Height growth of naturally established seedlings (<0.5 m tall initially) in mixed-conifer forest along a 55 km transect in Plumas County, California. The horizontal axis shows light measured at 1.3 m above ground. Average annual height change over 3 years is shown. Lines show the AIC_c best model of light-dependent growth.
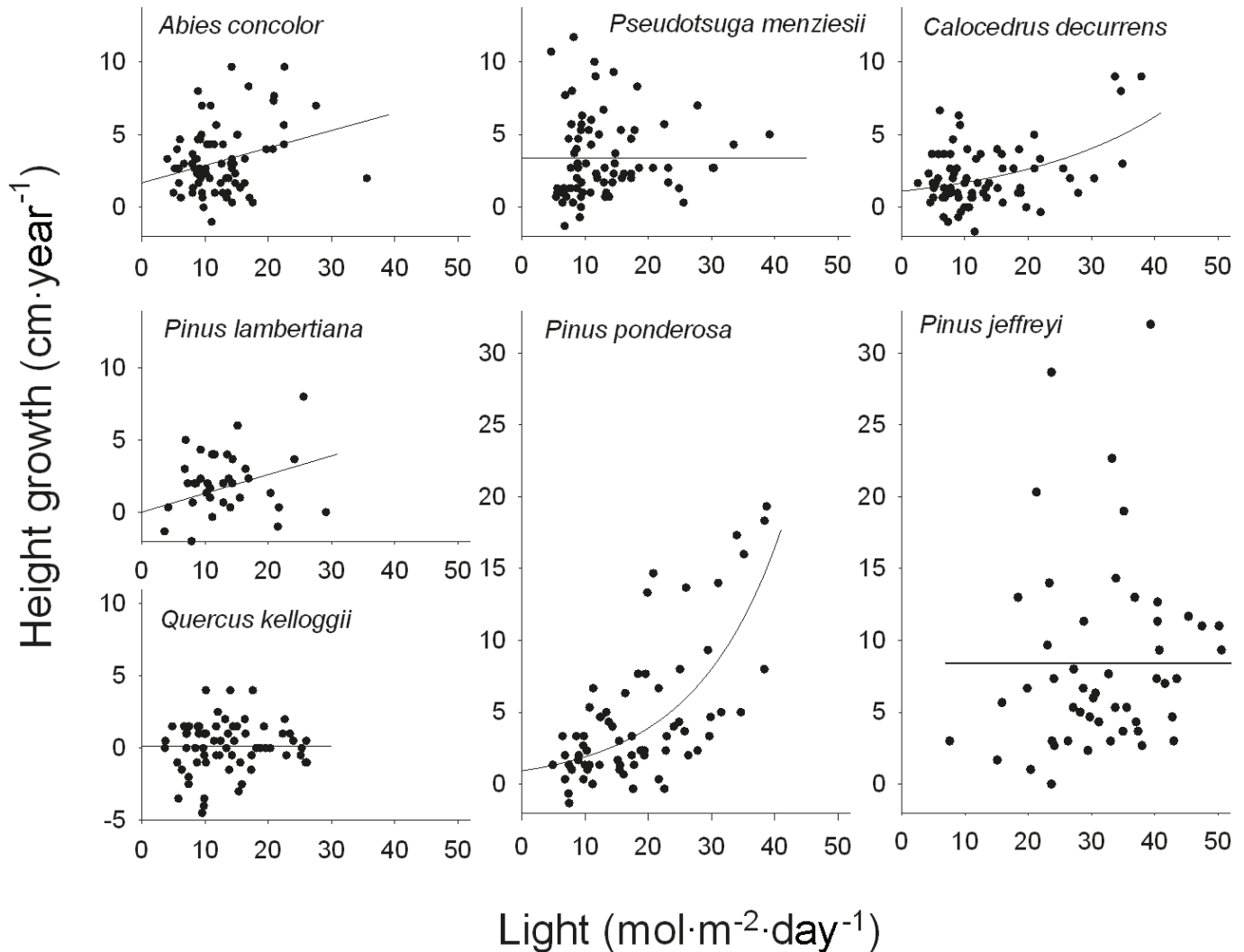
(Table 4). Median light showed little change in control plots ($p = 0.81$) or lightly thinned plots ($p = 0.20$) from 2003 to 2010. Median light values were significantly higher in moderately thinned plots than in lightly thinned plots. Median light values in treated plots did not change significantly from immediately after treatment in 2007 to 3 years after treatment in 2010 ($p = 0.55$).

The regression of the proportion of light observations >CPI (*P. ponderosa – A. concolor*) against canopy cover in control and thinned plots showed a trend at $p = 0.051$, $r^2 = 0.44$. Up to 20% of light observations exceeded the CPI (*P. ponderosa – A. concolor*) in the plots thinned to 40% canopy cover, indicating that an equivalent area should be available for regeneration of shade-intolerant species (Fig. 5). The mean proportion of light observations >CPI was 89% (SD = 5%) in post-treatment group-selection openings.

Spherical densiometry assessment

The relationship between light estimated from hemispherical image analysis and point-based canopy closure from spherical densiometry was highly significant ($p < 0.001$).

The equation for the relationship was light (mol·m^{-2}·day^{-1}) = 45.8 (1.48) – 0.405 (0.023) × canopy closure (%). Values in parentheses are standard errors of estimates. The coefficient of determination (r^2) was 0.74 (Fig. 6).

Discussion

The CPI of common shade-tolerant and shade-intolerant tree species provides a benchmark for judging current light conditions in forest understories and for assessing the implications of a range of treatments for regeneration dynamics. Under current conditions in the Meadow Valley area of the Plumas National Forest (i.e., mean canopy cover of 60%–80%), <5% of ground area would receive enough light to assure rapid growth of shade-intolerant species (Fig. 5). Experimental results indicate that light thinning (e.g., a reduction to 50% canopy cover) will not greatly increase that figure, but a reduction to 40% canopy cover will provide high-light microsites in 10%–20% of stand area. Group-selection openings, even ones with large trees retained, will have ~90% of their area in high light.

Table 1. Best models of light-dependent height growth (average annual over 3 years) of naturally established seedlings along a 55 km transect in Plumas County, California.

Species	n	Best model	Mean model Δ_i*	R^2	a[†]	b
					Parameters and confidence limits	
Abies concolor	75	$a + bI$	5.2	0.08	1.7 (0.5–3.0)	0.12 (0.03–0.21)
Pseudotsuga menziesii	75	a	0	0	3.4 (2.7–4.0)	
Calocedrus decurrens	73	$\exp(a - bI)$	7.0	0.12	0.11 (–0.04–0.58)	–0.043 (–0.062 – –0.016)
Pinus lambertiana	69	$a + bI$	7.4	0.13	0.01 (–1.27–1.19)	0.13 (0.05–0.22)
Pinus ponderosa	70	$\exp(a - bI)$	39	0.45	–0.079 (–0.90–0.39)	–0.072 (–0.096 – –0.054)
Pinus jeffreyi	50	a	0	0	8.4 (6.5–10.4)	
Quercus kelloggii	66	a	0	0	0.13 (–0.31–0.55)	

*Indicates AIC$_c$ difference between best model and mean model.

[†]Note that the confidence intervals for *a* parameters of *C. decurrens*, *P. lambertiana*, *P. ponderosa*, and *Q. kelloggii* encompass zero.

Table 2. Crossover-point irradiances for species pairs with intersecting height–growth models.

	Abies concolor	*Pseudotsuga menziesii*	*Calocedrus decurrens*	*Pinus lambertiana*	*Pinus ponderosa*	*Pinus jeffreyi*
Abies concolor		**14.2 (4.2–38.9)**	**31.2 (0.36–45.8)**	—	**22.5 (14.6–28.9)**	—
Pseudotsuga menziesii	25.8 (7.6–70.7)		**29.0 (20.0–47.2)**	—	**19.5 (13.8–25.1)**	—
Calocedrus decurrens	56.7 (0.7–83.3)	52.7 (36.4–85.8)		**14.9 (3.7–34.6)**	**9.9 (0.6–20.0)**	—
Pinus lambertiana	—	—	27.1 (6.7–62.9)		**16.2 (2.0–48.7)**	—
Pinus ponderosa	40.9 (26.5–52.5)	35.5 (25.1–45.6)	18.0 (1.1–36.4)	29.5 (3.6–88.5)		**30.8 (10.3–35.5)**
Pinus jeffreyi	—	—	—	—	56 (18.7–64.5)	

Note: Bold values in the upper right are in quanta (mol·m^{-2}·day^{-1}) (median and 95% credible interval) and values in the lower left are in units of % of full sun. *Quercus kelloggii* is not shown because it had no crossover-point irradiances with any species. — indicates no crossover point.

Fig. 3. Canopy cover before, immediately after, and 3 years after experimental treatments in Meadow Valley, California. Error bars show standard deviations ($n = 3$) and the broken vertical line shows the date of experimental treatments.
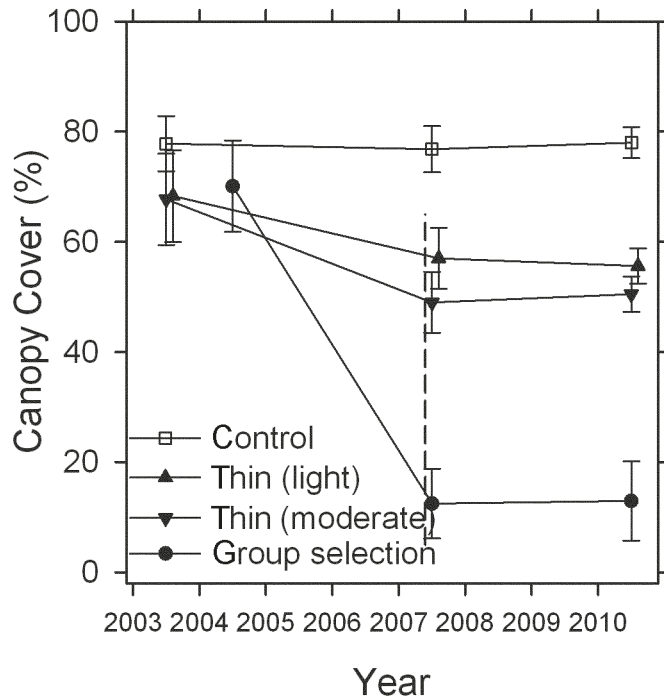

CPI

Performance rank reversals are thought to be important in determining patterns of succession and coexistence in forests (Latham 1992). The mechanistic basis of such reversals is likely related to differing patterns of biomass production with respect to leaf area (Gersonde and O'Hara 2005). The idea of CPI, or a threshold light level at which growth ranks of a pair of species switch, was formalized by Sack and Grubb (2001), and there has subsequently been debate on performance measures (Kitajima and Bolker 2003; Sack and Grubb 2003). The relative rate of dry mass accrual is an oft-used performance measure (e.g., Baltzer and Thomas 2007), but we used absolute height growth in the present study because of the mechanistic link between height growth and competitive ability. Taller individuals intercept more light while depriving shorter neighbors of it, thus gaining an asymmetric competitive advantage (Schwinning and Weiner 1998). Further, height growth is widely used by foresters as a basic metric of seedling and sapling performance.

Our data revealed some limitations to development of CPIs based on field measurements. Growth of most species was only weakly related to light (Table 1), with some individuals even displaying negative height growth. It is not uncommon for shade-tolerant species to display weak light-dependent growth because their growth approaches an asymptote at low light. However, the lack of light-dependent growth in the highly shade-intolerant *P. jeffreyi* was perplexing. Factors that may have introduced variation to the growth–light relationship include herbivory, disease, measurement error, variation in belowground resource availability, and variation in seedling age (e.g., Bigelow et al. 2009). Of these, the first

Table 3. Stand structure (canopy cover, basal area, quadratic mean diameter, and proportion of pines and black oak in stands) before and after treatment; means (with standard deviations) of three replicate blocks.

Treatment	Canopy cover (%)		Basal area (m²·ha⁻¹)		Quadratic mean DBH (cm)		Pine–oak proportion	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Control	77.9 (5.0)	76.8 (4.2)	64.3 (17.1)	68.0 (13.2)	27.7 (3.2)	29.3 (2.8)	0.09 (0.15)	0.09 (0.16)
Light thinning	68.3 (8.3)	57.0 (5.6)	54.0 (21.0)	49.1 (18.1)	32.6 (7.6)	37.7 (9.8)	0.32 (0.24)	0.39 (0.17)
Moderate thinning	67.8 (6.5)	49.1 (7.7)	62.3 (18.8)	48.8 (13.3)	34.7 (5.1)	41.0 (7.5)	0.17 (0.25)	0.19 (0.27)
Group selection	70.1 (8.3)	12.5 (6.4)	43.1 (13.4)	7.8 (2.6)	33.0 (5.8)	74.7 (5.0)	0.19 (0.20)	0.44 (0.06)

Fig. 4. Kernel density plots showing the distribution of understory light in experimental plots in mixed-conifer forest, Meadow Valley, California. Top panel, prior to treatment; middle panel, 1 month after treatment; bottom panel, 3 years after treatment. Light values from 10 to 50 mol·m^{-2}·day^{-1} in increments of 10 correspond to 18%, 36%, 55%, 73%, and 91% of full sun.
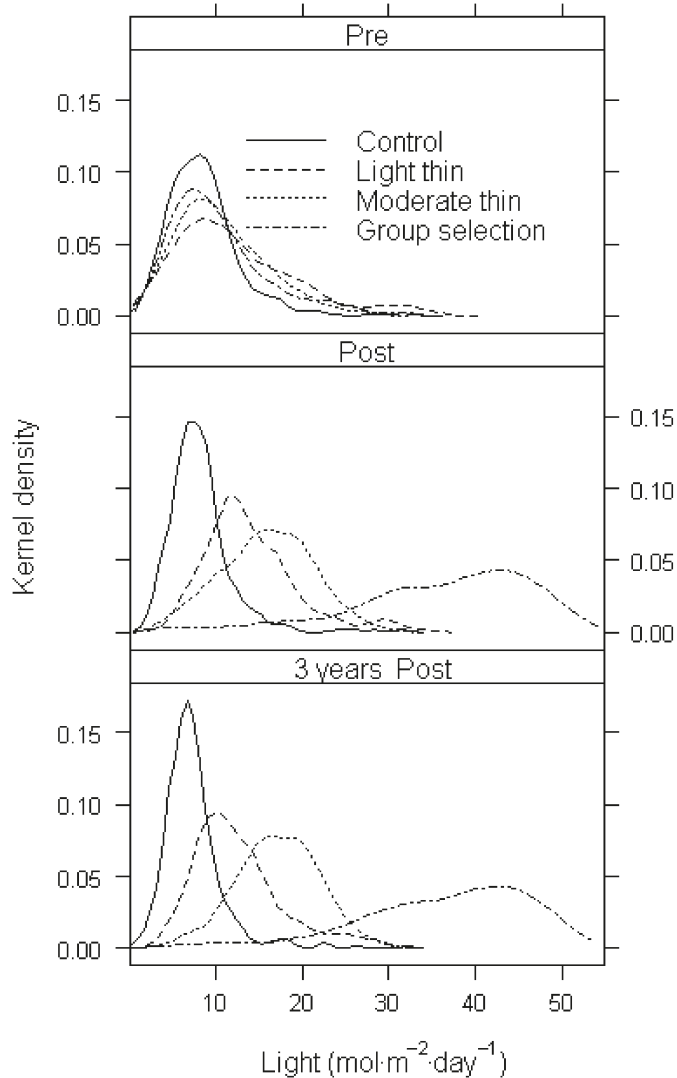
three might have been responsible for some of the negative growth values in our data. We present these values and included them in the analysis because they reflect the variable growth response that managers find under actual field conditions. Negative growth values mainly occurred at low light, however, and did not significantly influence the growth–light relationship for any species (1%–3% of observations for *A. concolor*, *P. menziesii*, and *P. jeffreyi*; 7%–8% of observations for *P. ponderosa* and *C. decurrens*) except perhaps *P. lambertiana*, which had several negative growth values at high light (19% of observations were negative). This species nevertheless displayed positive light-dependent growth.

Belowground resource limitation is unlikely to have obscured the growth–light relationship for *P. jeffreyi* or other species because tree growth in the Sierra Nevada is not tightly coupled to local variation in nutrient and water avail-

ability in surface soils (Powers 1980; Royce and Barbour 2001; Bigelow et al. 2009). Variation in seedling age is a possible source of variation. We did not assess seedling age but attempted to minimize age-related variation by selecting individuals <0.5 m high. Regardless of the cause, most species pairs had wide credible intervals around their CPI, indicating limited predictive power. Still, strong light-dependent growth of the common shade-intolerant species *P. ponderosa* resulted in well-defined CPIs with the three most shade-tolerant species *A. concolor*, *P. menziesii*, and *C. decurrens*. It is the need to know light levels at which height growth of shade-intolerant species will be favored over shade-tolerant species that is of most practical importance for forest managers.

Our study suggests 22.5 mol·m^{-2}·day^{-1} (41% full sun) as a minimum light level for competitive advantage of *P. ponderosa* over seedlings of co-occurring shade-tolerant species. Coincidentally, 40% of full sun was the minimum light required for accelerated diameter growth of *P. jeffreyi* saplings in a companion study (Bigelow et al. 2009), and 40% of full sun has been cited as a threshold value for competitive success of shade intolerants in other studies (Drever and Lertzman 2001; Gersonde et al. 2004). Two of three other related studies showed results that are consistent with our findings. York et al.'s (2003) study of 3 year height growth of mixed-conifer seedlings indicated minimal switching of height growth ranks across group-selection openings from 0.1 to 1.0 ha in size, yet mean light transmittance in the smallest (0.1 ha) openings, 40% of full sun (22 mol·m^{-2}·day^{-1}), was still higher than where most crossovers occurred in our data. McDonald (1976) demonstrated a reversal in height growth ranking between *P. ponderosa* and four shade-tolerant species along a treatment intensity gradient from single-tree selection to group selection. In the contrasting study, height growth of *A. concolor* exceeded that of *P. ponderosa* even at light transmittance up to 58% of full sun (Oliver and Dolph 1992). Except for this conflicting study, there is broad agreement that ~40% of full sun represents a threshold for light-driven competitive growth advantage of *P. ponderosa* in the Sierra Nevada. Having such a quantitative threshold allows investigation of stand area potentially available for shade-intolerant regeneration under various silvicultural treatments.
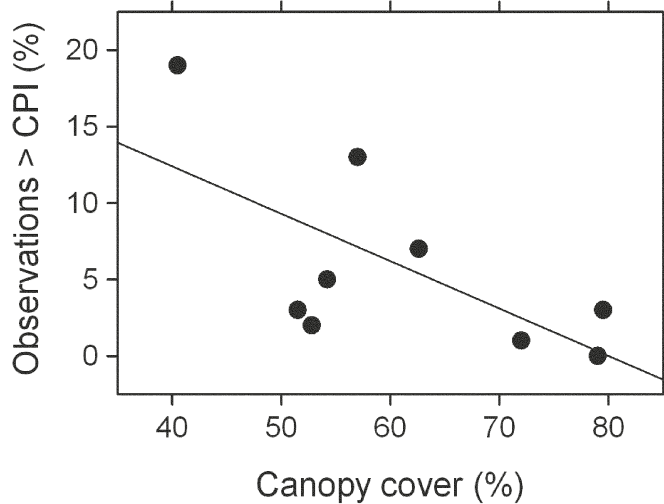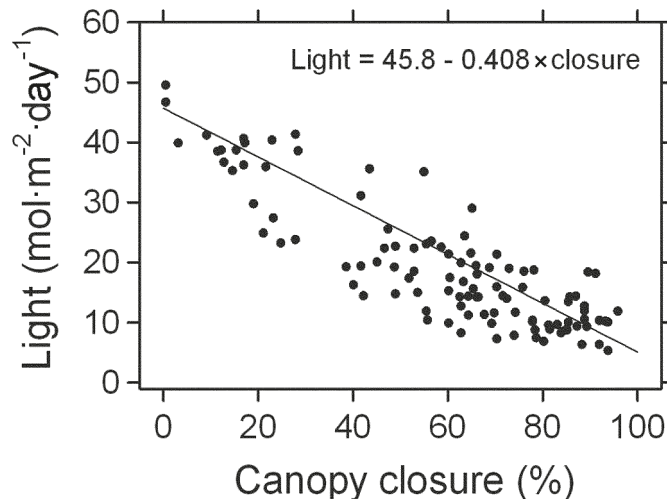
Light

Mean light levels in untreated forest in our study were moderately high (range of transmittance from 14% to 25% of above-canopy light) despite the preponderance of dense-crowned, shade-intolerant tree species. In contrast, a study in dense mixed-conifer stands in the central Sierra showed mean transmittance of only 16% (Blodgett Forest: Moghaddas et al. 2008). The distribution of light in our study forest was strongly skewed with rare bright patches among a mostly dark understory, as is often true of dense forests (Parker et al. 2002). The increases in light in our studies after treatment were consistent with the Blodgett Forest study; for example, the increase from 19% to 24% (not significant) in the light-thinning treatment of our study was similar to the 16%–21% (also not significant) increase from mechanical treatments in the Blodgett Forest study. Creation of group-selection openings, of course, led to large increases in understory light and switched the skew of the distribution to mostly bright with a

Table 4. Means of median irradiance (mol·m^{-2}·day^{-1})* in experimental stands before and after treatments.

Treatment	Pre-treatment	Post-treatment	3 years post-treatment
Control	7.8 (1.4)	7.5 (1.0)	6.8 (0.4)
Light thin	10.4 (2.7)	13 (1.3)	11.5 (0.6)
Moderate thin	9.3 (1.8)	15.5 (3.7)	16.9 (2.6)
Group selection	9.2 (1.6)	38.3 (6.2)	38.3 (5.3)

*Transmittance (proportion of full sun) can be calculated by dividing values by above-canopy light (55 mol·m^{-2}·day^{-1}).

Fig. 5. Percentage of understory light observations that exceeded the crossover-point irradiance (CPI) of *Pinus ponderosa* and *Abies concolor* in nine mixed-conifer stands in Meadow Valley, California, after treatment in 2007. Control and thinned stands only.

Fig. 6. Understory light as predicted by spherical densiometer estimates of canopy closure. Data are from stands that were either untreated or treated with fuels-reduction thinning or group selection.

few shaded areas (Fig. 4). Median light transmittance in group-selection openings, 70%, is slightly lower than that of the 1 ha openings at Blodgett Forest (from 70% along edges to 90% in the center: York et al. 2003).

Several studies have noted a strong relationship between canopy cover and mean transmittance of light through the canopy (Lhotka and Loewenstein 2006; Bigelow et al. 2009). Mean light would be useful for predicting area avail-

able for regeneration of intolerants, given a threshold value such as CPI, if the distribution of observations around the mean were known. Nevertheless, this is complicated by the change from a right-skewed to left-skewed light distribution as canopy cover decreases along the continuum from closed- to open-canopy forest. We avoided this complication by simply noting the empirical relationship between canopy cover and proportion of light observations (a proxy for area) exceeding the *P. ponderosa – A. concolor* CPI. The unexpected weakness of this relationship ($r^2 = 0.44$) was unrelated to the relative abundance of differing species in the stand overstories (data not shown), although species do differ predictably in crown light transmittance according to their shade-tolerance ranking (Canham et al. 1999). The degree of patchiness in the stands may have played a larger role in determining mean irradiance and distribution form and in introducing variation into the relationship between canopy cover and understory irradiance.

Restoration potential of silvicultural treatments

CPI provides a quantitative explanation for the success of *A. concolor* over *P. ponderosa* given understory light conditions prevailing in the present dense mixed-conifer forests of the Sierra Nevada. In our study, fuels-reduction treatments did sufficiently increase understory irradiance to favor shade intolerants in a limited area. The fuels-reduction treatment that resulted in the lowest canopy cover (~40%) only provided high light (i.e., irradiance > CPI) for about 20% of its area. Retaining 40% canopy cover is considered a heavy thin; for example, the most intensive treatment (mechanical thinning plus prescribed fire) at Blodgett Forest only reduced canopy cover to 50%. Granted, restoration of shade-intolerant species is not the primary objective of fuels-reduction thinning (Reinhardt et al. 2008), but given the ubiquity of fuels-reduction thinning treatments (Schoennagel and Nelson 2011), it is reasonable to ask how fuels-reduction treatments may contribute to the longer-term goal of restoring fire-tolerant species such as *P. ponderosa*, which is highly shade intolerant. Group-selection openings, in contrast, had abundant light, and the retention of large trees within the openings did not adversely affect shade-intolerant regeneration opportunities. Nevertheless, openings of 1 ha have a substantial visual impact on the landscape and may affect habitat connectivity under some circumstances (e.g., Bigelow and Parks 2010). Creating smaller openings may be a means of providing regeneration opportunities for shade-intolerant trees; openings of 0.1 ha (equivalent to a 36 m diameter circle) in similarly dense forest had mean light levels at or above the *A. concolor – P. ponderosa* CPI (York et al. 2003).

Direct planting is a possible solution to increasing the representation of shade-intolerant regeneration in treated stands. The equation relating mean understory light to canopy clo-

sure (i.e., the proportion of sky hemisphere obscured by vegetation above a point) (Fig. 6) provides a basis for estimating whether a point in the forest is irradiated well enough to support rapid growth of a given species. The relationship is not tight ($r^2 = 0.75$) but is comparable with the $r^2 = 0.68$ value of Lhotka and Loewenstein (2006). Converted to units of transmittance (percentage of full sun) rather than irradiance, the formula $83 - 0.74 \times$ canopy closure (%) suggests that a spherical densiometer reading of 58% canopy closure would be equivalent to 40% of full sun. This relationship is influenced by factors such as site aspect and latitude, but it provides a rule of thumb for using a common and inexpensive forestry instrument to determine suitability for planting of shade intolerants.

Small openings could be created by spatially aggregating retained trees, leaving clumps and gaps. Thinning treatments in our experiment were applied to leave an approximately evenly distributed residual stand, consistent with the silvicultural objective of maximizing growth of residual trees and the fuels-reduction objective of maximizing separation of crowns of adjoining trees. If the thinning prescription were applied in a patchier manner, leaving larger openings and denser clusters of remaining trees, the range of light values would increase (Drever and Lertzman 2003). This might require reevaluation of fuels-reduction thinning effectiveness, but otherwise, regeneration opportunities for shade-intolerant species are severely limited in thinned stands.

In addition to adequate light, natural regeneration of *P. ponderosa* and *P. jeffreyi* requires a seed source. Fuels-reduction thinning treatments do not contribute to this because current thinning prescriptions do not emphasize placement of larger openings where there are residual shade-intolerant trees, leaving seed dispersal to appropriate openings to chance. It is unlikely, therefore, with only a modest proportion of the stand understory available for shade-intolerant restoration that current fuels-reduction treatments will have much influence on guiding species composition toward earlier composition of shade-intolerant, fire-resistant trees.

Conclusions

CPI is a useful concept that may improve prediction of which species will have superior height growth given a known light environment. Predictions of CPI, however, will be less accurate in forests where other resources such as water or nitrogen availability most affect tree seedling height growth. Our results suggest that fuels-reduction thinning treatments in Sierran mixed-conifer forest will only produce a very limited area with sufficiently high light to favor the shade-intolerant *P. ponderosa*, but group selection will produce a much larger area for rapid *P. ponderosa* growth, even when large trees (i.e., >75 cm DBH) are retained within group openings. The CPI may help in design of novel treatments that balance multiple objectives such as maximizing diversity of regeneration and minimizing wildfire hazard.

Acknowledgments

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Appendix A. Light estimation from hemispherical image analysis

Growing season photosynthetic photon flux density (PPFD) was estimated from hemispherical image analysis (HIA) photographs. A Nikon Coolpix 4500 camera with FC-E8 fisheye converter was mounted on a tripod, leveled, and oriented north–south. Photographs were analyzed with GLA V2 (Frazer et al. 2000) using the parameters Kt (cloudiness index) of 0.8 for generally clear skies, spectral fraction (ratio of energy in visible wavelengths to all wavelengths) of 0.45, beam fraction (ratio of direct solar radiation to total solar radiation) of 0.9, and a growing season from 1 April to 30 September (Bigelow et al. 2009). Accuracy of HIA estimates of understory PPFD ($PPFD_{HIA}$) was assessed with quantum sensors ($PPFD_{Qs}$). Four sensors (0–2500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ range, 400–700 nm wavelength; Onset Computer Corp., Bourne, Massachusetts) were deployed in stands of varying structure for up to one growing season and then moved to a different stand the following year for 3 consecutive years ($n = 12$). Output was recorded at 15 min intervals with dataloggers (Hobo Microstation; Onset Computer Corp.). Hemispherical lens images taken at sensor locations were analyzed over the same range of dates as the accompanying $PPFD_{Qs}$ record and values were normalized to mean daily PPFD (moles per square metre per day). HIA provided precise prediction of PPFD ($r^2 = 0.987$) but HIA analyses of PPFD were consistently 12% greater than quantum sensor estimates. The discrepancy was probably due to the use of a spectral fraction of 0.45; a spectral fraction of 0.40 would likely be more appropriate for our location (Meek et al. 1984). HIA-derived estimates of PPFD were corrected to make them consistent with quantum sensor estimates. PPFD values presented in this paper can be expressed as a proportion of above-canopy light by dividing by 55.0 $mol \cdot m^{-2} \cdot day^{-1}$, which is the estimated above-canopy light based on a 0.40 spectral fraction.

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