

Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests

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Abstract: We characterize understory light of seven stands that varied along a gradient of tree retention. Using hemispherical canopy photographs and digital image, we estimated gap light or solar radiation reaching the understory through the canopy. Using nonlinear regressions, we related gap light to several structural attributes in the examined silvicultural treatments. The silvicultural treatments affected both the median and range of gap light in the understory. As overstory removal increased from uncut second growth to green-tree retention, the median value of light increased from 8 to 68% full sun, while the range of light increased from 3–22% to 26–88% full sun. We found strong, significant, and negative nonlinear relationships between gap light at a particular microsite (0.04 ha) in the understory and the height, diameter at breast height, density, and volume of surrounding retained trees ($r_a^2 = 0.77\text{--}0.94$). These relationships can aid planning of treatments that retain forest structure, such as variable retention, by allowing predictions of understory light from commonly used field data. These predictions allow forest managers to understand some of the ecological consequences and tradeoffs associated with retaining structure during harvesting.

Résumé : Nous avons caractérisé la lumière du sous-bois de sept peuplements situés le long d'un gradient de coupe avec réserves. À l'aide de photographies hémisphériques du couvert et de l'analyse d'images digitales, nous avons estimé la quantité de lumière dans les trouées, c'est-à-dire la radiation solaire atteignant le sous-bois après avoir traversé le couvert. À l'aide de la régression non linéaire, nous avons corrélié la quantité de lumière dans les trouées à plusieurs attributs structuraux en fonction des traitements sylvicoles examinés. Les traitements sylvicoles ont altéré à la fois la médiane et le domaine des valeurs de quantité de lumière dans les trouées. Lorsque l'enlèvement du couvert augmente en passant des peuplements de seconde venue non coupés à ceux coupés avec préservation d'arbres vivants, la valeur médiane de la quantité de lumière augmente de 8 à 68 % de la pleine lumière, alors que le domaine des valeurs observées passe d'entre 3 à 22 % à entre 26 à 88 % de la pleine lumière. Nous avons trouvé des relations non linéaires fortes, significatives et négatives entre la quantité de lumière dans une trouée, pour un microsite particulier (0,04 ha) dans le sous-bois, et la hauteur, le diamètre à hauteur de poitrine, la densité et le volume des arbres restants avoisinants ($r_a^2 = 0,77$ et $0,94$). Ces relations peuvent aider à planifier des traitements qui conservent la structure de la forêt comme la coupe à rétention variable pour permettre de prédire la quantité de lumière du sous-bois à partir de mesures récoltées de façon usuelle. Ces prédictions permettent aux aménagistes forestiers de comprendre quelques-unes des conséquences écologiques et les compromis associés au maintien de la structure au moment de la récolte.

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Introduction

Increasingly, forest managers wish to implement silvicultural systems that retain live trees, snags, and other aspects of forest structure as alternatives to clear-cutting (Franklin et al. 1997; Weyerhaeuser Co. 2000). These treat-

ments maintain structural diversity in harvested areas by retaining trees in different densities, spatial arrangements, and age, size, and life-stage classes (Hansen et al. 1995a; Acker et al. 1998). Retaining forest structure can help meet ecological objectives because maintaining structural diversity is thought to conserve biological diversity and ecosystem function in harvested areas (McComb et al. 1993; Hansen et al. 1995b). Moreover, partial cutting treatments can allow managers to address various, and sometimes contradictory, management objectives within a given treatment unit. For example, it is possible to implement harvesting treatments that meet objectives of timber production while maintaining mature-forest characteristics (Neitlich and McCune 1997; Rose and Muir 1997), maintaining wildlife habitat (Cole 1996; Curtis et al. 1998), conserving functional communities of soil organisms (Barg and Edmonds 1999; Marshall 2000), or mitigating the microclimatic effects of forest removal (Barg and Edmonds 1999). However, the tradeoffs among these diverse management objectives are often uncertain. It

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is especially unclear how retaining forest structure will affect the growth and survival of regenerating trees, either already present in the stand as natural and (or) advance regeneration or as planted trees (Birch and Johnson 1992; Franklin et al. 1997).

Partial cutting treatments span a wide range of intensities of overstory removal and can incorporate more traditional silvicultural approaches, such as seed-tree and single-tree selection. This diversity of treatments may best be conceptualized using the notion of “variable retention” (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995; Franklin et al. 1997). Variable retention recognizes a gradient of structural retention and describes silvicultural treatments according to various attributes of retained structure. Typical attributes of structure include density, basal area, volume, mean height of standing trees, and other descriptors of structure in the forest such as snags or species composition.

The extent of partial overstory removal directly affects light in the understory (Coates et al. 1997). Changes in the overstory influence the angle of incidence of solar radiation, the timing and duration of sunflecks, and the mix of diffuse and direct solar radiation (Canham 1988; Chazdon 1988). In this study, we sought to quantify the relationships between light in the understory of partial cutting treatments and the amount and type of retained structure. Understanding these relationships is key for predicting the impacts of retaining forest structure on light and how light affects various aspects of the post-harvest stand (Leiffers et al. 1999), e.g., survival and growth of regeneration (Klinka et al. 1997; Wright et al. 1998), development of shrub and other understory species (Ricard and Messier 1996; Naumburg and DeWald 1999), and microclimatic conditions in the understory (Brososke et al. 1997; Zheng et al. 2000). Therefore, the objectives of this study were to (i) characterize light in the understory of partial cutting treatments, and (ii) to quantify the relationships between understory light and attributes of stand structure, as determined from readily available field data. Understanding these relationships will help address some of the uncertainty regarding the successful implementation of silvicultural treatments that retain structure, as well as aid in their planning and design. Drever and Lertzman (2001), in a companion piece to this work, examine the growth response to light for two silviculturally important species; these light–growth responses can be used to predict the performance of regeneration under partial canopies. While the treatments we examined pre-dated variable retention, we expect our analyses to provide tools for planning variable retention and other innovative silvicultural treatments that retain forest structure.

Materials and methods

Study area

Drever and Lertzman (2001) provide further details regarding the study area and the use of hemispherical canopy photography for estimating light. The study area lies on the east coast of Vancouver Island, near Campbell River, British Columbia, Canada (49°57'N, 125°16'W). The sampled areas are almost exclusively second-growth coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests that regenerated naturally after large forest fires in the

1930s (S. Lackey, Regional forester, TimberWest Forest Products Ltd., personal communication). Smaller amounts of western hemlock (*Tsuga heterophylla* (Raf) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and western white pine (*Pinus monticola* Dougl. ex D. Don) are present. Salal (*Gaultheria shallon* Pursh), red huckleberry (*Vaccinium parvifolium* Smith), and dull Oregon-grape (*Mahonia nervosa* Pursh) typically dominate the shrub understory. Vanilla leaf (*Achlys triphylla* Smith) and sword fern (*Polystichum munitum* (Kaulf.) K. Presl.) are common in the herb layer. All the stands sampled in this study occur in the very dry maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHxm) (Meidinger et al. 1991; Green and Klinka 1994). The study area is generally flat, and all the sampled stands have slopes of less than 3%. Soils of this area are primarily Orthic Dystric Brunisols and Humo-Ferric Podzols (Keser and St. Pierre 1973). The parent materials are marine and glacio-marine deposits that vary between silt and clay and gravelly, sandy, or clayey veneer, normally over till (McCammom 1977).

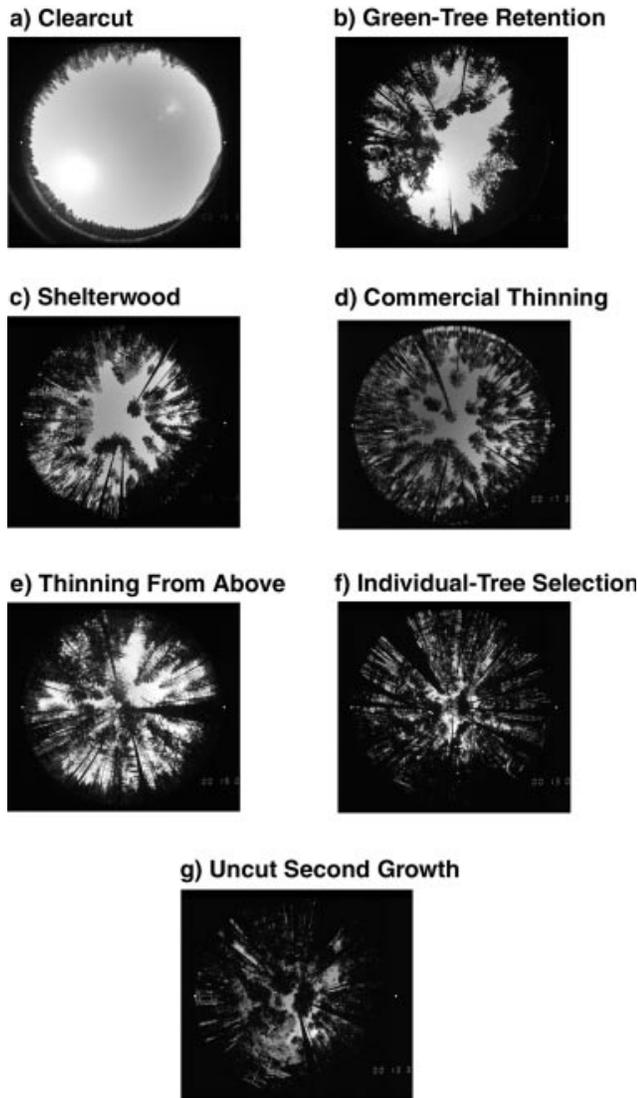
Sampling light and stand structure in partially cut stands

In the summer of 1997, we sampled light and forest structure in seven stands that varied in the abundance and distribution of retained structure (Fig. 1). The treatments that created this variation represent a gradient of retention. Ranked from low to high density of retained trees, the treatments were clearcut, green-tree retention, commercial thinning, thinning from above, shelterwood, individual-tree selection, and uncut second growth (Table 1). Stands were chosen from forest cover maps provided by TimberWest Forest Products Inc. From these maps, we chose stands with a similar preharvest date of establishment (1920–1935) and stand composition (Douglas-fir leading).

The silvicultural treatments in the seven stands we sampled (Table 1) were

- (1) Clearcut (CC): a one-pass removal of all standing trees completed in the spring of 1996.
- (2) Green-tree retention (GTR): a one-pass modified clearcut. Completed in the spring of 1993, this cut removed 95% of the merchantable timber, retaining structurally sound snags and 5–15 dominant Douglas-fir per hectare as well as any immature western hemlock, lodgepole pine, and western redcedar.
- (3) Shelterwood (SW): the first cut of a planned two-pass uniform shelterwood treatment. Completed in the spring of 1993, this cut removed 75% of stand volume and retained 80–100 dominant Douglas-fir per hectare as well as 10–25 suppressed and codominant western redcedar per hectare.
- (4) Commercial thinning (CT): the first commercial cut of a planned two-pass harvest of Douglas-fir. Completed in 1994, this cut removed about 75% of the trees and retained 400–450 Douglas-fir per hectare homogeneously distributed for subsequent harvest.
- (5) Thinning from above (TFA): a one-pass harvest of all dominant Douglas-fir that retained a multistory canopy of subdominant and understory Douglas-fir, western

Fig. 1. Representative hemispherical photographs of the canopy in seven stands that varied along a gradient of retained tree structure.



hemlock, lodgepole pine, and western redcedar. Harvesting was completed in 1994.

- (6) Individual-tree selection (ITS): the first cut of a planned multiple-pass harvest of dominant trees in a series of light thinnings at intervals of 4 to 10 years. Harvesting was completed in the fall of 1991.
- (7) Uncut second growth (USG): no silvicultural treatment.

To characterize light in these stands, we took a hemispherical canopy photograph every 30 m along a straight 900-m randomly initiated transect in each stand ($n = 30$). Photographs were taken at least 30 m from the stand edge. We used a Minolta X700 camera mounted with a Minolta fish-eye lens ($f = 7.5$ mm). To characterize structure, at the location of every third photograph, we measured the diameter at breast height (DBH; 1.3 m), species, and height of all trees >2 m, including stumps and snags, in an 11.3 m radius circular plot (0.04 ha). From these data, we computed volume, basal area, mean height, mean DBH, percent composition of component species, and various other structural

attributes for each sampled plot and for each of the seven stands. Estimates of stand structural attributes were separated into live and total (live plus dead) biomass.

The photograph was taken at the plot centre. We chose the 2-m threshold of sampling height because forest structure greater than 2 m likely has an impact on the light environment of regenerating trees and understory shrubs. We sampled light 30 times, rather than only 10 as for the structure assessment, to more fully characterize the variation in light within the seven stands.

To assess the effect of spatial distribution of retained trees on understory light, we calculated the Morisita index of dispersion for each treatment type. This density-based index provides a proxy of the spatial aggregation of stems at the 0.04-ha scale by incorporating stem density in the 10 plots of stand structure of each treatment type (Krebs 1989). Lower values (i.e., close to zero) indicate a uniform pattern of stems, and values closer to the sample size (i.e., 10) indicate a clumped pattern of stems.

Quantifying light

Hemispherical photographs of the canopy allow characterization of the amount of photosynthetically active radiation at a given spot in the understory (Anderson 1964; Frazer et al. 1997). These photographs capture the geometry and orientation of canopy structure and, combined with digital image analysis, are used to estimate an index of light in the understory. In this study, we used canopy photographs to determine an index of light availability for the entire growing season, rather than an estimate for a particular point in time. This index, measured in units of percent of full sun, was determined using GLI/C version 2.0 light modelling software developed by C.D. Canham (Scientist, Institute of Ecosystem Studies, Millbrook, N.Y.). GLI/C, like other image analysis systems, measures “gap light”, an index of the amount of light available for photosynthesis for the whole growing season (Canham 1988). More specifically, gap light is an estimate of the solar radiation that reaches the understory directly through an opening in the canopy, without passing through or reflecting off leaves or branches (Canham 1988). Estimating gap light involves combining the diurnal and seasonal paths of the sun, the mix of direct and diffuse solar radiation, and the spatial distribution of the surrounding canopy (Frazer et al. 1997). Under relatively open conditions, gap light accounts for the vast majority of incident radiation. On the other hand, under a heavily closed canopy, a large fraction of incident radiation in the understory is transmitted through or reflected off foliage and is not captured by a photograph (Canham 1988).

Data analysis

We assessed different structural attributes as predictors of gap light at two different spatial scales: the microsite and the stand. At the microsite scale (i.e., the 0.04-ha plots), we were able to easily measure attributes of stand structure and estimate light. At the stand scale (i.e., 9–35 ha), sampling multiple plots in each stand allowed inferences about how variation in light relates to variation in stand structure and to variation in the spatial distribution of retained trees.

We fit the following nonlinear model to the light and structure data:

Table 1. Selected stand structural attributes of the sampled partial cutting treatments, separated by live biomass and total (live and dead) biomass of trees >2 m in height.

Treatment	Live tree biomass				Total tree biomass					
	Mean DBH (cm)	Mean height (m)	Basal area (m ² /ha)	Density (stems/ha)	Volume (m ³ /ha)	Mean DBH (cm)	Mean height (m)	Basal area (m ² /ha)	Density (stems/ha)	Volume (m ³ /ha)
Clearcut	0	0	0	0	0	0	0	0	0	0
Green-tree retention	22 (12)	16 (7)	15 (15)	184 (179)	167 (174)	43 (33)	13 (7)	59 (62)	247 (222)	167 (175)
Shelterwood	37 (15)	28 (11)	30 (12)	284 (183)	356 (126)	37 (15)	27 (11)	30 (12)	294 (191)	358 (125)
Commercial thinning	28 (5)	26 (4)	21 (7)	319 (60)	209 (104)	28 (5)	25 (4)	21 (7)	329 (63)	211 (103)
Thinning from above	19 (5)	16 (3)	22 (5)	628 (309)	200 (70)	19 (5)	16 (3)	22 (5)	656 (321)	203 (70)
Individual-tree selection	31 (5)	28 (3)	56 (12)	691 (194)	682 (93)	30 (5)	26 (3)	73 (18)	858 (257)	704 (80)
Uncut second growth	21 (3)	21 (2)	44 (6)	1157 (227)	388 (85)	20 (2)	19 (2)	46 (7)	1376 (204)	398 (91)

Note: Values are means with SDs in parentheses. $n = 10$ plots in each treatment.

$$[1] \quad Y = a e^{-bX} + \epsilon$$

In this model, Y is the measure of gap light, X is the structural attribute, ϵ is the error term, and a and b are model parameters. At this stage, we also assessed the effect of removing the dead biomass component from the data on the capacity of structural attributes to predict understory light.

Nonlinear regressions provided an excellent fit of the model to the data, with low mean square error of residuals and high predictive capacity (i.e., high r_a^2). Plots of the residuals against predicted values strongly suggested a curvilinear relationship between gap light and the structural attributes. To ensure the assumptions of nonlinear least squares regressions were met, we examined plots of the residuals for normality and homoscedasticity.

Results

Gap light under partial cutting treatments

The various harvesting treatments we examined create a wide variety of understory light environments. Harvesting affected both the overall range of gap light in a stand and the specific maximum and minimum light levels (Fig. 2). As the extent of overstory removal increased from uncut second growth (USG) to green-tree retention (GTR), the median value of light increased from 8 to 68% full sun, while the range of light increased from 3–22% full sun to 26–88% full sun (Fig. 2). Individual-tree selection (ITS) created a narrow range of low gap light (2–22% full sun), whereas GTR created a wider range of relatively higher levels of gap light. Generally, as tree retention increased from GTR to ITS, the width of the range in gap light decreased and lay closer to the range found in USG (Fig. 2).

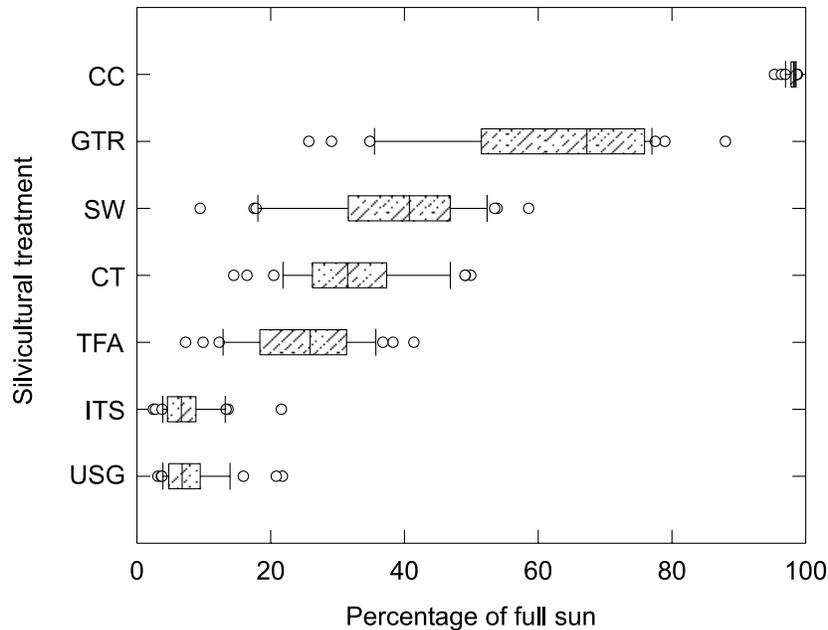
Light and structure at the microsite scale

Several attributes of forest structure proved statistically significant predictors of whole season light availability in the understory. The four structural attributes best able to predict light at the centre of the circular plots were density of stems in a plot, volume of retained stems, total DBH of all stems in the plot, and total height of all stems in the plot (i.e., the summed height of all measured stems) (Fig. 3). Summed variables, e.g., total height, provided better predictive capacity than averaged attributes, e.g., mean height.

In general, as the value of the attributes of structure increased, gap light decreased (Fig. 3). For example, plots with 200 stems/ha had a mean gap light of roughly 50% full sun, whereas plots with 1200 stems/ha had a mean gap light of less than 10% full sun (Fig. 3). The predictive capacity of these structural attributes was better for high light levels (>50% full sun) than for low light levels (<20% full sun). At light levels of less than 20% full sun, a wide range of any given structural attribute produced similar light environments, e.g., 10% full sun occurred in plots having from 380 to 1600 stems/ha (Fig. 3).

With one exception, removing dead biomass from the data had little effect on the capacity of retained structure to predict light at the microsite scale. The exception is total DBH. Using only the live biomass to assess the capacity of total DBH to predict light ($Y = 94.4 e^{-0.003X}$) increased the r_a^2 value from 0.89 to 0.94.

Fig. 2. The range of light in seven stands that varied along a gradient of retained tree structure. Treatment types are CC, clearcut; GTR, green-tree retention; SW, shelterwood; CT, commercial thinning; TFA, thinning from above; ITS, individual-tree selection; USG, uncut second growth. $n = 30$ for each treatment. The boundaries of the box plots closest to zero indicate the 25th percentile, the centre lines within the boxes indicate the median, and the boundaries of the boxes farthest from zero indicate the 75th percentile. Error bars are the 10th and 90th percentiles, and dots are data outlying the 10th and 90th percentiles.



Light and structure at stand scale

Generally, structural attributes that proved good predictors of light at the microsite scale were good predictors of light at the stand scale. As stand density, total DBH, mean height, and total height of retained trees increased, the mean value of gap light decreased (Fig. 4). The total height of retained stems proved a particularly good predictor of stand-level gap light ($r_a^2 = 0.99$) (Fig. 4).

Including dead tree biomass in the structural data improved the predictive capacity of two attributes: volume and mean height. Variation in the volume of dead plus live biomass explained slightly more of the variation in light ($r_a^2 = 0.85$; $Y = 98.3 e^{-0.004X}$), than variation in volume of only live biomass ($r_a^2 = 0.82$) (Fig. 4). The r_a^2 values for mean height were 0.72 ($Y = 98.5 e^{-0.002X}$) for dead and live biomass and 0.67 for live biomass only (Fig. 4).

The spatial distribution of stem density for retained trees directly affects the abundance and distribution of light in the understory. The Morisita index of dispersion showed significant, positive linear relationships with both the mean and variance of gap light in a stand. As clumping of stems increased, the mean of gap light increased ($r_a^2 = 0.64$, $P = 0.03$, intercept = -54.0 , slope = 69.5), as did the variance in gap light ($r_a^2 = 0.86$, $P = 0.01$, intercept = -534.0 , slope = 557.3). A caveat is necessary here about our use of the Morisita index. Little variation exists in the degree of clumping among the treatments we examined: the Morisita index varies only about 0.5 units over all treatments on the theoretical 10-point scale. It would be instructive to reexamine this relationship more thoroughly using a range of partial cutting treatments that retain structure which varies more widely along a clumping gradient.

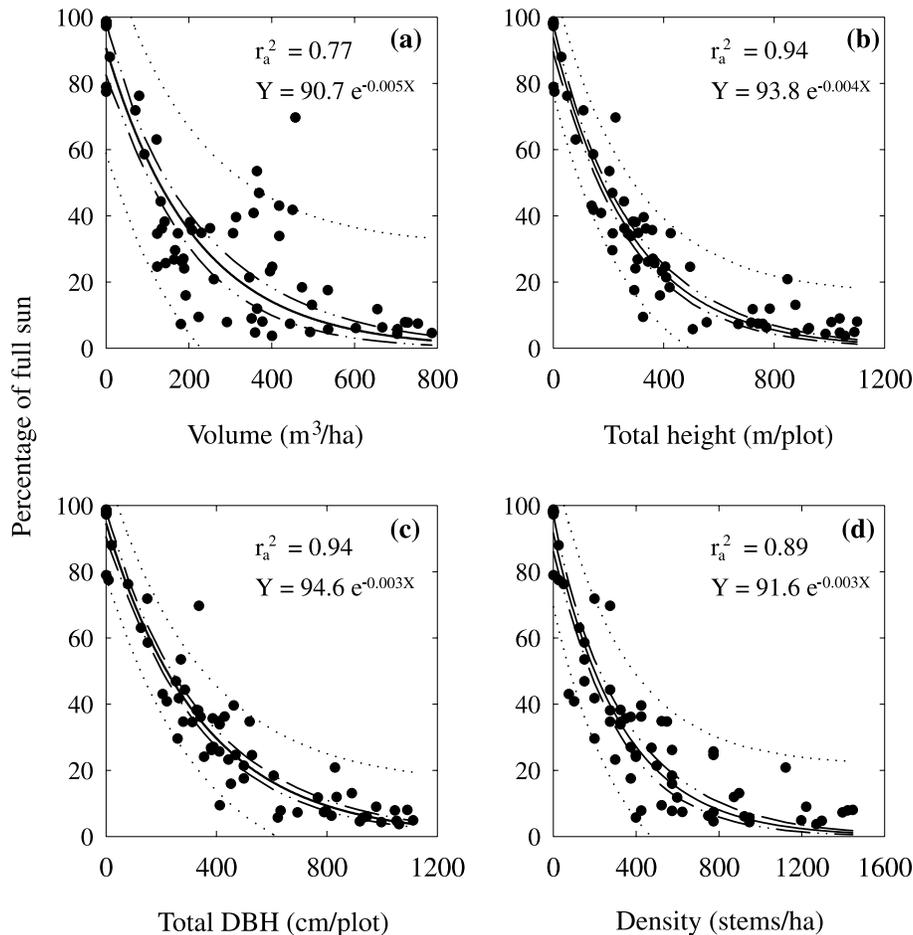
Discussion

Light under partial cutting treatments

As retention of forest structure increased, gap light in sampled stands more closely resembled that of uncut forest (Fig. 2). Light intensity in the uncut forest we examined is similar to that reported for understories beneath other conifer-dominated canopies at northern latitudes (e.g., Vales and Bunnell 1988; Canham et al. 1999). In the understory of closed coniferous canopies, sunflecks contribute about half of the total growing season photosynthetically active radiation (Canham et al. 1990; Easter and Spies 1994), light is predominantly diffuse (Parker 1997), and most of the light that penetrates to the forest floor comes from regions of the sky near the zenith (Canham et al. 1990, 1994). Generally, as the amount of retention decreased from uncut second growth (USG) to green-tree retention (GTR), the size of openings and the clumping of retained trees increased while density decreased. This changes the quantity and quality of light, as well as its directionality and variability, so that more of the forest floor receives direct solar radiation and sunflecks become longer and more intense (Liefers et al. 1999; Gendron et al. 2001). Overall, this trend is reflected in an increasing median and range in understory light as retention decreased (Fig. 2). Removing all standing trees eliminated this variation.

At high levels of retention, the structural attributes and the spatial arrangement of retained trees proved especially important in shaping understory light. For example, the commercial thinning (CT) treatment had the most homogeneously distributed retained trees of all the treatments we examined and had a high enough stand volume and density to create a

Fig. 3. Regressions of structural attributes of live trees and light at microsite scale (i.e., 0.04-ha plots). Dotted lines are the 95% CI for the predicted values and dotted-dashed lines are 95% CI for the population means. $n = 70$.



small range of gap light with a median of roughly 33% full sun (Fig. 2). The CT treatment created a range of gap light similar to that of the shelterwood (SW) treatment. However, the light environment of the SW treatment resulted from retained trees that were more clumped, but had a higher volume and mean height and a lower density than those in the CT treatment. The thinning from above (TFA) treatment had the lowest retained tree volume of these three treatments but the highest density and total height, resulting in a lower median value of gap light. The high gap light of the GTR treatment resulted from its relatively clumped distribution, as well as the low density, volume, and total height of the retained trees.

The above examples illustrate that very different stand structural conditions can result in similar light conditions. Moreover, they illustrate the flexibility available to forest managers seeking to manipulate stand structure to create a given light environment as well as illuminate the need to pay heed to several different structural attributes in doing so. It is possible to use simulation models, such as SORTIE (Canham et al. 1994), MIXLIGHT (Stadt and Loeffers 2000), and others (e.g., Cescatti 1997a, 1997b) to evaluate the effects of various gradients of retention on understory light. Such models could be particularly useful for understanding under what precise amounts, types, and distributions of for-

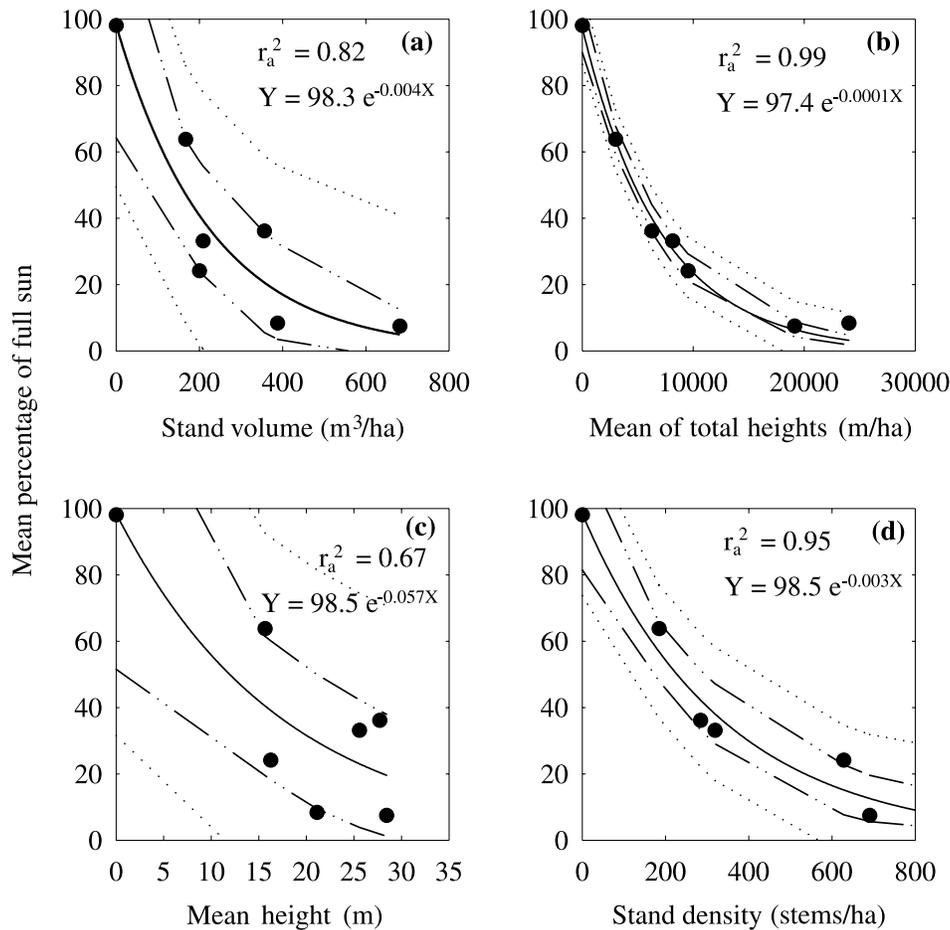
est structure understory light will begin to significantly differ relative to other structural conditions.

Stand structure and light

Stand structural attributes determined from readily available field data are strong predictors of understory light. We found statistically significant relationships between gap light and the density, total height, total DBH, volume, and spatial arrangement of retained trees. Interestingly, these structural attributes describe properties of the woody biomass of trees, rather than the biomass principally responsible for intercepting light as it travels to the understory, namely tree foliage. Measures associated with woody biomass of trees are thus a good proxy measure of crown structure and size in these stands, as has been observed elsewhere (Canham et al. 1999).

The negative nonlinear relationship of structural attributes with understory light has been previously documented in other forests. Other studies reported nonlinear decreases in light with increasing stem density (Brown and Parker 1994), canopy height (Clark et al. 1996; Martens et al. 2000), basal area (Palik et al. 1997), and stem volume (Sequeira and Gholz 1991). Furthermore, a number of studies noted the importance of spatial heterogeneity of canopy structure in shaping the range and distribution of light environment

Fig. 4. Regressions of structural attributes of live trees and light at the stand scale (9–35 ha). Dotted lines are the 95% CI for the predicted values and dotted–dashed lines are 95% CI for the population means. $n = 7$.



within a stand (e.g., Gholz et al. 1997; Van Pelt and Franklin 2000).

The total or summed height of retained trees proved an especially good predictor of gap light ($r_a^2 = 0.99$). The reasons for this are both structural and mathematical. The structural reason is that a direct relationship exists between canopy height and the angle of incidence of solar radiation to the forest floor. As the height of the trees surrounding a particular spot in the understory increases, the range of solar angles providing direct sunlight decreases (Canham 1988). The mathematical reason is that calculating total height involves two variables, height and density (i.e., the total number of trees whose height was summed). A regression of total height with light therefore combines the predictive capacity of both these variables.

Averaged variables for structural attributes, such as the mean volume per tree, mean tree height, or mean basal area, explain less of the variation in gap light than the summed values of the structural attributes in a plot, such as total height in a plot. As alluded to above, this presumably occurs because the averaged variables do not reflect the total amount of structure actually present to intercept light traveling through the canopy.

Species composition was only weakly related to the amount of light in the understory of the partial cutting treatments. Of the species we examined, only variation in the

percentage of Douglas-fir in the species mix of the retained canopy explained some of the variation in understory light (data not shown). This differs from other studies of intact forests where significant differences were evident in understory light of stands with canopies dominated by different species (e.g., Canham et al. 1994; Hunter et al. 1999). Therefore, our result is likely a consequence of the relatively low number of different species in the retained canopies we examined (i.e., typically, only three conifer species), as well as the much higher canopy openness in the partial cutting treatments relative to intact forests.

A wide range of values for various structural attributes creates similar low light environments (Figs. 3 and 4). If the retained structure has a high density, total height, or volume, the amount of light in the understory is greatly influenced by the spatial distribution and orientation of trees relative to the path of the sun (Canham et al. 1990; Clark et al. 1996). This is likely a consequence of the spatial distribution and orientation of the trees affecting the temporal and spatial distribution of sunflecks. The contribution of diffuse light to the overall light environment is greater at high levels of retained structure than at low levels of retained structure. At high levels of retention, the penetration of low angle light and the contribution of sunflecks also become important in determining the overall light environment (Canham et al. 1990; Clark et al. 1996). This effect is not as important at low

levels of retention because the canopy blocks a smaller proportion of the path of the sun and light is primarily direct (Canham et al. 1990).

There are two important caveats about the light–structure relationships described above. First, since no replication was possible for all the different treatments we examined, the relationships between structure and light at the stand scale are meant to illustrate the type of light environments that can possibly be created by these treatments. They are not meant to be representative of all the variation in light possible under these treatments types as carried out elsewhere. For example, although the ITS treatment appears to have produced only a small effect on gap light relative to the USG, this is a consequence of different pre-harvest conditions between the stands. Even after the selection harvesting, basal area remained higher in the ITS than in the USG (Table 1). Second, the sites we examined were fairly homogeneous Douglas-fir leading stands. The relationships above may not be as strong in more mixed or complex stands, particularly those with a much larger deciduous component.

Management implications

Retaining structure at the levels found in the green-tree retention treatment creates opportunities for efficiently regenerating shade-intolerant species while meeting multiple management objectives. The GTR treatment created a wide range of light environments, including up to about 90% full sun (Fig. 2). Such bright environments are especially possible if retained trees are clumped rather than dispersed uniformly and gaps between clumps are relatively large (i.e., greater than 1400 m²) (Palik et al. 1997; Coates 1998). Aggregated arrangements of retained trees create light environments that allow growth rates of shade intolerant species, such as Douglas-fir, that can approximate those expected in clearcuts (Wright et al. 1998; Drever and Lertzman 2001). For example, Douglas-fir saplings have mean leader increments of 45 cm/year under 60% full sun on mesic and rich sites, roughly 60% of the growth that can be expected at full sun in similar sites (Drever and Lertzman 2001). Such growth rates should be encouraging to forest managers seeking to efficiently regenerate an area following timber harvesting without compromising other ecological objectives provided by retained structure. Aggregated retention allows the maintenance of a broad variety of stand structural elements such as snags, downed wood, large live trees, and understory and midstory deciduous trees (Franklin et al. 1997). Retained trees, either singly or in patches, provide a number of important ecological functions, from wildlife habitat to sources of inocula for ectomycorrhizal fungi (e.g., Coates and Steventon 1994; Simard et al. 1997). Because retaining trees in clumps allows the retention of intact patches of understory plant communities and undisturbed forest floor, there is increasing emphasis on group retention in variable-retention blocks (Weyerhaeuser Co. 2000). Our results corroborate these findings and suggest that a strategy of aggregated retention, or aggregates mixed with a low density of individual trees, can provide both good silvicultural and conservation opportunities in partially cut stands.

The light levels under heavy retention treatments are likely insufficient to ensure survival and growth of regener-

ating shade-intolerant species in the study area (Carter and Klinka 1992; Drever and Lertzman 2001). Coastal Douglas-fir, for example, needs at least 20% full sun to ensure survival and 40% full sun to develop crown conditions that allow efficient capture of solar radiation (Mailly and Kimmins 1997). ITS and TFA, as carried out in the stands we studied, are not suitable options for regenerating shade-intolerant species in this area. The single- and multiple-tree gaps (about 300–500 m² as estimated in the field) created in the ITS and TFA treatments did not strongly alter understory light intensity, as compared with other examined treatments. These treatment types are suitable for regenerating shade-tolerant species, like western hemlock and western redcedar, which have low light requirements for survival and maximum height and diameter growth (Wang et al. 1994; Coates 2000).

The selection of a silvicultural treatment increasingly requires consideration of multiple and diverse management objectives (Franklin et al. 1997). In this study we assessed silvicultural treatments only by their impact on light, while ignoring the uncertainty regarding other important considerations such as harvesting logistics and costs, changes in retained canopy structure over time, and dynamics of understory plant communities. Fortunately, partial cutting treatments are the focus of many recent research efforts (e.g., McComb et al. 1993; Coates et al. 1997), some of which conclude that partial cuttings are less costly and less logistically difficult than previously believed (e.g., Coates 1997; Howard and Temesgen 1997). The relationships elucidated in this study can contribute to the further development of partial cutting systems by aiding in the design of understory light regimes that can provide competitive growth rates for a wide range of tree species while retaining ecologically significant elements of stand structure. These relationships can also aid planning for other phenomena associated with understory light, such as microclimatic conditions and shrub growth. Applications of hemispherical photography such as ours may also provide measures of subtle changes in the openness that can be important to various other organisms (e.g., Endler 1993) and thus aid managers in planning the post-harvest environment for a wide range of resources.

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