MADE IN THE SHADE: REGENERATING COASTAL DOUGLAS-FIR AND WESTERN REDCEDAR UNDER PARTIAL CUTTING TREATMENTS

by

Charles Ronald Drever

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Abstract

Partial cutting treatments that retain forest structure in harvested areas are increasingly being used to address ecological management objectives during timber extraction. However, the shading effects of retained forest on the growth rates of regenerating trees remain unclear. I examined relationships between light and sapling growth in partial cutting treatments on Vancouver Island, British Columbia. I described the growth response to light for Douglas-fir and western redcedar regenerating on sites of different soil moisture and nutrient regimes, and characterized the light environment of 7 stands that varied along a gradient of tree retention. I used hemispherical canopy photographs and digital image analysis to quantify the light environments in the neighbourhood of saplings of each species and in partial cutting treatments. Using nonlinear regressions, I related the light environment to both the growth characteristics of the saplings and to the structural attributes of the examined silvicultural treatments.

Light is a good predictor of both height and radial growth rates for Douglas-fir and western redcedar (r_a^2 = 0.52 to 0.85). For Douglas-fir saplings, differences in the response of height growth to light among sites of various soil moisture and nutrient regimes become apparent in light environments of about 43 % full sun or greater. For radial growth, such a divergence in the growth response among sites varying in site quality is

apparent only at light environments higher than about 60 % full sun. Western redcedar approaches its maximum radial and height growth rates at about 30 % full sun.

Partial harvesting affects both the median value and the range of light environments in forest stands. As overstory removal increases from uncut second growth to green tree retention, the median value of light increases from 8 % full sun to 68 % full sun, while the range of light environments increases from between 5 – 10 % full sun to between 35 – 77 % full sun. I found strong, significant, and negative non-linear relationships between light environment at a particular site in the understory and the summed height, summed diameter at breast height, density, and volume of surrounding residual trees (r_a^2 = 0.77 to 0.94).

The management implications of these relationships include the ability to predict the growth of Douglas-fir and western redcedar under partial canopies by characterizing retained forest structure. Green tree retention is a silvicultural alternative that can meet ecological management objectives while allowing height growth for regenerating Douglas-fir that exceeds 50 cm / yr. The shade tolerance of western redcedar permits implementing many partial cutting treatments that do not compromise growth rates.

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Introduction

Silvicultural treatments that retain live trees and add structural diversity to a harvested area are increasingly being used as alternatives to clearcutting (Franklin et al. 1997). These partial cutting treatments retain trees in different densities, spatial arrangements, and age and size classes (Hansen et al. 1995a; Acker et al. 1998). Retaining forest structure has important ecological consequences; maintaining a diversity of forest structure preserves biological diversity and ecosystem function in harvested areas (Harmon et al. 1986; McComb et al. 1993; Hansen et al. 1995b; Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995; Franklin et al. 1997). Partial cutting treatments can allow forest managers to address multiple, and sometimes conflicting, management objectives within a given treatment unit. For example, forest managers can implement harvesting treatments that meet objectives of timber production while maintaining mature-forest characteristics (McComb et al. 1993; Rose and Muir 1997), preserving wildlife habitat (Coates and Steventon 1994; Hansen et al. 1995b), conserving functional communities of soil organisms (Perry 1994), or mitigating microclimatic effects of forest removal (Franklin et al. 1997). However, the tradeoffs between these disparate management objectives are often uncertain, especially about how retaining mature green trees after harvesting affects the growth rates of regenerating trees, either already present in the stand as advance regeneration or as outplanted trees (Birch and Johnson 1992; Franklin et al. 1997).

Partial cutting treatments span a wide range of degrees of overstory removal and can incorporate more traditional silvicultural approaches, such as seed tree and single tree selection (Coates and Burton 1997). 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 using attributes of stand structure. Typically, stand structure is quantified using stand structural attributes such as the density, basal area, volume, mean height of standing trees, and other descriptors of the amount of structure in the forest (Smith 1986).

The extent of partial overstory removal affects the light environment of the understory (Coates 1997; 1998). 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; Canham et al. 1994; Sequeira and Gholz 1997). In this study, I sought to quantify the relationships between the light environments in partial cutting treatments and the amount and type of retained structure. Understanding these relationships is key for designing and planning partial cutting treatments and for predicting the impacts of retained structure on the growth rates of regeneration (Franklin et al. 1997).

The effect of partial overstory removal on the growth rates of regeneration is species-specific (Carter and Klinka 1992). Each tree species reacts differently to various light levels, according to its shade tolerance and other autoecological constraints. I chose two species common in the study area and of silvicultural significance: coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and western redcedar (*Thuja plicata* Donn ex D. Don). These species are typically described as shade intolerant and shade tolerant, respectively (Carter and Klinka 1992). I sought to characterize the growth response of these two species across the range of light environments created by partial cuttings.

In addition to light, site quality is an important factor influencing the growth of regenerating trees. Saplings respond differently to varying light levels in sites with different regimes of soil moisture and soil nutrients (Carter and Klinka 1992). For example, some evidence suggests that Douglas-fir may be more shade tolerant when growing in dry sites than in wet sites (Carter and Klinka 1992). I sought to quantify the growth response to light for Douglas-fir saplings growing in sites of different regimes of soil moisture and nutrients. This allowed me to make conclusions about how the choice of partial cutting treatment affects the growth rates of regenerating Douglas-fir in sites of various soil nutrients and moisture.

Therefore, in order to address some of the uncertainty regarding the successful implementation of partial cutting treatments, the objectives of this study were:

a) to characterize the growth response to light for:
    i) Douglas-fir saplings in four different regimes of soil moisture and nutrients in which they commonly naturally regenerate, and,
    ii) western redcedar saplings in sites of a common regime of soil moisture and nutrients.
b) to characterize the light environment of partial cutting treatments.
c) to quantify relationships between attributes of stand structure and the light environment in partial cutting treatments.

Methods

Study area

The study area is on the east coast of Vancouver Island, near Campbell River, British Columbia (Figure 1). The sampled areas are almost exclusively second growth coastal Douglas-fir forests that regenerated naturally after large forest fires in the 1930s (Lackey, S., pers. comm.). Smaller amounts of western hemlock (*Tsuga heterophylla* (Raf) Sarg.), western redcedar, lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and western white pine (*Pinus monticola* Dougl. ex D. Don) are also present. Common understory shrubs include salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*), and dull Oregon-grape (*Mahonia nervosa*). Vanilla leaf (*Achlys triphylla*) and sword fern (*Polystichum munitum*) typically dominate the herb layer.

All the stands and saplings I sampled are in the Very Dry Maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHxm) (Pojar et al. 1987; Meidinger et al. 1991; Green and Klinka 1994). This low elevation (0-150 m) subzone receives 1100-2721 mm of precipitation annually and has warm, dry summers (160-565 mm precipitation between May and September) and moist, wet winters with little snow (26-234 mm mean annual snowfall) (Green and Klinka 1994). The growing season begins in mid-April and ends in late August (Brix 1993). Water deficits occur during the summer on sites of average soil moisture and nutrients for the region (Green and Klinka 1994). The study area is generally flat; all the sampled stands have slopes 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 (McCammon 1977).

Quantifying the light environment

Hemispherical photographs of the canopy allow characterization of the amount of photosythetically active radiation at a given spot in the forest (Canham 1988; Canham 1995; Frazer et al. 1997; Frazer et al. *in press*). These photographs capture the geometry and orientation of canopy trees and, combined with digital image analysis, can be used to estimate the light environment at a particular spot. More specifically, I used hemispherical canopy photographs to determine an index of whole growing season light availability. This index, measured in units of percent of full sun, was determined using GLI/C 2.0 light modelling software (Frazer et al. 1997; Canham 1988). GLI/C 2.0 calculates the amount of light available for photosynthesis for the whole growing season by 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 (Canham 1988; Canham 1995; Pacala et al. 1994). I used a Minolta X700 camera mounted with a Minolta fish-eye lens (f = 7.5 mm).

Light and growth of saplings

During the 1997 growing season, I destructively sampled 294 Douglas-fir and 43 western redcedar saplings (4-45 years old). These saplings were growing across gradients of light environments, soil moisture regime, and soil nutrient regime (Table 1). I searched for saplings growing in mature second growth stands (80-100 years old), under canopy openings, along road edges, and in clearcut and partially cut stands. I did not sample in recently disturbed areas (i. e., < 5 years ago) to avoid sampling trees growing in a recently modified light environment. I selected sample trees that reflected the optimum growth at a given light environment, i. e., trees with the most consistent and largest leader increments, free of kinks, scars, and bent stems. Furthermore, I sampled trees under primarily coniferous overstories to avoid variation in light environment resulting from seasonal changes of deciduous canopies.

For each sapling, I recorded species, height, diameter at breast height (1.3 m, dbh), and length of leader increment for the last three to five growing seasons. I also cut a stem disk 10 cm above the ground for estimating radial growth. After cutting the stem, I took a hemispherical canopy photograph 1 - 1.5 m above the stump.

In the laboratory, I determined radial growth increments for the last three to five growing seasons (1992-1996) with a Velmex – Accurite sliding stage system, a high-resolution video camera connected to a microscope (7x - 45x magnification), and the MEDIR measuring program (Grissino-Mayer 1996). I measured the width of each year's growth along 2 radii of a randomly drawn diameter line through the pith. Care was taken to avoid areas of reaction wood. I then averaged the two estimates of each year and calculated an average growth rate for the last three to five years. Using more than three to five years increases the probability that the canopy photograph does not accurately reflect the light environment in which the sapling grew.

For the first 50 saplings measured, I calculated the radial growth rate using 4 radii of 2 perpendicular diameter lines. I then randomly picked 2 of the 4 radii and compared the estimates of radial growth derived from 2 and 4 radii. I found no statistical difference between the average growth rate determined using 2 or 4 radii (ANOVA, F-stat.= 0.02; P = 0.99; df = 9). Two radii were used to calculate radial growth for the remaining sampled trees.

Determining site series

Site series is an index of the soil moisture and nutrient regime at given site (Meidinger and Pojar 1991). I estimated site series for the site where each of the sampled saplings grew using the Biogeoclimatic System of Ecosystem Classification developed for the Vancouver Forest Region in British Columbia (Green and Klinka 1994). This procedure combines an assessment of the relative abundance of indicator plants with a characterization of the topographical and soil morphological properties for each site. Soil moisture regime is based on the annual water balance and the depth of water table. Soil nutrient regime refers to the amount of available essential soil nutrients, particularly nitrogen, and the turnover of organic matter.

I sampled Douglas-fir and western redcedar saplings in the four site series where Douglas-fir regenerates naturally in the shrub layer (Green and Klinka 1994). These site series encompass three soil moisture regimes lumped into two classes (Moderately Dry, and Slightly Dry to Fresh) and five soil nutrient regimes again lumped into two classes (Very Poor to Medium, and Rich to Very Rich). For simplicity, I labeled the site series as: Dry, Poor (03); Dry, Rich (04); Fresh, Poor (01); and Fresh, Rich (05).

Light environment and stand structure in partial cuts

I sampled the light environment and stand structure of 7 stands representing a gradient of tree retention: clearcut (CC); green tree retention (GTR); shelterwood (SW); commercial thinning (CT); thinning from above (TFA); individual tree selection (ITS); and uncut second growth (USG) (Table 2). The lack of availability of replicates for three of the treatment types required adopting the regression framework used in this study. The stands were chosen from forest cover maps provided by TimberWest Forest Products Inc. I ensured the stands had a similar pre-harvest date of establishment (1920-1935), stand composition, and productivity class (High, Medium, Low).

The silvicultural treatments I examined varied in the amount and distribution of retained structure following harvest (Table 2). The treatments are characterized as follows:

Clearcut (CC) - One pass removal of all standing stems.

Green Tree Retention (GTR) - A one pass modified clearcut. This cut removed 95% of merchantable timber, retaining structurally sound snags and 5-15 large dominant Douglas-fir per hectare as well as any immature western hemlock, lodgepole pine, and western redcedar.

Shelterwood (SW) - First cut of a planned two pass shelterwood harvest. This cut removed 75% of stand volume and retained 80-100 large dominant Douglas-fir and 10-25 suppressed / codominant western redcedar per hectare.

Commercial Thinning (CT) – First commercial cut of a planned two pass harvest of Douglas-fir. This cut removed about 75% of the trees and retained 400-450 Douglas-fir trees / ha homogeneously distributed for subsequent harvest.

Thinning From Above (TFA) - A one pass harvest of dominant Douglas-fir that retained a multi-story canopy of subdominant and understory Douglas-fir, western hemlock, lodgepole pine, and western redcedar.

Individual Tree Selection (ITS) - First cut of a planned multiple entry harvest of dominant trees in a series of light thinnings at intervals of 4 to 10 years.

Uncut Second Growth (USG) - No silvicultural treatment.

The clearcut and uncut second growth treatments represent the extremes of a gradient of tree retention.

To characterize the light environment in these 7 stands, I took a hemispherical canopy photograph every 30 m along a 900-m transect (n = 30) in each stand. Photographs were taken at least 30 m from the stand edge. At the location of every third photograph, I measured the dbh, species, and height of all trees > 2 m, including stumps and snags, in a 11.3-m radius circular plot for which the photograph location was the plot centre. I 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. From these data, I computed volume, basal area, mean height, mean dbh, percent composition of component species, and other structural attributes for each sampled plot and for each of the seven stands. It is worth noting that these attributes of stand structure include both live and dead biomass. Typically, estimates of basal area and volume include only live material above a certain threshold in tree size, e.g., the minimum dbh considered merchantable.

To assess the effect of the spatial distribution of retained trees on light environment, I calculated the Morisita index of dispersion for each treatment type. This density-based index is a measure of the spatial aggregation of stems that incorporates 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.

Data analysis

Response of sapling growth to light

I tested three nonlinear models to characterize the growth response of Douglas-fir and western redcedar to a range of light environments: the Michaelis-Menton equation, the Michaelis-Menton equation with a non-zero X intercept, and a sigmoidal growth equation. These equations, obtained from previous studies of light-dependent growth response (e. g., Wright et al. 1998; Wright et al. 1999), have parameters that are interpretable biologically. For example, the Michaelis-Menton equation with a non-zero X intercept was used to test for a whole-plant compensation point, with the non-zero intercept being the minimum light level required for positive net carbon balance. I estimated the best-fit estimates of the model parameters using the nonlinear regression procedure in SPSS 8.0 with the sequential quadratic programming method to minimize the sum of squared residuals (SPSS 1996).

I chose the Michaelis-Menton equation [1] to characterize the growth response to light of Douglas-fir and western redcedar across different site series. This equation has the following form:

[1] $Y = ((a \times X) / ((a / s) + X) + \varepsilon$

where Y represents the mean rate of height growth (cm / yr) or $\log_{10}$(mean rate of radial growth (mm) + 1) and X is the index of light over the growing season (in units of percent full sun). Parameters *a* and *s* represent the asymptote of growth rate at high light and the slope of the curve at zero light, respectively, and ε represents the error term. A $\log_{10}$ transformation of the radial data was necessary to stabilize variance and normalize the residuals.

The Michealis-Menton equation consistently provided a better model fit to data, i. e., had the lowest mean square error (MSE) of the residuals, than both the Michealis-Menton equation with a non-zero X intercept and the sigmoidal growth equation. Although the sigmoidal growth equation fit the data better than the Michaelis-Menton equation for Douglas-fir in one of the site series, residuals plots for other site series were generally heteroscedastic and not normally distributed. The Michaelis-Menton equation with a non-zero X intercept was not very informative; most of the non-zero intercepts were not significantly different from zero and model fits were not as good as those for the Michaelis-Menton equation.

The means of radial and height growth over 3 to 5 years consistently provided better model fits than estimates of growth based on a single year. Hence, these were selected for intra- and inter-specific comparisons of growth responses. I used the 95% confidence intervals of the parameters, of the predicted values of the regression, and of the population means of the regression for comparing between and within species, and among different site series. I deemed regions where the 95% CI did not overlap as statistically significantly different ($P \leq 0.05$).

The light environment of partial cuts

I assessed different stand structural attributes as predictors of the light environment at two different spatial scales - the site and the stand. At the site scale (i. e., 400 m^2), I was able to easily measure attributes of stand structure and estimate light environment. At the stand scale (i. e., 9 - 35 ha), having 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 residual trees . As mentioned previously, I used the Morisita index of dispersion (Krebs 1989) to describe the degree of clumping or uniformity across the stand.

Linear regression analyses allowed determining which structural attributes had potential for significantly explaining the most variation in light, i. e., high adjusted-r^2 (r_a^2) values. For the structural attributes with high potential for explaining variation in light, I fit the following nonlinear model to improve the model fit to data (i. e., lower MSE of residuals) and the predictive capacity (i. e., increase r_a^2) for the most predictive structural attributes:

[2] $Y = ae^{bX} + \varepsilon$

In this model, Y represents the measure of light environment, X is the stand structural attribute, ε represents the error term, and *a* and *s* are model parameters.

Nonlinear regressions provided better model fits to data and better satisfied the normality and homoscedasticity assumptions than linear regression. Although many of the linear regressions of stand structural attributes and light environment were statistically significant, the residuals of these linear regressions were neither homoscedastic nor distributed normally. Rather, plots of the residuals against predicted values strongly suggested a curvilinear relationship between light environment and these stand structural attributes.

I used the stepwise multiple regression procedure of SPSS 8.0 to ascertain the most parsimonious combination of stand structural attributes that explained the highest proportion of the variation in light environment. To ensure the assumptions of nonlinear least squares regressions were met, I examined plots of the residuals for normality and homoscedasticity.

Results

Growth responses of saplings to light

The index of light availability is an excellent predictor of the growth rates of saplings. As mentioned above, this index estimates the percent of full open photosynthetic active radiation received between April 15 and August 15, the length of the typical growing season on the east coast of Vancouver Island (Canham 1988; Brix 1993). For western redcedar in Dry, Poor sites and for Douglas-fir in all site series, the variation in light explains over half the variation in both height and radial growth rates ($r_a^2 = 0.52$ to 0.85; Table 3 and 4). Generally, as whole season light availability increases, the rates of radial and height growth increase.

Height growth

Variation in light explains 62 % to 81 % of the variation in height growth for Douglas-fir saplings in the four site series examined

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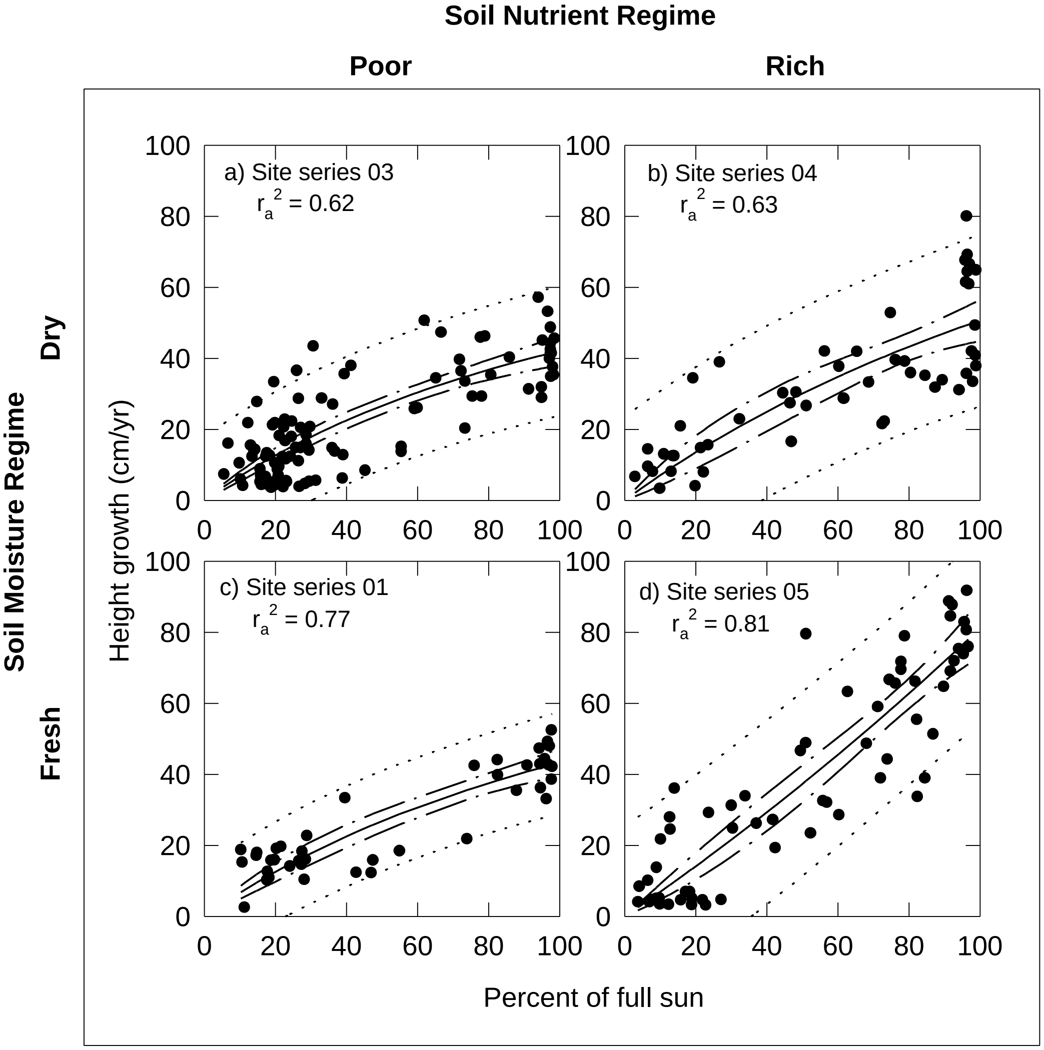

Figure 3; Table 3). The percentage in variation of growth explained by the variation in light increases as sites improve in their soil nutrient and moisture regime, i. e., from 03 to 05 sites

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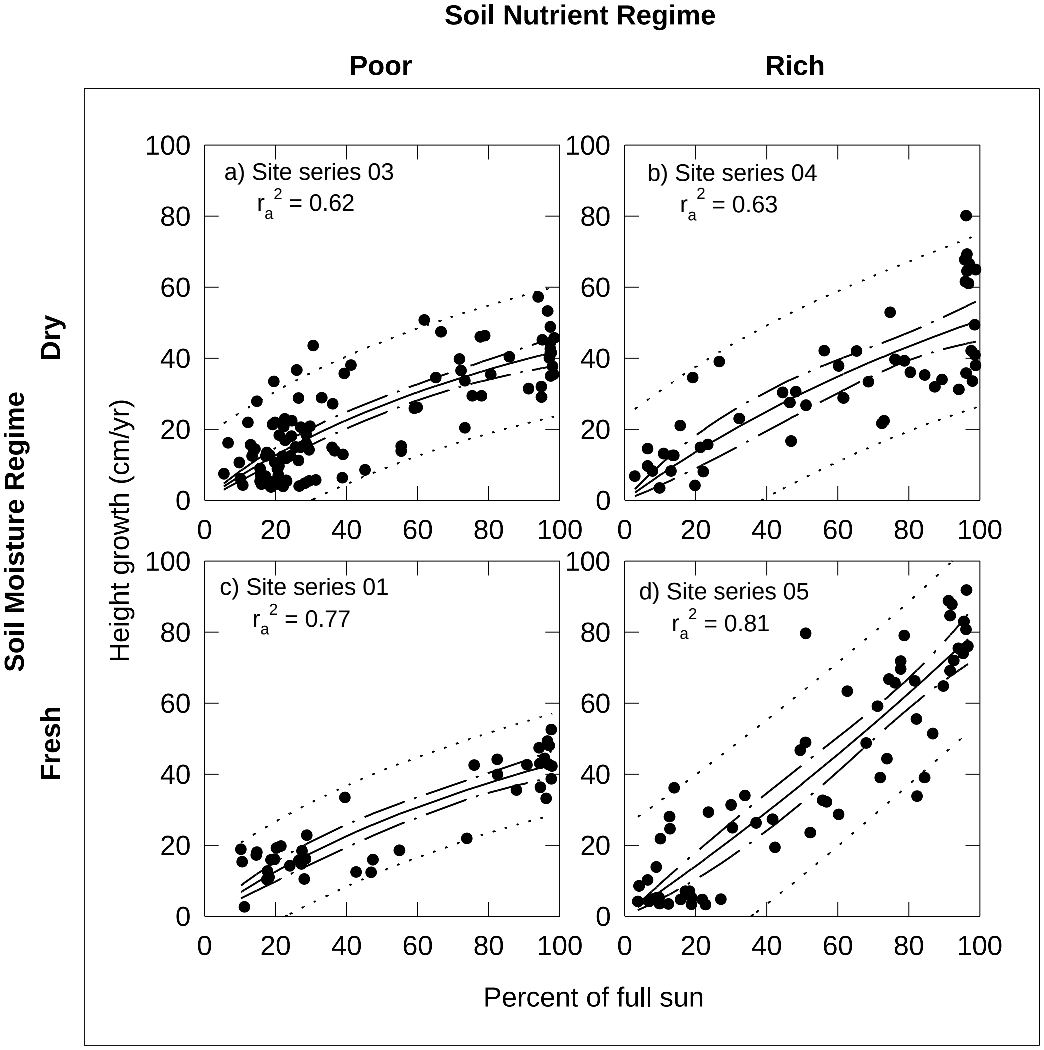

Figure 3). Variation in light can explain 62 % of the variation in height growth for Douglas-fir saplings growing on Dry, Poor sites, whereas variation in light explains 81 % of the variation in height growth for Douglas-fir saplings growing on Fresh, Rich sites.

This trend of light accounting for higher percentages of the variation in growth for Douglas-fir saplings in sites of higher quality is also reflected in the asymptote of growth at high light (the *a* parameter). This parameter is a theoretical maximum for growth rate at 100 % full sun (Table 3). The *a* parameter is higher for Fresh, Rich sites than for Dry, Poor sites. For Douglas-fir saplings in Fresh, Rich sites, the *a* parameter is so large that the growth response is nearly linear (Table 3).

The responses of height growth to light for Douglas-fir saplings differ among sites of different soil moisture and nutrient regimes. This is illustrated by the lack of overlap between the 95% confidence intervals (CI) of the population means for the different site series over parts of the range of light (

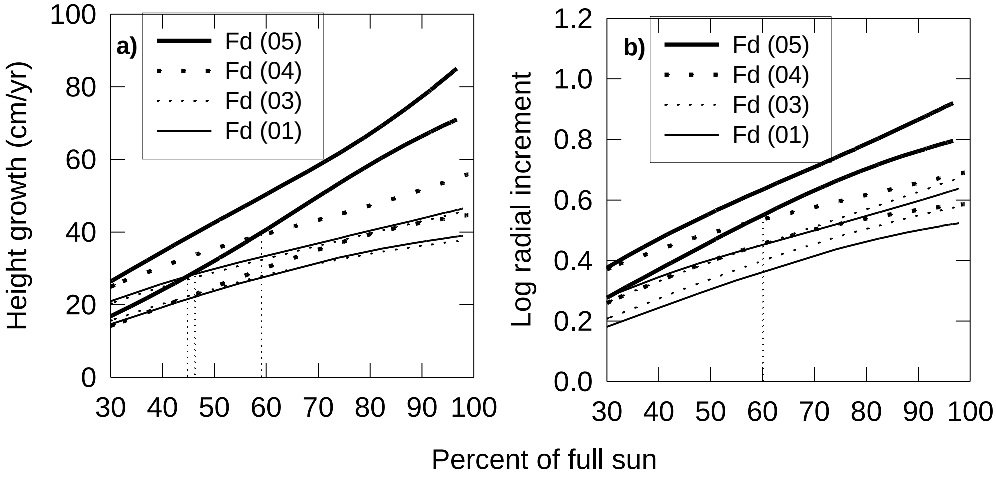

Figure **4**). For Fresh, Rich sites (05), the rates of height growth diverge from those of Dry, Poor sites (03) and Fresh, Poor sites (01) at about 43 % and 46 % full sun, respectively. The point of divergence for the growth responses between Dry, Rich (04) sites and Fresh, Rich (05) sites is about 58% full sun. Values of divergence reflect the thresholds of light environment above which differences in the population means of the light-growth response are statistically significant. Interestingly, although the growth response of height for Douglas-fir saplings growing on 05 sites showed a statistically significant difference from the responses in 03, 04, and 01 sites, I found no statistically significant difference among these latter three site series.

Western redcedar saplings show a response of height growth to light that is more consistent with shade tolerant species. Between 0 to 20 % full sun, height growth increases rapidly with light (Figure 5). However, height growth increases to a low asymptote near 30% full sun (Figure 5). Variation in light accounts for 52 % of the variation in height growth for redcedar saplings growing on Dry, Poor sites.

Large variation exists in the rate of height growth among saplings of both species at a given light level (Figures 3 and 5). Such variation in height growth at a given light level is reflected in the parameter estimates of the nonlinear regressions and in the 95% CI for the predicted values of growth of individual saplings (Table 3). No statistically significant differences exist among the parameter estimates of the regression of height growth for Douglas-fir saplings among the four site series (Table 3). In addition, the 95% CI for the predicted values of individual Douglas-fir saplings overlap among all site series across the entire range of light (Figure 3). This result seems reasonable given these 95% CI incorporate uncertainty in the regression parameters. Therefore, for individual Douglas-fir saplings, the variation in growth at a given light level overshadows any site series-dependent effect on height growth.

Radial growth

With one exception, the radial growth responses to light of Douglas-fir saplings do not differ among sites of varying soil moisture regime and soil nutrient regime. The radial growth responses of Douglas-fir have overlapping 95% CI of the population mean over the entire range of light on Dry, Poor (03), Fresh, Poor (01), and Dry, Rich (04) sites (Figure 6). The radial growth response in Fresh, Rich (05) sites differs from that of other site series only at about 60 % full sun. This is indicated by a region of non-overlap of the 95% CI of the population mean with those of the other site series at this 60 % full sun threshold (Figure 6).

The radial growth response of western redcedar shows a similar plateau at low light to that observed for height growth. The radial growth rate increases rapidly as light increases from 0 % to about 30 % full sun (Figure 5). Above 30 % full sun, the radial growth rate increases slowly with increasing light (Figure 5). Variation in light explains 59 % of the variation in radial growth (Table 4).

Inter-specific comparisons of growth response to light

Douglas-fir saplings differ strikingly from western redcedar in their light-dependent growth responses. At low light levels, redcedar saplings have higher growth rates than Douglas-fir as light increases between 0 and 20 % full sun. The slope of the curve through the origin (the *s* parameter) is significantly greater, as determined by the 95 % CI, than that of Douglas-fir on Dry, Poor sites. Interestingly, the s parameter for redcedar is significantly greater than that of Douglas-fir in all the site series examined (Table 3). This means redcedar saplings growing on Dry, Poor sites have greater rates of height growth at low light than Douglas-fir growing on Fresh, Rich sites. Conversely, redcedar has a much lower rate of height growth at light levels > 30 % than Douglas-fir. The regression of height growth for western redcedar has a lower and statistically significantly different asymptote at high light (the *a* parameter) than Douglas-fir growing on 03 sites (Table 3).

Radial growth is also greater in low light for western redcedar than for Douglas-fir. The *s* parameter is statistically significantly greater for redcedar than Douglas-fir in all site series examined (Table 4). However, the rate of radial growth at high light is the similar for both species. The *a* parameter was not significantly different from that of Douglas-fir. This indicates that although redcedar grows smaller rings at high light than

Douglas-fir, these radial increments are within the range of variability of Douglas-fir.

Light environment of partial cuts

Different harvesting methods result in different light environments. Harvesting affects both the width of the range of light environments in a stand and where the range occurs in the full gradient between 0 % and 100 % full sun (Figure 7). As overstory removal increases from uncut second growth to green tree retention, the median value of light increases from 8 % full sun to 68 % full sun, while the range of light environments increases from between 5 – 10 % full sun to between 35 – 77 % full sun (Figure 7). Effectively, the treatments sampled in this study represent a broad range of light environments over most of this gradient. Individual Tree Selection, for example, creates a narrow range of low light environments, whereas Green Tree Retention creates a wide range of light environments closer to 100 % full sun. Generally, as tree retention increases from green tree retention to individual tree selection, the width of the light range decreases and lies closer to the range of light found in Uncut Second Growth (Figure 7).

Light and structure at the site scale

Forest structural attributes retained in partial cutting treatments are statistically significant predictors of whole season light availability at a given spot in the understory. The four structural attributes best able to predict light at the centre of the circular plots are the volume of retained stems, the summed height of all stems in the plot, the summed dbh of all stems in the plot, and the density of stems in a plot (Table 5 and Figure 8). Generally, as the value of these attributes of stand structure increases, the light environment decreases (Figure 8). For example, plots with 200 stems have light environments with a mean of ca. 50 % full sun, whereas plots with 1200 stems have light environments with a mean less than 10 % full sun (Figure 8). The predictive capacity of these structural attributes is better for high light levels (> 50 % full sun) than for low light levels. At light levels less than 20 % full sun, a wide range of structural attributes can produce similar light environment, e. g., 10 % full sun occurs in plots having between 380 to 1600 stems / ha (Figure 8).

It is worth noting that the structural attributes presented here incorporate total biomass (i. e., live and dead biomass). Standard usage of these attributes by forest managers typically incorporates only live biomass. Additional analyses of the data shown here could involve comparisons of the relationships between structure and light using only live biomass and the same relationships using both living and dead biomass. This would allow detecting any effect of dead biomass on light environment.

Most of the variation (89%) in light can be explained by variation in plot density and the average height of the five tallest trees in a plot. A multiple stepwise linear regression of the six variables with the highest r_a^2 values (Table 5) provided the following relationship (F-stat. = 266.811, P = 0.000, df = 2, $r_a^2 = 0.89$):

[3] Percent of full sun = 94.803 - 0.4345 x (Average height of five tallest trees) - 0.931 x (Plot density).

The residuals of this regression are homoscedastic and do not strongly violate the assumption of normality.

Light and structure at stand level

Generally, variables that proved good predictors of light at the site level proved good predictors of light at the stand level (Table 6). As stand density, summed dbh, mean height, and summed height of residual trees increases, the mean value of light environment decreases (Figure 9). The summed height of residual stems is a particularly good predictor of stand-level light environment, having an $r_a^2 = 0.99$ (Figure 9). As the variance in stand volume increases, the variance of light environments in a stand also increases (Table 5).

The spatial distribution of retained structure in a stand 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 light environments in a stand (Figure 10). As clumping of stems in a stand increases, the mean of the light environments increases ($r_a^2 = 0.64$; P = 0.03; Intercept = - 54.0; Slope = 69.5), as does the variance in light environments ($r_a^2 = 0.86$; P = 0.01; Intercept = - 534.0; Slope = 557.3).

A caveat is necessary here about the Morisita index. Little variation exists among the treatments in their degree of clumping. The Morisita index varies only about 0.5 units over all treatments on the theoretical 10 point scale. It would be instructive to re-examine this relationship more thoroughly using a range of partial cutting treatments that vary more widely along a clumping gradient.

Discussion

Light-growth responses of Douglas-fir and western redcedar

For Douglas-fir saplings growing below about 43 % full sun, light is the primary factor affecting height growth. I detected no significant differences in the response of height growth among the different site series below 43 % full sun. This suggests that at lower than this threshold, light is the primary determinant of growth, irrespective of the soil moisture and nutrient regime. Above 43 % full sun, variation in height growth across sites with similar light regimes increases, leading to statistically significant differences in height growth for Douglas-fir saplings among sites of different regimes of soil moisture and nutrients (Figure 6). These results corroborate other findings that light has the greatest effect on growth at low light levels (e. g., Chazdon 1988; Wang et al. 1994) and that a threshold level of light exists above which juvenile trees show an increase in variation of growth (e. g., Carter and Klinka 1992; Wang et al. 1994). Furthermore, the detection of a threshold of light is consistent with findings that leaf-level photosynthesis of Douglas-fir and other conifers reaches a light saturation point between 20-40 % full sun (Horn 1971; Leverenz 1981; Perry 1994; Lavender 1990).

The role of soil moisture and nutrient regime

The soil nutrient regime appears a more important factor affecting the response of height growth of Douglas-fir saplings than soil moisture regime. The divergence between the growth response on Fresh, Rich sites (05) and that of Fresh, Poor (01) sites occurs at ca. 46 % full sun, whereas the divergence between the growth response on 05 sites and that of Dry, Rich (04) sites occurs at ca. 60 % full sun (Figure 6). Douglas-fir saplings respond to changes in soil nutrient regime more than to changes in soil moisture regime. This suggests that Douglas-fir saplings are better adapted to dealing with moisture stress than with nutrient stress.

I found no evidence of a soil moisture-dependent effect on shade tolerance for Douglas-fir in the study area. The slope of the growth rate at low light (the *s* parameter) was not significantly different for sites with different soil moisture regimes (Table 3). Furthermore, the radial and height response to light of Douglas-fir does not change with increasing soil moisture, i. e., between site series 03 and 01 and between 04 and 05 at low light levels

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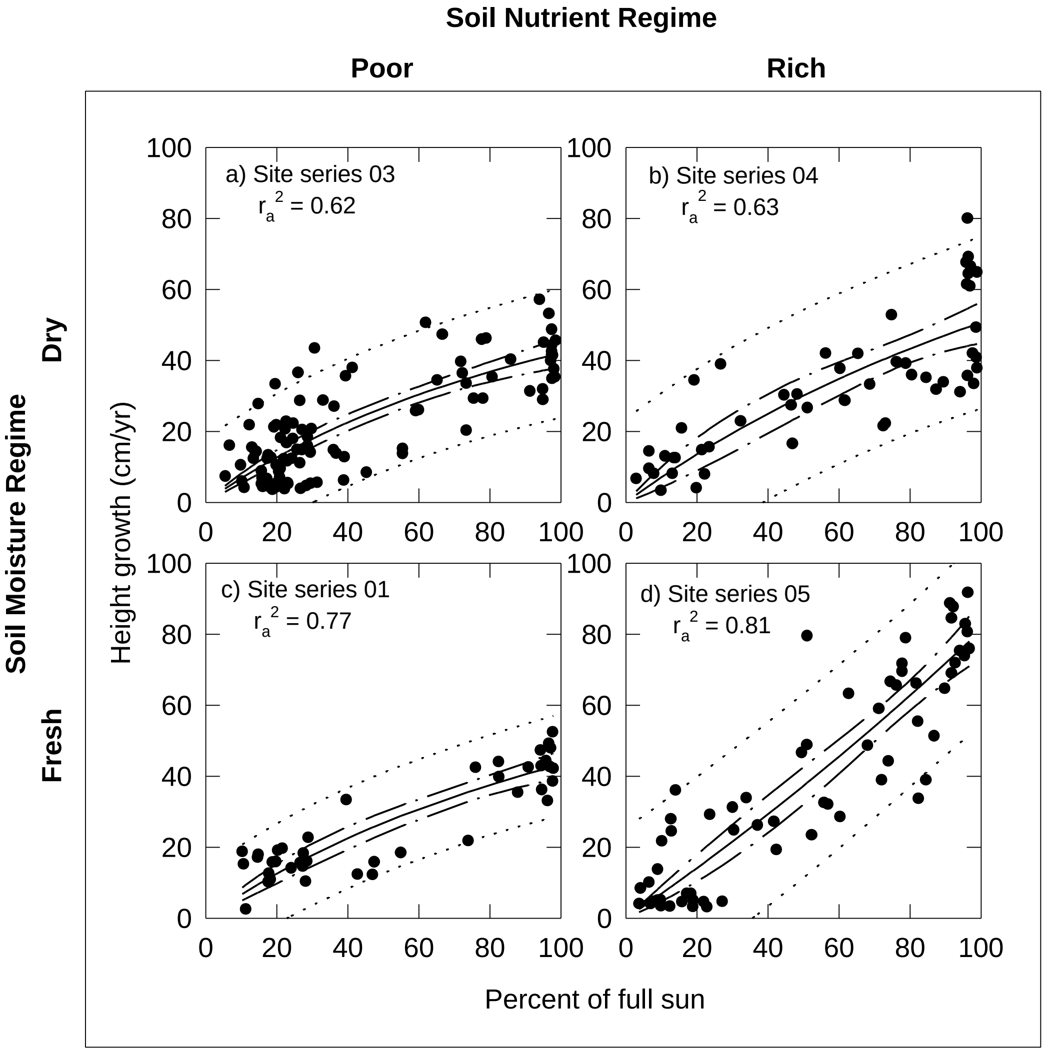


Figure 3 and 4). These results support neither the hypothesis that shade tolerance of Douglas-fir increases with decreasing soil moisture (Atzet and Waring 1970; Marshall 1986) nor the hypothesis that the shade tolerance of

Douglas-fir decreases with soil moisture (Carter and Klinka 1992). The lack of support for either hypothesis may result from the use of absolute rather than relative values of growth or from differences among studies in the range of soil moisture analyzed (Carter and Klinka 1992). Alternatively, my results may simply reflect that growth is primarily light-dependent when light is limiting, irrespective of site-specific effects on growth.

Radial growth of Douglas-fir saplings is not as responsive as height growth to differences in site quality. The only statistically significant difference among site series occurred above 60 % full sun, where the growth response on Fresh, Rich sites differed from the response on other site series (Figure 6). This is consistent with the finding that shade intolerant species like Douglas-fir tend to allocate photosynthate to height growth rather than to lateral growth in order to reach the forest canopy more quickly (Tilman 1988; Chen 1997).

Interspecific differences in growth response

The inter-specific differences I detected in growth response are similar to results of other field studies of light-dependent growth responses (e. g., Carter and Klinka 1992; Wang et al. 1994; Mailly and Kimmins 1997; Coates 1998; Wright et al. 1998) and are consistent with traditional classifications of shade tolerance. Documented classifications of shade tolerance rank Douglas-fir as less shade tolerant than western redcedar (e. g., Carter and Klinka 1992). Shade tolerant species typically have higher growth rates at low levels of light, and shade intolerant species typically have higher growth rates at high light levels (Kobe and Coates 1997; Mailly and Kimmins 1997; Klinka et al. 1997). This was the pattern I observed for height growth and radial growth at low light for Douglas-fir and western redcedar. These results are consistent with the idea of a trade-off in the ability of saplings to survive and grow at low light levels with their ability to grow rapidly at high light levels (Pacala et al. 1994; Kobe and Coates 1997; Wright et al. 1998).

Variation of individual trees at a given light level

It is difficult to predict accurately the growth rate for an individual tree at a given light level. Variation in the growth of individual trees results from many factors, including genetics (Lester et al. 1990), mycorrhizal associations (Simard et al. 1997), previous periods of suppression (Wright et al. 1999), disturbance history (Horn 1971), competition for resources (Vitousek et al. 1982), morphological differences (Chen et al. 1996; Wang et al. 1994), and variation within site series in the amount of soil nutrients and moisture present. It is likely that all these factors influence the presented data set of sapling growth. It is important for managers to bear this variation in mind when setting re-stocking targets for partial cutting treatments, even if the treatment creates a homogenous stand of evenly dispersed light environments (e. g., commercial thinning), and especially if advance regeneration is incorporated into the re-stocking target. It is possible to mitigate some of this variation by appropriate stocking practices (Lester et al. 1990).

Stand structure and light

The amount and distribution of retained structure shape the light environment of regenerating trees in partially cut stands. I found statistically significant relationships between the light environment in the understory and the density, summed height, summed dbh, volume, and spatial arrangement of residual trees (Figure 8 and 10). The negative relationship of these structural attributes with light corroborates a previously documented process regarding light in forests. Namely, that the density of photosynthetically active photon flux decreases exponentially as the amount of leaf material increases when light travels through the canopy (Nobel and Long 1985). Other studies reported such nonlinear decreases in light with increasing stem density (Brown and Parker 1994), canopy height (Clark et al. 1996), basal area (Palik et al. 1997), 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 within a stand (Sequeira and Gholz 1991; Gholz et al. 1997; Walter and Himmler 1996). Quantifying the relationship between these attributes of stand structure and light provides the basis for planning and predicting the effects on partial cutting treatments on regeneration.

The summed height of residual trees is an especially good predictor of light environment (Table 7 and Figure 9). This is likely a result of the direct relationship 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). This finding is important because tree height is a key variable in the emerging design of variable retention treatments (e. g., MacMillan Bloedel 1999).

Many structural attributes show little predictive capacity for light environment (Table 5). Such attributes include the stand composition of component species, average volume per tree, average tree height, and average basal area of trees. Interestingly, the summed values of the structural attributes in a plot explain a higher percentage of the variation in light environment than the averaged values of those attributes, e. g., summed height of stems rather than average height of stems in a plot. This presumably occurs because the averaged variables do not reflect the total amount of structure actually present to intercept light travelling through the canopy.

Similar low light environments are created by a wide range of values of structural attributes. At high densities, summed heights, or volumes of retained structure, the amount of light at any one location in the understory is greatly influenced by the spatial distribution and orientation of stems relative to the path of the sun (Clark et al. 1996; Canham et al. 1990). This is likely a consequence of the spatial distribution and orientation of the stems affecting the temporal and spatial distribution of sunflecks. At high values of structural attributes, the contribution of diffuse light to the overall light environment is greater than at low levels of retained structure. Moreover, the penetration of low angle light and the contribution of sunflecks become important at determining the overall light environment (Canham et al. 1990; Clark et al. 1996). This effect is not as important at low values of the structural attributes because the canopy blocks a smaller proportion of the path of the sun and light is primarily direct (Canham et al. 1990).

Light in partial cuts

At higher levels of retention, the light environment more closely resembles the light regime of uncut second growth (Figure 7). In the understory of closed Douglas-fir forests, sunflecks contribute about half of the total growing season photosynthetically active radiation (Canham et al. 1990) and light is predominantly diffuse (Parker 1997). This is insufficient to guarantee survival of regenerating Douglas-fir, which needs at least 20 % full sun to ensure survival (Mailly and Kimmins 1997). Therefore, individual tree selection and thinning from above, as carried out in the sites I studied, should not be considered plausible options for regenerating Douglas-fir. The single and multiple tree gaps (i. e., 300-500 m^2) created by the individual tree selection and thinning from above treatments have little influence on the understory light regime of these forests.

The combination of different structural attributes and the spatial arrangement of residual trees shape the light environment of silvicultural treatments with high levels of retention. For example, the commercial thinning treatment has the most homogeneously distributed residual trees of all the treatments I examined and has a high enough stand volume and density to create a small range of light environments with a mean of roughly 40 % full sun (

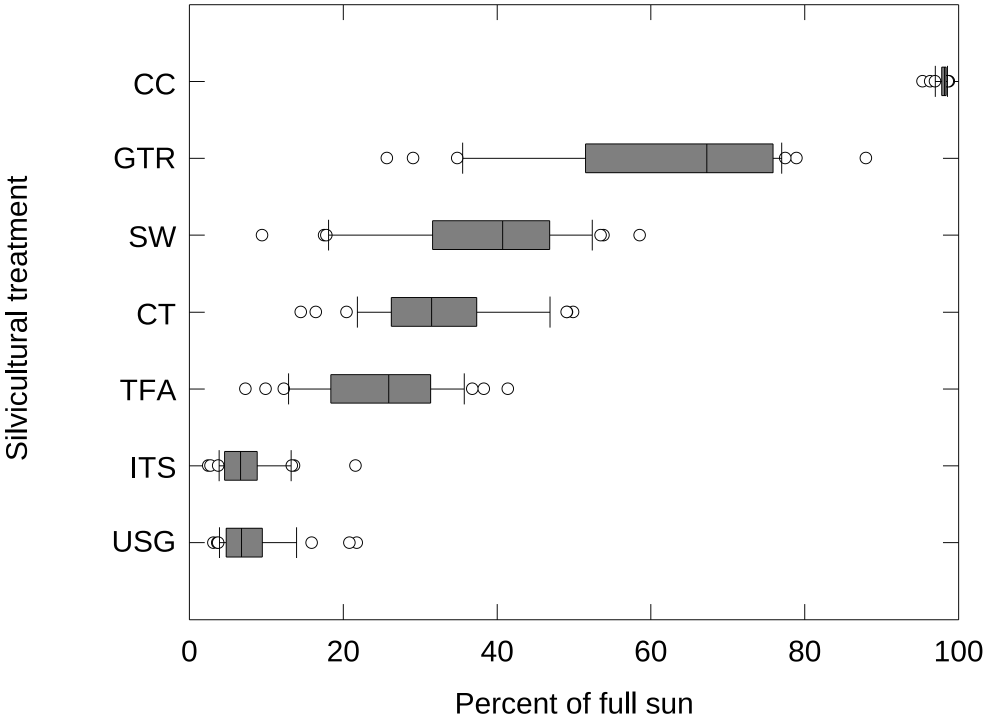


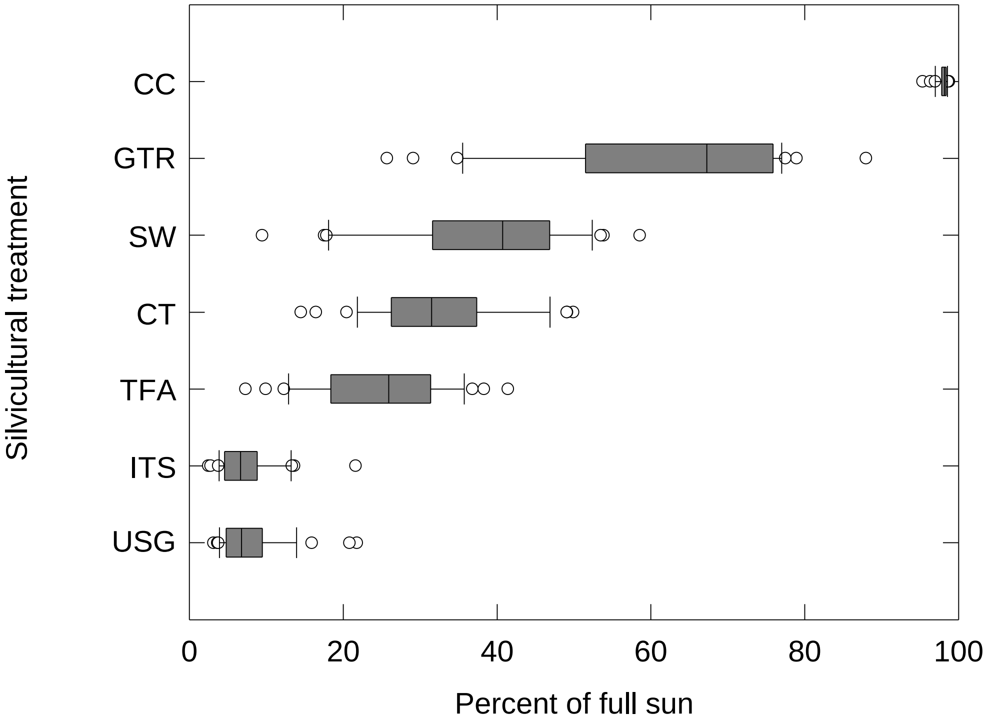
Figure 7). Although the shelterwood treatment has a mean light environment similar to that of commercial thinning, the light environment of the shelterwood treatment is created by residual trees that are more clumped, and have a higher volume and mean height and a lower density. The thinning from above treatment has the lowest residual tree volume of these three treatments but the highest density and summed heights, resulting in a lower mean light environment. The high mean light environment of the green tree retention treatment results from its relatively clumped distribution, and low density, volume, and summed height of residual trees. These examples illustrate that forest managers can modify stand structure in a number of different ways to create a stand of a given mean light environment.

Management implications

Partial cutting treatments are the focus of many recent research efforts (e. g, Lundqvist 1994; Van Der Kamp 1995; Dolph et al. 1995; Maraj 1999). However, many of the ecological and economic consequences of these treatments remain uncertain (McComb et al. 1993; Franklin et al. 1997). Given the potential of partial cutting treatments for meeting the increasingly broad set of management objectives demanded from forest lands, this uncertainty should not stop managers from implementing these treatments. Rather, this uncertainty calls for an adaptive management approach when implementing partial cutting treatments. Such an approach would allow lessons to be drawn from management actions and comparisons to be made regarding the efficacy of different silvicultural treatments in meeting their management objectives (Swanson and Franklin 1992).

Forest managers seeking to regenerate Douglas-fir and western redcedar using partial cutting treatments should consider the following: *1) It is possible to predict the shading effects of retained structure on the growth rates of regenerating trees*. For example, silvicultural treatments that create light environments similar to those of thinning from above (i. e., ranging between about 8 – 42 % full sun) (Figure 11) will result in leader increments for Douglas-fir regenerating on Fresh, Rich sites that vary between about 8 – 38 cm / yr. in (Figure 3), or approximately 8 – 40 % of what would be expected under 100 % full sun (Figure 11). Furthermore, setting specific targets for retained structure to meet ecological objectives allows characterization of the trade-offs regarding the growth rates of regeneration. For example, if 200 large trees / ha are retained during harvest with a total volume of 200 m^3 / ha and a summed height of 8000 m / ha, the mean of the light environments created by this treatment will be between 40 – 65 % full sun (Figure 9). The growth rates for regenerating Douglas-fir on Fresh, Rich sites in this range of light environments are about 40 – 65 % of the growth rates expected under full sun (Figure 11).

2) Green tree retention provides an opportunity for regenerating shade intolerant species, like Douglas-fir, while meeting multiple management objectives. - Residual trees, either singly or in patches, provide a number of important ecological functions, from wildlife habitat to sources of innocula for ectomycorrhizal fungi (e. g., Coates and Steventon 1994, Simard et al. 1997). Green tree retention can create light environments with up to ca. 90 % full sun (**Figure 7**). Such bright environments are possible if residual trees are clumped rather than dispersed uniformly and gaps between clumps are



relatively large (i. e., greater than 1400 m^2) (Palik et al. 1997; Coates 1998). An aggregated arrangement of residual trees can allow growth rates of regeneration in more open areas that approximate those expected in clearcuts (Figure 11). Furthermore, aggregated retention allows the maintenance of broader variety of stand structural elements (e. g., snags, downed logs) than dispersed retention (Franklin et al. 1997; MacMillan Bloedel 1999).

3) *Tailoring the harvesting pattern to the distribution of site series within a harvest area and the use of appropriate reforestation techniques may mitigate the shading effect of retained green trees on regeneration.* – The data presented here suggest it is possible to optimize the distribution of potential growth rates of Douglas-fir regeneration by allocating openings in a harvest area according to the distribution of site series within that area. Douglas-fir saplings show a relatively greater decrease in growth rates relative to their potential at 100 % full sun on Fresh, Rich sites than Dry, Poor over the range of light environments created by partial cutting treatments (Figure 11). This means that larger openings, such as those created in the green tree retention treatment I examined (i. e., 0.5 – 1 ha), should be created in Fresh, Rich sites rather than in poorer or drier sites.

Appropriate reforestation techniques can abate shading effects of retained green trees through thoughtful species choice and microsite selection (Coates 1998; Rose and Muir 1997). Areas of high light in larger gaps and on the eastern and southern exposures of retained patches should be replanted with shade intolerant species, while the more shaded areas of smaller gaps and western and northern exposures should be replanted with western redcedar and other shade tolerant species. Such a spatial allocation of different species within a harvested area results in a more efficient use of growing space as it allocates the light environments created by logging to the species best able to maximize growth in those environments.

4) *The shade tolerance of western redcedar allows a wide range of silvicultural options that result in growth rates similar to those expected in clearcut environments*. - Redcedar approaches its maximum growth rate at ca. 30 % full sun (Figure 5). Therefore, partial cutting treatments that create similar light environments to those of the green tree retention, shelterwood, and commercial thinning treatments may be considered without compromising growth rates of regenerating redcedar. Even the light environment of the individual tree selection treatment, which has a median light environment of less than 10 % full sun, is associated with growth rates of regenerating redcedar that approximate 50 % of the growth rates expected in clearcuts (Figure 11). This shade tolerance allows great flexibility for forest managers in choosing the amount and distribution of retained structure.

The selection of a silvicultural treatment increasingly requires consideration of multiple and diverse management objectives (Franklin et al. 1997). This study considers selection of silvicultural treatments only by their impact on the growth rates of regeneration, while ignoring important considerations such as harvesting logistics, logging costs, and other forest values. However, these other considerations are the subject of much recent research effort, much of which concludes partial cuttings are less costly and less logistically difficult than previously believed (e. g., Coates 1997; Howard and Temesgen 1997). Furthermore, it is worth noting that Douglas-fir saplings show average leader increments of 60 cm / yr under 60 % full sun on Fresh, Rich sites

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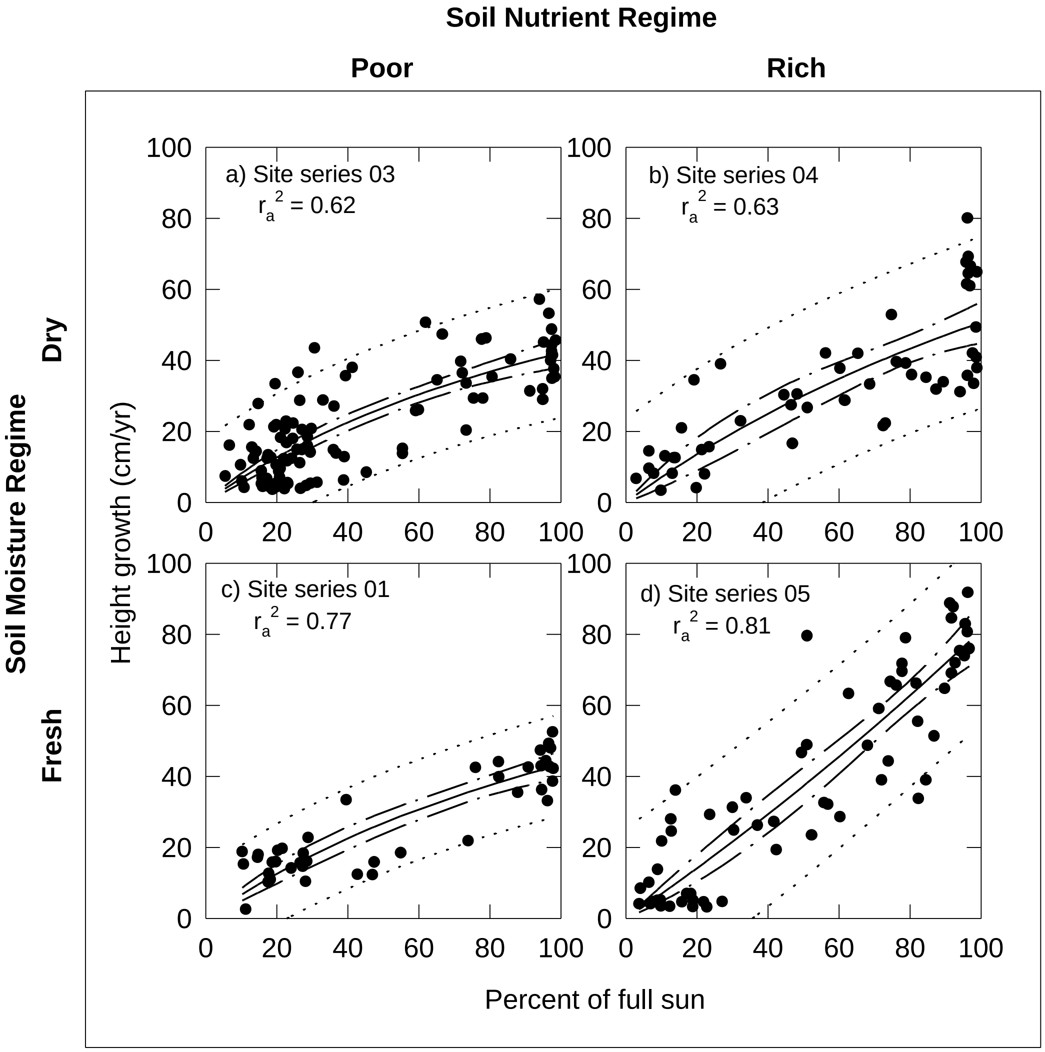

Figure 3). Such growth rates should be encouraging to forest managers seeking to efficiently regenerate an area following timber harvesting without compromising other ecological objectives for the stand.

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Tables

Table 1. Average height and dbh of saplings sampled among site classes. Standard deviations are in parentheses. SMR = Soil moisture regime, SNR = soil nutrient regime.

Site series	SMR	SNR	Species	n	Height (m)	dbh (cm)
03	Moderately Dry	Very Poor to Medium	Fd	101	3.95 (1.67)	4.09 (1.90)
04	Moderately Dry	Rich to Very Rich	Fd	52	3.26 (1.42)	3.42 (1.90)
05	Slightly Dry to Fresh	Rich to Very Rich	Fd	64	3.99 (1.63)	4.45 (2.30)
01	Slightly Dry to Fresh	Very Poor to Medium	Fd	41	2.95 (1.43)	2.96 (1.75)
03	Moderately Dry	Very Poor to Medium	Cw	43	3.74 (0.94)	4.97 (1.97)

Note: Fd = Douglas-fir; Cw = western redcedar

Table 2. Selected attributes of stand structure for both live biomass and total biomass (live and dead) in the partial cutting treatments sampled. Data are derived from 10 plots of stand structure in each treatment. Standard deviations are in parentheses.

	Live biomass					**Total biomass**				
Treatment	**Mean dbh (cm)**	**Mean height (m)**	**Basal area[1] (m^2/ha)**	**Density (stems/ha)**	**Volume (m^3/ha)**	**Mean dbh (cm)**	**Mean height (m)**	**Basal area[1] (m^2/ha)**	**Density (stems/ha)**	**Volume (m^3/ha)**
Clearcut	0	0	0	0	0	0	0	0	0	0
Green Tree Retention	24	17	15	184	167	43	13	59	247	167
	(9)	(7)	(15)	(179)	(174)	(33)	(7)	(62)	(222)	(175)
Shelterwood	37	28	30	284	356	37	27	30	294	358
	(15)	(11)	(12)	(183)	(126)	(15)	(11)	(12)	(191)	(125)
Commercial Thinning	28	28	21	319	209	28	25	21	329	211
	(5)	(5)	(7)	(60)	(104)	(5)	(4)	(7)	(63)	(103)
Thinning From Above	19	16	22	628	200	19	16	22	656	203
	(5)	(3)	(5)	(309)	(70)	(5)	(3)	(5)	(321)	(70)
Individual Tree Selection	31	28	56	691	682	30	26	73	858	704
	(5)	(3)	(12)	(194)	(93)	(5)	(3)	(18)	(257)	(80)
Uncut Second Growth	21	21	44	1157	388	20	19	46	1376	398
	(3)	(2)	(6)	(227)	(85)	(2)	(2)	(7)	(204)	(91)

[1] This estimate of basal area includes all trees above 2-m in height.

Table 3. Goodness of fit and parameter estimates for predicted height growth of Douglas-fir and western redcedar saplings using the Michaelis-Menton equation (Predicted Radial Growth = (*a* x Light) / ((*a*/*s*) + Light). Light represents the index of whole season light availability. Height growth is the mean of height growth over the sampled years (1992-1996). Parameter *a* is the asymptote of the function at high light and parameter *s* is the slope of the relationship at zero light. See Table 1 for sample sizes.

				a			***s***	
Species	**Site series**	r_a^2	***a***	**Lower 95 % CI**	**Upper 95% CI**	***s***	**Lower 95 % CI**	**Upper 95% CI**
Fd	05	0.81	2.216E05	0.000	2.399E08	0.785	0.538	1.033
Fd	04	0.63	159.634	-38.601	357.869	0.743	0.385	1.099
Fd	01	0.77	111.748	41.573	181.922	0.707	0.481	0.932
Fd	03	0.61	100.346	51.781	148.912	0.727	0.547	0.906
Cw	03	0.52	11.057	9.976	12.138	2.035	1.193	2.877

Note: Fd = Douglas-fir; Cw = western redcedar

Table 4. Goodness of fit and parameter estimates for predicted radial growth of Douglas-fir and western redcedar using the Michaelis-Menton equation (Predicted Radial Growth = (a x Light) / ((a/s) + Light). Light represents the index of whole light availability. Radial growth is $\log_{10}$ (mean of radial growth increment + 1). Parameter *a* is the asymptote of the function at high light and parameter *s* is the slope of the relationship at zero light. See Table 1 for sample sizes.

				a			***s***	
Species	**Site series**	r_a^2	***a***	**Lower 95 % CI**	**Upper 95% CI**	***s***	**Lower 95 % CI**	**Upper 95% CI**
Fd	05	0.85	3.213	0.366	6.060	0.012	0.009	0.015
Fd	04	0.71	1.150	0.128	2.429	0.014	0.009	0.020
Fd	01	0.76	1.761	0.185	3.337	0.009	0.006	0.012
Fd	03	0.76	2.384	0.686	4.083	0.009	0.007	0.010
Cw	03	0.59	0.677	0.571	0.782	0.052	0.032	0.073

Note: Fd = Douglas-fir; Cw = western redcedar

Table 5. Linear regressions of stand structural attributes and whole season light availability. n = 10.

Variable	r_a^2	P
Snag composition	-0.01	0.743
Percent composition of Pl	-0.01	0.683
Mean basal area of 5 tallest trees	-0.01	0.657
Basal area/tree	-0.01	0.495
Percent composition of deciduous	-0.01	0.472
Volume/tree	0.01	0.217
Percent composition of Cw	0.01	0.210
Percent composition of Hw	0.01	0.206
Mean dbh	0.02	0.112
Height variance	0.04	0.065
Range of dbh	0.10	0.004
Basal area/ha	0.27	0.000
Percent composition of Fd	0.33	0.000
Height range	0.34	0.000
Mean height	0.36	0.000
Plot volume of trees	0.57	0.000
Plot density of trees	0.61	0.000
Mean height of 5 tallest trees	0.62	0.000
Summed height / summed dbh	0.63	0.000
Summed height	0.68	0.000
Summed dbh	0.71	0.000

Note: Fd = Douglas-fir; Cw = western redcedar; Hw = western hemlock; Pl = lodgepole pine

Table 6. Selected linear regressions of structural attributes and the light environment of partial cutting treatments at the stand scale.

Variable	r_a^2	P	Intercept	Slope
(1) DEPENDENT:				
Mean light environment				
INDEPENDENT:				
Height means (m)	0.56	0.03	87.8	-2.7
Stand volume (m^3/ha)	0.57	0.03	72.7	-0.1
Summed heights (m/ha)	0.61	0.02	88.3	-0.5
Stand density (stems/ha)	0.62	0.02	69.6	-1.4
Summed dbh (cm/ha)	0.70	0.01	76.7	-0.01
(2) DEPENDENT:				
SD in light environment				
INDEPENDENT:				
Mean basal area (m^2)	0.72	0.01	2.6	60.7
SD of stand volume	0.75	0.01	-2.1	181.5
(3) DEPENDENT:				
Variance in light environment				
INDEPENDENT:				
Mean basal area (m^2)	0.82	0.00	-17.9	1348.7
Variance in stand volume	0.87	0.00	-39.8	34840.5

Note: Unless otherwise stated, all independent variables are means of all the plots (n = 10) in each stand.

Table 7. Adjusted r^2 values, mean square error of residuals, and best-fit parameter estimates for nonlinear regressions of selected stand structural attributes and mean light environment using the model $Y = ae^{bX}$.

Structural attribute	r_a^2	MSE	*a*	*b*
Site scale				
Plot density (stems/plot)	0.87	129.661	92.205	-0.069
Plot volume (m^3/ha)	0.77	233.304	90.935	-0.004
Summed dbh in plot (cm/plot)	0.89	116.210	96.191	-0.026
Summed height in plot (m/plot)	0.94	63.485	94.431	-0.003
Stand scale				
Stand density (stems/ha)	0.94	78.311	98.086	-0.003
Stand volume (m^3/ha)	0.85	184.595	98.262	-0.004
Mean height in stand (m)	0.72	352.765	98.466	-0.002
Summed height in stand (m/ha)	0.99	13.149	98.022	-0.000

Figures

Figure 1. Distribution of stands and saplings sampled within the study area. The ellipse indicates the approximate boundary for the sampling of saplings. The acronyms refer to treatment type: CC, clearcut; GTR, green tree retention; SW, shelterwood; CT, commercial thinning; TFA, thinning from above; ITS, individual tree selection; USG, uncut second growth.

Figure 2. Hemispherical photographs of the canopy in: clearcut (CC), green tree retention (GTR), shelterwood (SW), commercial thinning (CT), thinning from above (TFA), individual tree selection (ITS); and uncut second growth (USG).

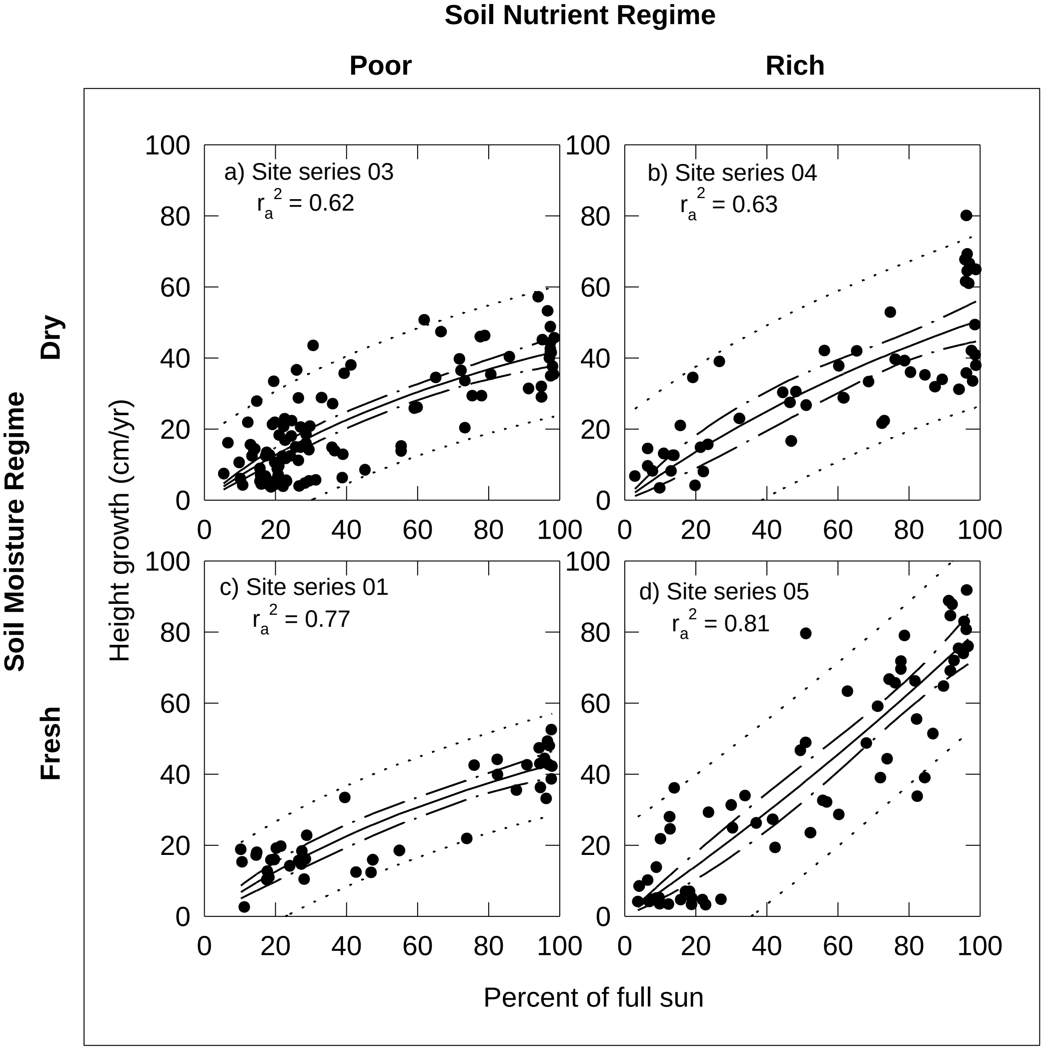

Figure 3. Response of height growth to light for Douglas-fir saplings in sites of varying soil moisture and soil nutrient regimes. Dotted lines are the 95% CI for the predicted values of growth of individual saplings at a given light level. Lines of dots and stripes are 95 % CI for the predicted values of the population mean of growth at a given light level. The site series are: Dry, Poor (03); Dry, Rich (04); Fresh, Poor (01); and Fresh, Rich (05). See Table 1 for sample sizes and Table 3 for regression equations and parameter estimates.

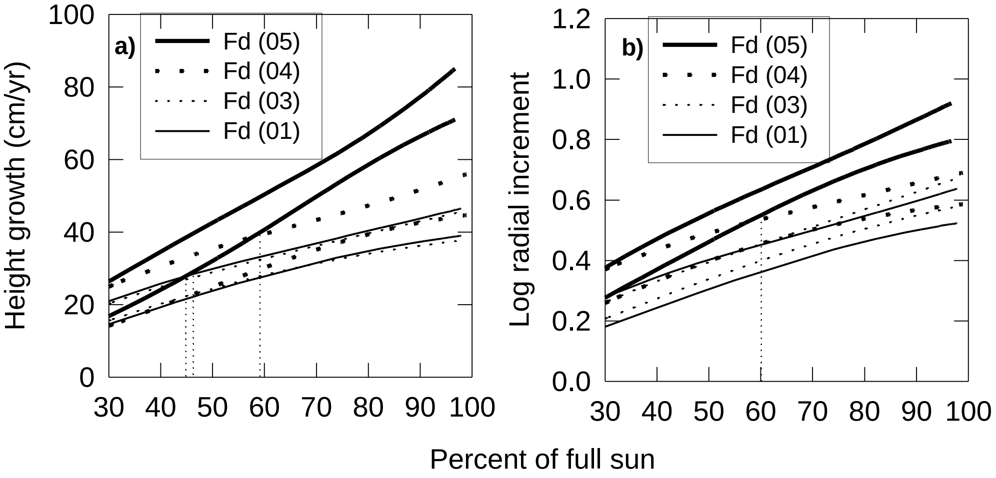

Figure 4. Upper and lower bounds of the 95 % CI for the population mean of Douglas-fir response in (a) height growth and (b) radial growth in different site series. Dotted lines indicate the light level above which the 95 % CI no longer overlap. The site series are: Dry, Poor (03); Dry, Rich (04); Fresh, Poor (01); and Fresh, Rich (05).

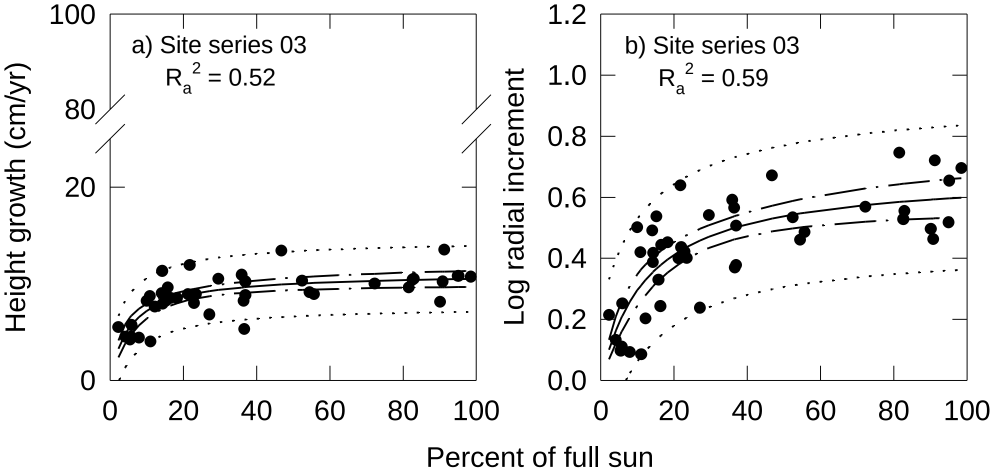

Figure 5. Height and radial growth response to light for western redcedar saplings in Dry, Poor (03) sites. Dotted lines are the 95% CI for the predicted values of growth of individual saplings at a given light level. Lines of dots and stripes are 95 % CI for the predicted values of the population mean of growth at a given light level. See Table 1 for sample sizes and Tables 3 and 4 for regression equations and parameter estimates.

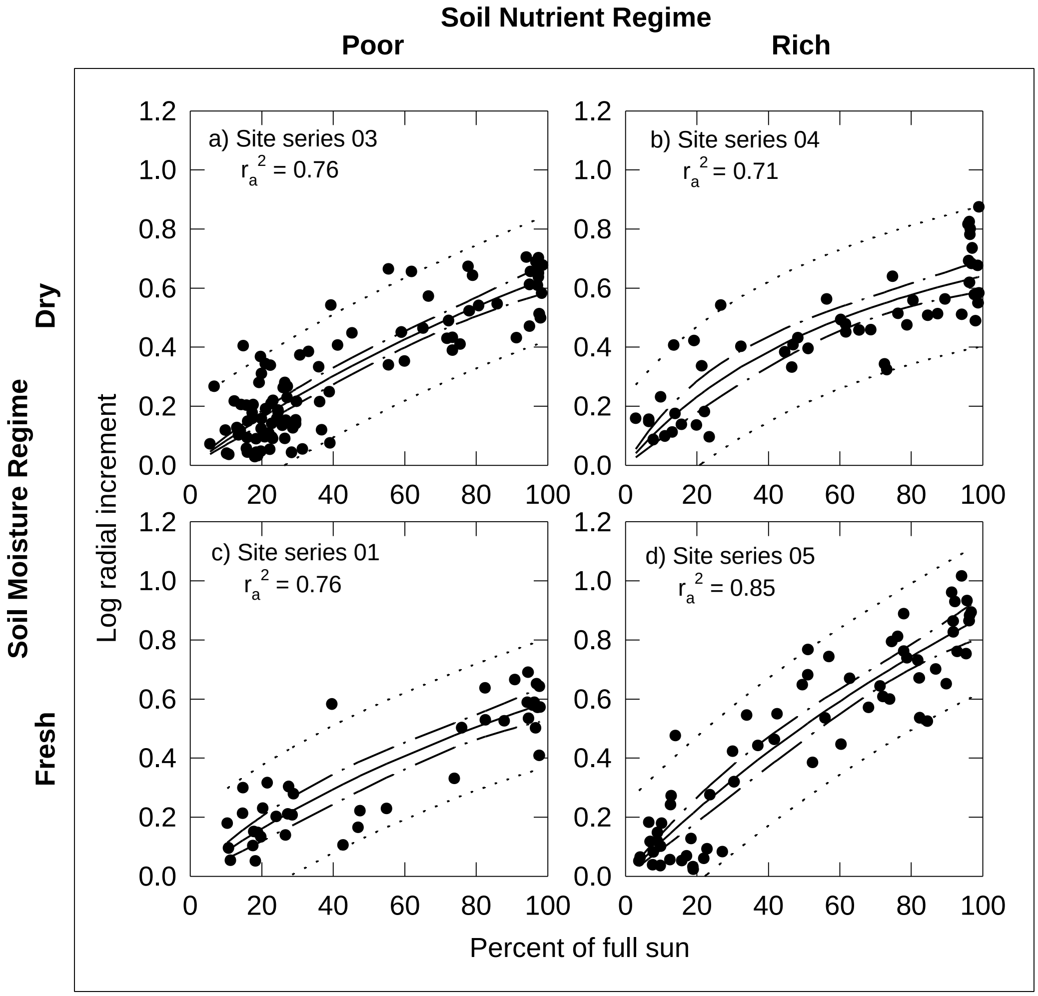

Figure 6. Radial growth response to light for Douglas-fir saplings in sites of varying soil moisture and soil nutrient regimes. Dotted lines are the 95% CI for the predicted values of growth of individual saplings at a given light level. Lines of dots and stripes are 95 % CI for the predicted values of the population mean of growth at a given light level. The site series are: Dry, Poor (03); Dry, Rich (04); Fresh, Poor (01); and Fresh, Rich (05). See Table 1 for sample sizes and Table 4 for regression equations and parameter estimates.

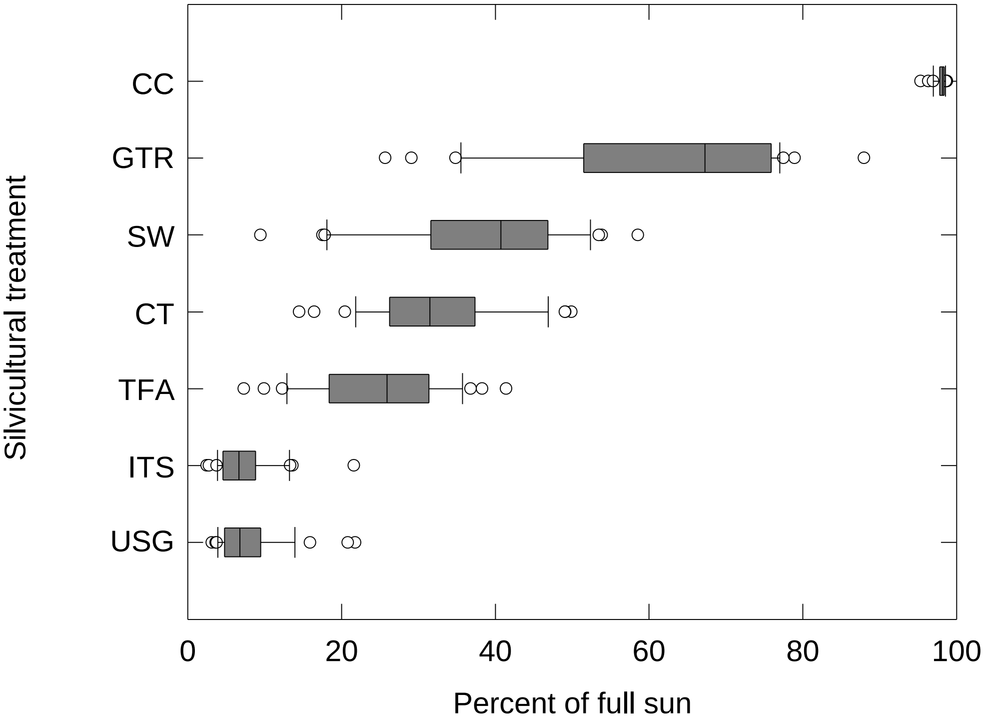

Figure 7. The range of light environments in partial cutting treatments. The acronyms refer to treatment type: CC, clearcut; GTR, green tree retention; SW, shelterwood; CT, commercial thinning; TFA, thinning from above; ITS, individual tree selection; USG, uncut second growth. n = 30 for each treatment type.

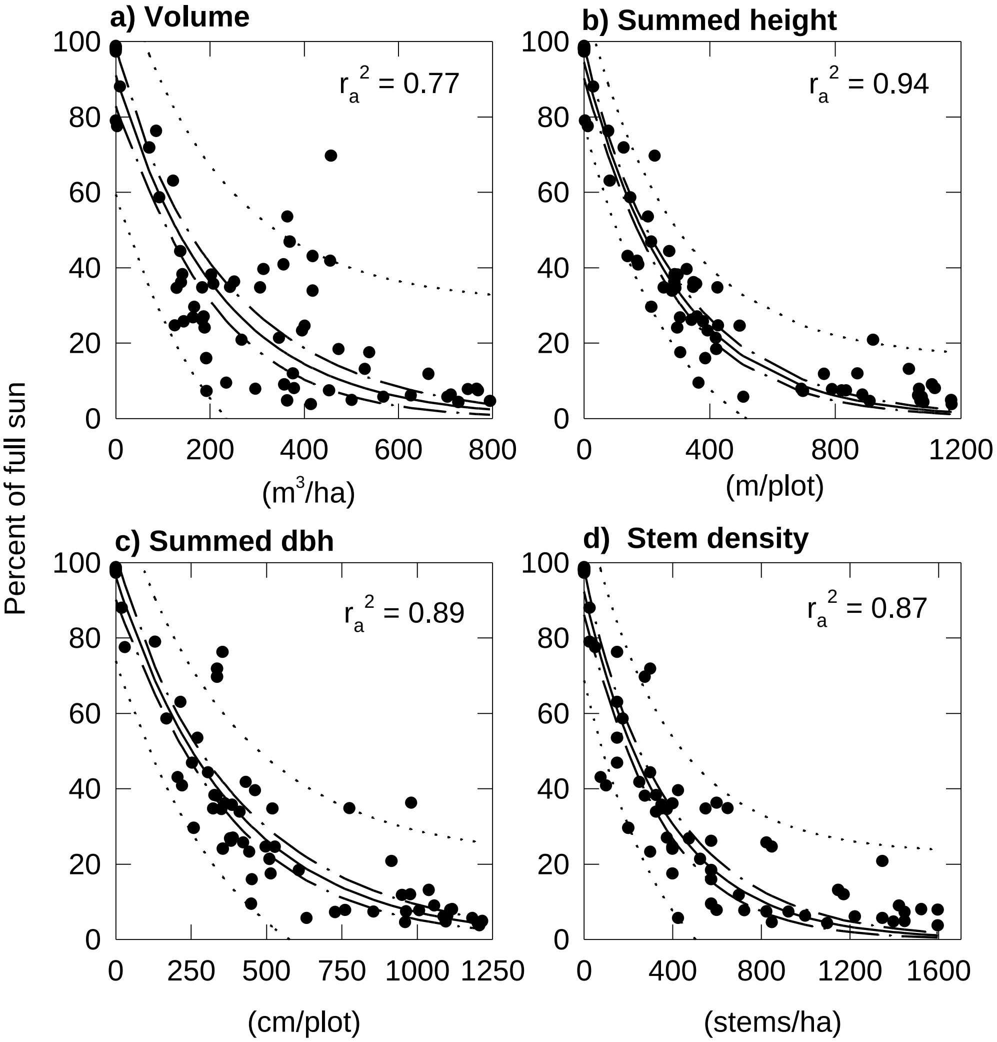

Figure 8. Regressions of structural attributes and light at the site scale. Dotted lines are the 95 % CI for the predicted values and lines of dots and stripes are 95 % CI for the population means. See Table 7 for regression equations and parameter estimates. n = 70.

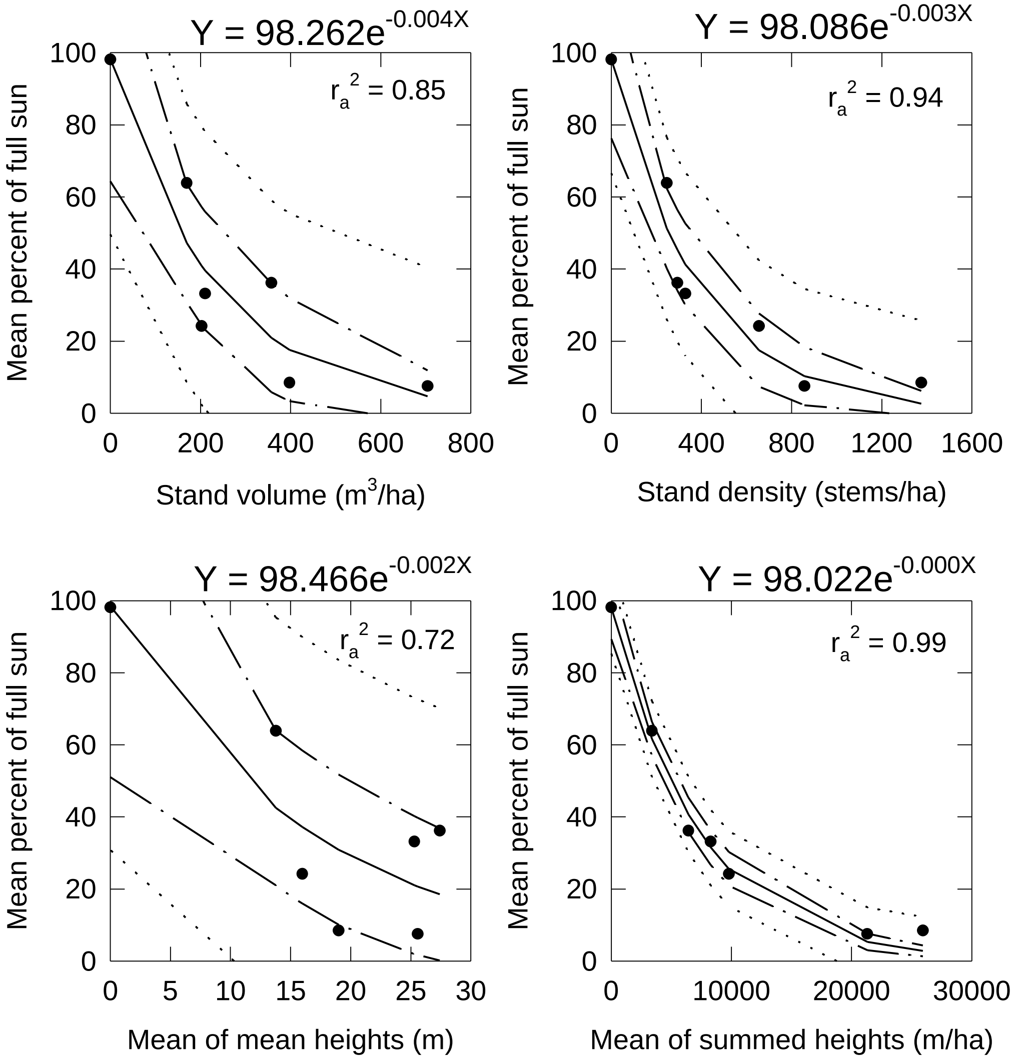

Figure 9. Regressions of structural attributes and light at the stand scale. Dotted lines are the 95 % CI for the predicted values and lines of dots and stripes are 95 % CI for the population means. See Table 7 for regression equations and parameter estimates. n = 7.

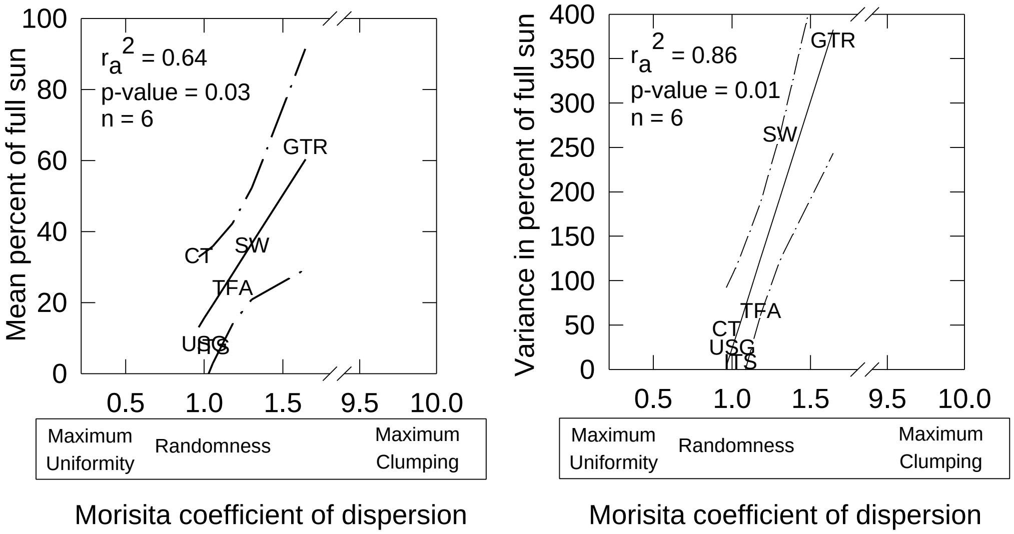

Figure 10. Morisita coefficient of dispersion for residual trees in partial cutting treatments and its relation to the mean and variance in light environment. n = 6.

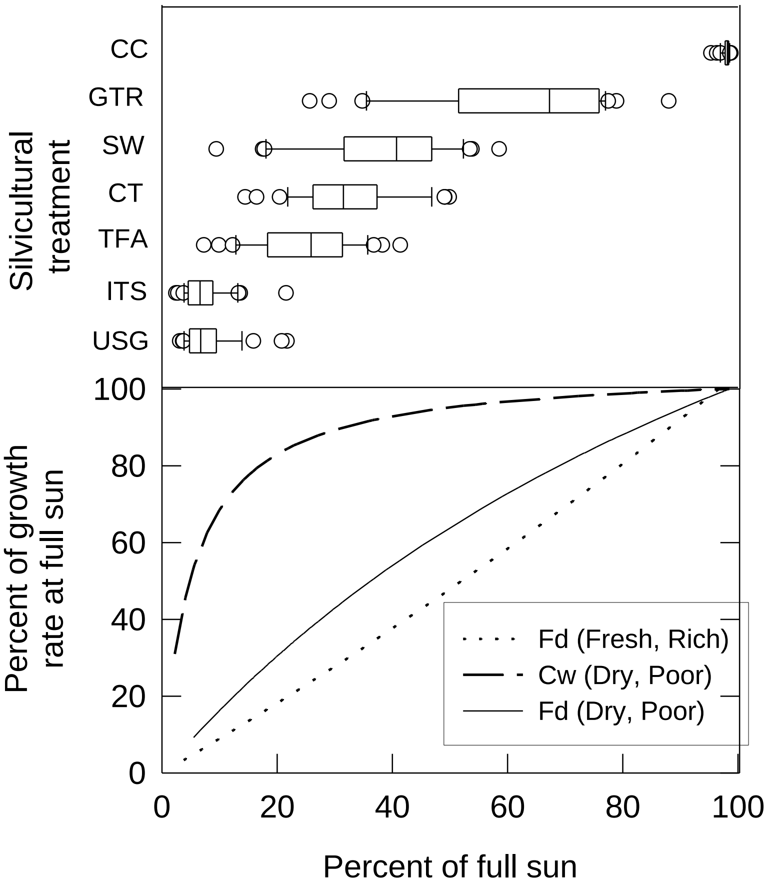

Figure 11. The distribution of light environments in partial cutting treatments and the growth rates of saplings under varying light conditions as a percentage of that expected under 100 % full sun. The acronyms refer to treatment type: CC, clearcut; GTR, green tree retention; SW, shelterwood; CT, commercial thinning; TFA, thinning from above; ITS, individual tree selection; USG, uncut second growth.