Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients

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Abstract: We characterized the radial and height growth response to light for coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and western redcedar (*Thuja plicata* Donn ex D. Don) saplings growing in sites of different regimes of soil moisture and nutrients on the east coast of Vancouver Island, British Columbia. We determined that at low light levels, site quality has little effect on the growth response of Douglas-fir saplings. At light levels above approximately 40 and 60% full sun, Douglas-fir saplings show statistically significant differences in height and radial growth, respectively, that reflect the differences in soil moisture and nutrient regimes of the sites we examined. Western redcedar approaches its maximum radial and height growth rates at about 30% full sun. Our data suggest that partial-cutting treatments need to create light environments greater than about 40% full sun to achieve growth that represents a high proportion of the site growing potential for Douglas-fir at full sun, while the high shade tolerance of western redcedar allows silvicultural treatments that retain a high amount of forest structure without compromising growth rates of young trees.

Résumé : Nous avons caractérisé la réponse à la lumière de la croissance radiale et en hauteur de semis de sapin de Douglas côtier (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) et de thuya géant (*Thuja plicata* Donn ex D. Don) croissant dans des sites à régimes nutritifs et d'humidité du sol différents sur la côte est de l'île de Vancouver, en Colombie-Britannique. Nous avons déterminé que sous une faible luminosité, la qualité du site avait peu d'influence sur la réponse de croissance des semis de sapin de Douglas. À partir d'intensités lumineuses supérieures à 40 et 60% de la pleine lumière, les semis de sapin de Douglas montrent des différences statistiquement significatives respectivement dans leur croissance en hauteur et radiale, qui reflètent les différences entre les régimes d'humidité du sol et nutritifs des sites que nous avons examinés. Le thuya géant approche ses taux maximums de croissance radiale et en hauteur à approximativement 30% de la pleine lumière. Nos données suggèrent que des traitements de coupe partielle doivent créer des conditions de luminosité supérieures à 40% de la pleine lumière afin d'obtenir une croissance qui s'approche du potentiel de croissance du sapin de Douglas en pleine lumière, alors que la forte tolérance du thuya géant à l'ombre permet des traitements sylvicoles qui préservent pratiquement la structure de la forêt sans compromettre les taux de croissance des jeunes arbres.

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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 clear-cutting (Swanson and Franklin 1992; Hansen et al. 1995*a*; Franklin et al. 1997; Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995). 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. 1995*b*; Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995; Franklin et al. 1997). Partial-cutting treatments can allow forest managers to ad-

dress multiple, and sometimes conflicting, management objectives within a given treatment unit (Coates and Burton 1997). 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. 1995*b*; Maraj 1999), conserving functional communities of soil organisms (Perry 1994; Durall et al. 1999), or mitigating microclimatic effects of forest removal (Franklin et al. 1997). However, the trade-offs among these disparate management objectives are often uncertain. In particular, there is concern regarding how shade cast by retained mature green trees after harvesting affects the growth rates of regenerating trees, either already present in the stand as advance regeneration, as newly established seedlings, or as outplanted trees (Birch and Johnson 1997; Franklin et al. 1997).

The effect of partial overstory removal on the growth rates of regeneration is species specific (Carter and Klinka 1992; Coates 1998). Each tree species reacts differently to various light levels, according to its shade tolerance and other autoecological constraints. This diversity means forest managers

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need to make species-specific decisions when planning partial-cutting treatments and predicting their long-term consequences. We sought to characterize the growth response of two ecologically and silviculturally important species across the range of light environments created by partial cuttings in one portion of their geographic range. These species, coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and western redcedar (*Thuja plicata* Donn ex D. Don), are common in the southern coast of British Columbia. They are typically described as shade intolerant and shade tolerant, respectively (Krajina 1969; Carter and Klinka 1992; Wang et al. 1994). In this study, we examine shade tolerance solely as it relates to growth in low light, bearing in mind that another related aspect of shade tolerance, namely low-light survival, is an important influence on the dynamics of forest understories (Kobe et al. 1995; Kobe and Coates 1997).

In addition to light, site quality is an important factor influencing the growth response to light of regenerating trees. Saplings show intraspecific variation in growth under varying light levels in sites with different regimes of soil moisture and soil nutrients (Carter and Klinka 1992; Wright et al. 1998; Wang et al. 1994, 1998). Evidence of this variation is sometimes contradictory. 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; Marshall 1986). An alternative hypothesis is that Douglas-fir saplings actually exhibit less shade tolerance in dry sites than in wet sites (Atzet and Waring 1970). In this study, we quantify the growth response to light of Douglas-fir in sites of varying soil nutrients and moisture to better understand the effects of site quality on shade tolerance of Douglas-fir regeneration. Understanding such shifts in shade tolerance along varying conditions of soil nutrients and moisture can improve the planning and successful regeneration of silvicultural treatments that retain forest structure, as well as improve predictions of effects of these treatments on stand structure and composition (Klinka et al. 1990, 1994; Franklin et al. 1997; Coates and Burton 1999; Drever 1999).

Methods

Study area

The study area is on the east coast of Vancouver Island, near Campbell River, B.C. (49°57′N, 125°16′W). The sampled areas are almost exclusively second-growth coastal Douglas-fir forests that regenerated naturally after large forest fires in the 1930s (S. Lackey, Regional Forester, TimberWest Forest Products, personal communication). 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* Pursh), red huckleberry (*Vaccinium parvifolium* Smith), and dull Oregon-grape (*Mahonia nervosa* Pursh). Vanilla leaf (*Achlys triphylla* Smith) and sword fern (*Polystichum munitum* (Kaulf.) K. Presl.) are typical dominants in the herb layer.

All the saplings we sampled are in the Very Dry Maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHxm) (Pojar et al. 1987; Meidinger and Pojar 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). Growing-season 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 saplings were sampled from areas with 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; Frazer et al. 1997, 2000). These photographs capture the geometry and orientation of canopy trees and other vegetation above the spot where they are taken. With the use of digital image analysis and light modeling software, hemispherical canopy photographs can be used to estimate the light environment at a particular spot. In this study, we used hemispherical canopy photographs to determine an index of light availability over the whole growing season. This index, measured in units of percent of full sun, was determined using GLI/C version 2.0 light modeling software (Canham 1988; Frazer et al. 1997, 2000). GLI/C version 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; Pacala et al. 1994; Frazer et al. 2000). We used a tripod-mounted Minolta® X700 camera with a Minolta® fish-eye lens (f = 7.5 mm) and Fujichrome® Sensia 400 colour slide film.

Light and growth of saplings

During the 1997 growing season, we destructively sampled 294 coastal Douglas-fir and 43 western redcedar saplings (4–45 years old). We searched for saplings growing across gradients of light environments, soil moisture regime, and soil nutrient regime (Table 1). These saplings were growing in mature second-growth stands (80–100 years old), under canopy openings, along road edges, and in clear-cut and partially cut stands. We did not sample in recently disturbed areas (i.e., <5 years ago) to avoid sampling trees growing in a recently modified light environment, thereby helping ensure the measured growth reflected the available light rather than a recent release or suppression. A limitation of this method is that it precludes inferences about the degree and timing of growth for saplings during release or suppression. On the other hand, it makes our estimates of growth at various light levels suitable for predicting long-term growth of released saplings for the years following the partial cutting.

We selected sample trees that showed the best 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, we sampled trees under primarily coniferous overstories to avoid variation in light environment resulting from seasonal changes of deciduous canopies. We also ensured that each sampled sapling was at least 30 m away from other sampled trees to avoid pseudoreplication in light environment.

For each sapling, we recorded species, height, diameter at breast height (DBH, 1.3 m), and length of leader increment for the last three to five growing seasons. To estimate radial growth, we cut a stem disk 10 cm above the ground. After cutting the stem, we took a hemispherical canopy photograph 1–1.5 m above the stump. Shooting the canopy photographs at a relatively fixed height allowed for sampling efficiency and consistency in aligning the camera with the cardinal orientations. Understory light does not vary very much with height in the size range of our sampled saplings,

Table 1. Height and diameter at breast height (DBH) of saplings sampled among site series.

Site series	Soil moisture regime	Soil nutrient regime	Species	n	Height (m)	DBH (cm)
Dry, poor (03)	Moderately dry	Very poor to medium	Fd	101	3.95 (1.67)	4.09 (1.90)
Dry, rich (04)	Moderately dry	Rich to very rich	Fd	52	3.26 (1.42)	3.42 (1.90)
Fresh, rich (05)	Slightly dry to fresh	Rich to very rich	Fd	64	3.99 (1.63)	4.45 (2.30)
Fresh, poor (01)	Slightly dry to fresh	Very poor to medium	Fd	41	2.95 (1.43)	2.96 (1.75)
Dry, poor (03)	Moderately dry	Very poor to medium	Cw	43	3.74 (0.94)	4.97 (1.97)

Note: Values for height and DBH are means with SDs given in parentheses. Fd, Douglas-fir; Cw, western redcedar.

and camera height has been shown to have little influence on modeled light estimates at the low heights we sampled (Robison and McCarthy 1999).

In the laboratory, we 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 (7–45× magnification), and the MEDIR measuring program (Grissino-Mayer 1996). We measured the width of each year's growth along two radii of a randomly drawn diameter line through the pith. Care was taken to avoid areas of reaction wood. We then averaged the two estimates for each year and calculated a mean growth rate for the last 3–5 years.

For the first 50 saplings measured, we calculated the radial growth rate using four radii of two perpendicular diameter lines. We then randomly picked two of the four radii and compared the estimates of radial growth derived from two and four radii. We found no statistical difference between the mean growth rate determined using two or four radii (ANOVA, $F = 0.02$; $P = 0.99$; df = 49). Two radii were used to calculate radial growth for the remaining sample trees.

For the majority of the Douglas-fir saplings we sampled, mean growth rate was derived from 5 years of growth. For a small number of saplings that were 5 years or younger (25 of 294), we averaged only 3 years of growth to avoid the early years during which the sapling was still growing to its potential for a given set of light and soil conditions. We felt this would provide a more accurate estimate of growth. There was no significant difference between the estimates of mean growth derived this way and the estimates of mean growth for all the saplings derived from only 3 years of data ($t = 1.96$, $P = 0.23$, df = 564).

Determining site series

We assessed the soil moisture and nutrient regime for each sapling by determining the site series where each sampled tree grew. Site series is a qualitative index of the soil moisture and nutrient regime at a given site (Meidinger and Pojar 1991). It represents the finest scale of ecosystem classification, as determined by the Biogeoclimatic System of Ecosystem Classification (BEC) developed for the Vancouver Forest Region in British Columbia (Meidinger and Pojar 1991; Green and Klinka 1994). The BEC procedure combines an assessment of the relative abundance of indicator plants with a characterization of the topographical and soil morphological properties for each site. This type of site classification is a characterization of the moisture and nutrient status of sites within a biogeoclimatic subzone inferred from site, soil, and vegetation characteristics rather than quantitative chemical or moisture assessments.

The soil moisture regime describes the average amount of soil water actually available for plants at a given site based on the annual water balance and the depth of water table for the biogeoclimatic subzone in question. For example, a "moderately dry" soil moisture regime means rooting-zone groundwater is absent during the growing season, and a water deficit occurs that lasts between 1.5 and 3 months. In contrast, a "fresh" soil moisture regime

means no water deficit occurs, as plants are able to meet their water needs during groundwater absence utilizing soil-stored water.

Soil nutrient regime indicates, in a relative way, the ability of the soil to supply nutrients essential for plant growth, particularly nitrogen. The primary factors used to assess soil nutrient regime in the field are soil depth, texture, and coarse fragment content. Others include seepage water, humus form, and the geological source of the parent material.

We sampled Douglas-fir saplings in the four site series where Douglas-fir regenerates naturally in the shrub layer of unmanaged forests (Green and Klinka 1994). These site series encompass three soil moisture regimes that are typically grouped into two classes (moderately dry and slightly dry to fresh) and five soil nutrient regimes again grouped into two classes (very poor to medium and rich to very rich) (Green and Klinka 1994). For simplicity, we labeled the site series as dry, poor (03); dry, rich (04); fresh, poor (01); and fresh, rich (05).

Time and resources prevented us from sampling western redcedar saplings on site series other than dry, poor. However, estimates of growth at various light levels in these sites may be considered "minimums" or conservative estimates. The light-growth response for redcedar elucidated here is still somewhat useful for predicting growth of regeneration in richer and wetter site series than in the one we examined and where redcedar commonly regenerates.

Data analysis

Response of sapling growth to light

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

We chose the Michaelis–Menten equation to characterize the growth response to light of Douglas-fir and western redcedar across different site series. The Michaelis–Menten equation consistently provided a better model fit to data, i.e., had the lowest mean square error (MSE) of the residuals. Although the sigmoidal growth equation fit the data better than the Michaelis–Menten 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–Menten equation with a nonzero X intercept was not very informative; nonzero intercepts were not significantly different from zero and model fits were not as good as those for the Michaelis–Menten equation.

Table 2. Goodness of fit and parameter estimates for predicted height growth of Douglas-fir and western redcedar saplings using the Michaelis–Menten equation (predicted height growth = $(a \times \text{light})/((a/s) + \text{light})$), where light is the index of whole season light availability, height growth is the mean annual height growth over the sampled years (1992–1996), a is the asymptote of the function at high light, and s is the slope of the relationship at zero light.

Species	Site series	R_a^2	a			s		
			Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI
Fd	05	0.81	2.216×10^5	0.000	2.399×10^8	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: See Table 1 for sample sizes. Fd, Douglas-fir; Cw, western redcedar.

Table 3. Goodness of fit and parameter estimates for predicted radial growth of Douglas-fir and western redcedar using the Michaelis–Menten equation (predicted radial growth = $((a \times \text{light})/((a/s) + \text{light}))$), where light is the index of whole light availability, radial growth is $\log_{10}$(mean of radial growth increment + 1), a is the asymptote of the function at high light, and s is the slope of the relationship at zero light.

Species	Site series	r_a^2	a			s		
			Estimate	Lower 95% CI	Upper 95% CI	Estimate	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: See Table 1 for sample sizes. Fd, Douglas-fir; Cw, western redcedar.

The Michaelis-Menten equation has the following form:

$$[1] \qquad Y = \frac{aX}{(a/s) + X} + \varepsilon$$

where Y is the mean rate of height growth (cm/year) or $\log_{10}$(mean rate of radial growth (mm) + 1); X is the index of light over the growing season (in units of percent full sun); a and s are 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 means of radial and height growth over 3–5 years consistently provided better model fits than estimates of growth based on a single year. Hence, these were selected for intra- and interspecific comparisons of growth responses. We 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. We deemed regions where the 95% confidence intervals (CI) did not overlap as statistically significantly different ($P \leq 0.05$).

Results

Overall growth responses of saplings to light

The index of light availability we used is an excellent predictor of the rates of aboveground growth of saplings. As mentioned above, this index estimates the percentage of full open photosynthetic active radiation received between April 15 and August 15, the typical period for shoot and diameter growth for conifers growing on the east coast of Vancouver Island (Brix 1993). For western redcedar in dry, poor (03) sites and for Douglas-fir in all site series, variation in light explains over half the variation in both height and $\log_{10}$ radial growth rates ($r_a^2 = 0.52$–0.85; Tables 2 and 3). Generally, as whole season light availability increases, the rates of radial and height growth increase.
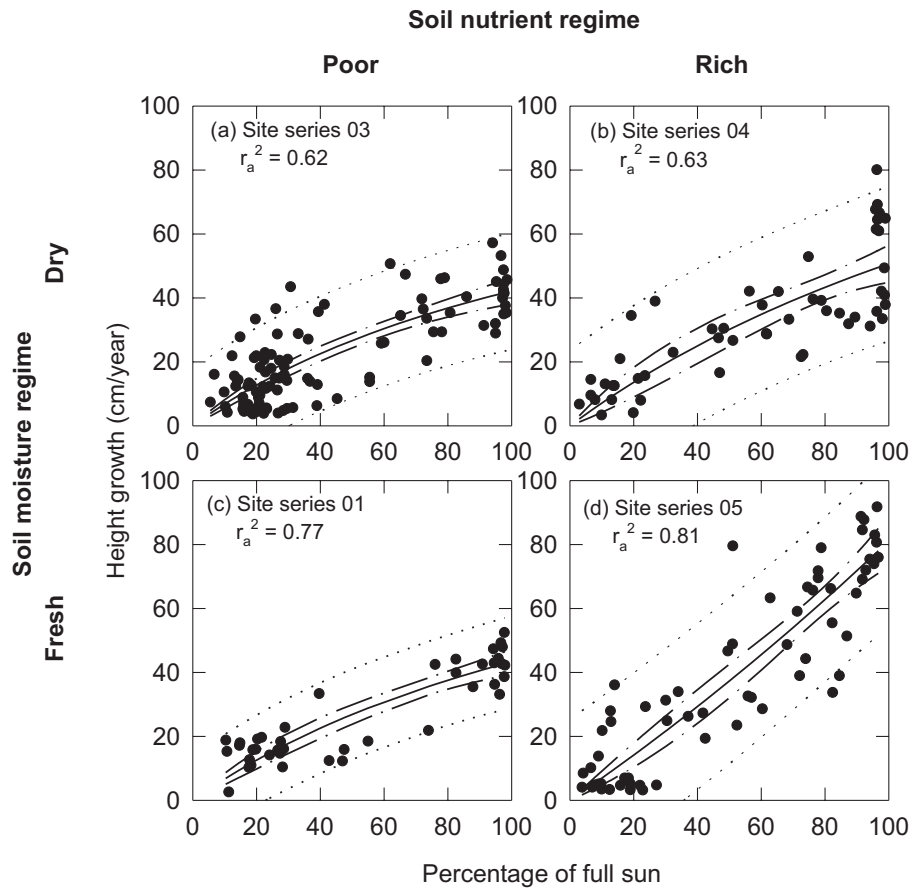
Height growth

Douglas-fir saplings show an almost linear increase in growth as a response to light with no clear plateau. Variation in light explains 62–81% of the variation in height growth for Douglas-fir saplings in the four site series examined (Fig. 1, Table 2). The percentage of variation of growth explained by the variation in light increases as sites improve in their soil nutrient and moisture regime, i.e., from dry, poor (03) to fresh, rich (05) sites (Fig. 1). Variation in light explains 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). The a parameter is higher for fresh, rich sites than for dry, poor sites. For Douglas-fir saplings in fresh, rich sites, a is so large that the growth response is nearly linear (Table 2).

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 among the 95% CI of the population means for the different

Fig. 1. Response of height growth to light for Douglas-fir saplings in sites of varying soil moisture and soil nutrient regimes. Two types of 95% CI are shown. Dotted lines are the 95% CI for the predicted values of growth of individual saplings at a given light level. Dot–dash lines 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.

site series over certain ranges of light levels (Fig. 2). For fresh, rich sites, the rates of height growth diverge from those of dry, poor sites and fresh, poor sites (01) at approximately 43 and 46% full sun, respectively. A similar divergence in the growth responses between dry, rich (04) sites and fresh, rich sites occurs at about 58% full sun. The range of light environments in which differences in the population means of the light-growth response are statistically significant is indicated by the region where the 95% CI of the population means no longer overlap. Although the growth response of height for Douglas-fir saplings growing on fresh, rich sites showed a statistically significant difference from the responses in dry, poor sites; dry, rich sites; and fresh, poor sites, we found no statistically significant difference among these latter three site series.

Western redcedar saplings show a response of height growth to light that is consistent with its designation as a shade-tolerant species. Between 0 and 20% full sun, height growth increases rapidly with light (Fig. 3). However, height growth reaches an asymptote near 30% full sun (Fig. 3). Variation in light accounts for 52% of the variation in height growth for redcedar saplings growing on dry, poor sites.

Substantial variation exists in the rate of height growth for individual saplings of both species at a given light level (Figs. 1 and 3). This variation is reflected in the 95% CI for

the predicted values of growth for individual saplings (as opposed to the 95% CI for population means) (Figs. 1 and 3). The 95% CI for the predicted values of individual Douglas-fir saplings overlap among all site series across the entire range of light (Fig. 1). Therefore, for individual Douglas-fir saplings, the variation in growth at a given light level overshadows any site series dependent effect on height growth. We could make no such inference for western redcedar, since we examined only one site series (03).
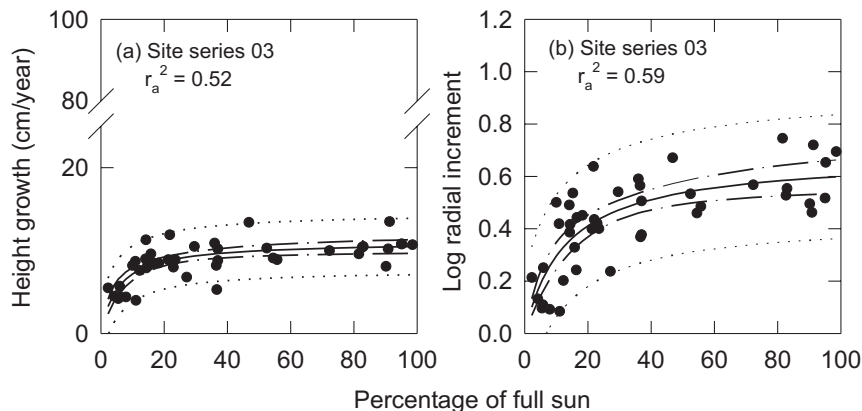
Radial growth

Radial growth for Douglas-fir saplings increases consistently as light increases and, as its height growth response, shows no clear plateau at a given light level. With one exception, the radial growth responses to light of Douglas-fir saplings do not differ significantly 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 sites; fresh, poor sites; and dry, rich sites (Fig. 4). The radial growth response in fresh, rich sites differs from that of other site series only at about 60% full sun. This is indicated by a region of nonoverlap of the 95% CI of the population mean with those of the other site series for light levels above 60% full sun (Fig. 2b).

Fig. 2. 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. Vertical dotted lines are 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).
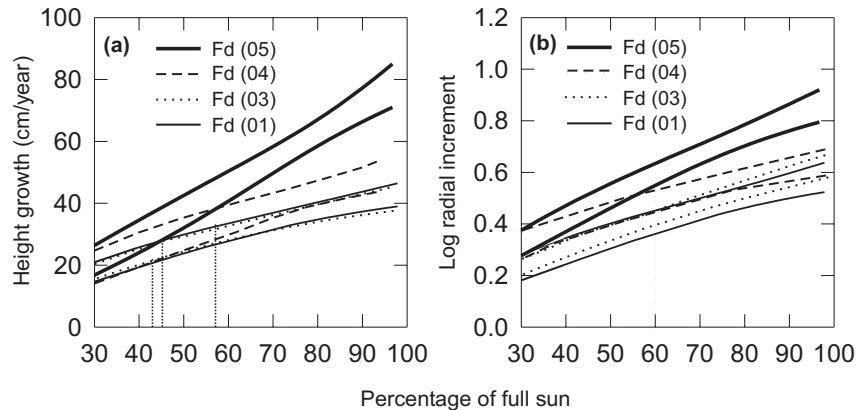
Fig. 3. Height and radial growth response to light for western redcedar saplings in dry, poor (03) sites. Two types of 95% CI are shown. Dotted lines are the 95% CI for the predicted values of growth of individual saplings at a given light level. Dot–dash lines are 95% CI for the predicted values of the population mean of growth at a given light level. See Table 1 for sample sizes and Tables 2 and 3 for regression equations and parameter estimates.

The radial growth response of western redcedar shows a plateau at low light levels similar to that observed for height growth. The radial growth rate increases rapidly as light increases from 0 to about 30% full sun (Fig. 3*b*). Above 30% full sun, the radial growth rate increases little with increasing light (Fig. 3*b*). Variation in light explains 59% of the variation in $\log_{10}$ radial growth (Table 3).

Interspecific comparisons of growth response to light

Douglas-fir saplings differ strikingly from western redcedar in their light-dependent growth responses. Redcedar saplings have higher rates of height growth than Douglas-fir at light levels 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 for all of the site series in which we examined Douglas-fir (Table 2). This means redcedar growing on dry, poor sites has 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 than Douglas-fir at light levels >30%. The regression of height growth and light for western redcedar has a lower and

statistically significantly different asymptote at high light (the *a* parameter) than Douglas-fir growing on dry, poor sites (Table 2).

Radial growth is also greater in low light for western redcedar than for Douglas-fir, as indicated by the *s* parameter (Table 3). This is consistent with the classification of redcedar as shade tolerant, as species that allocate more biomass to lateral growth have a greater advantage to capture light in light-limited environments (Oliver and Larson 1990, pp. 41–88; Klinka et al. 1992; Chen et al. 1996). However, the rate of radial growth in high light is similar for both species. The *a* parameter was not significantly different between the study species. 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.

Discussion

Light-growth responses of Douglas-fir and western redcedar

For Douglas-fir saplings growing below approximately 43% full sun, light is the primary factor affecting height

Fig. 4. Radial growth response to light for Douglas-fir saplings in sites of varying soil moisture and soil nutrient regimes. Two types of 95% CI are shown. Dotted lines are the 95% CI for the predicted values of growth of individual saplings at a given light level. Dot–dash lines 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.
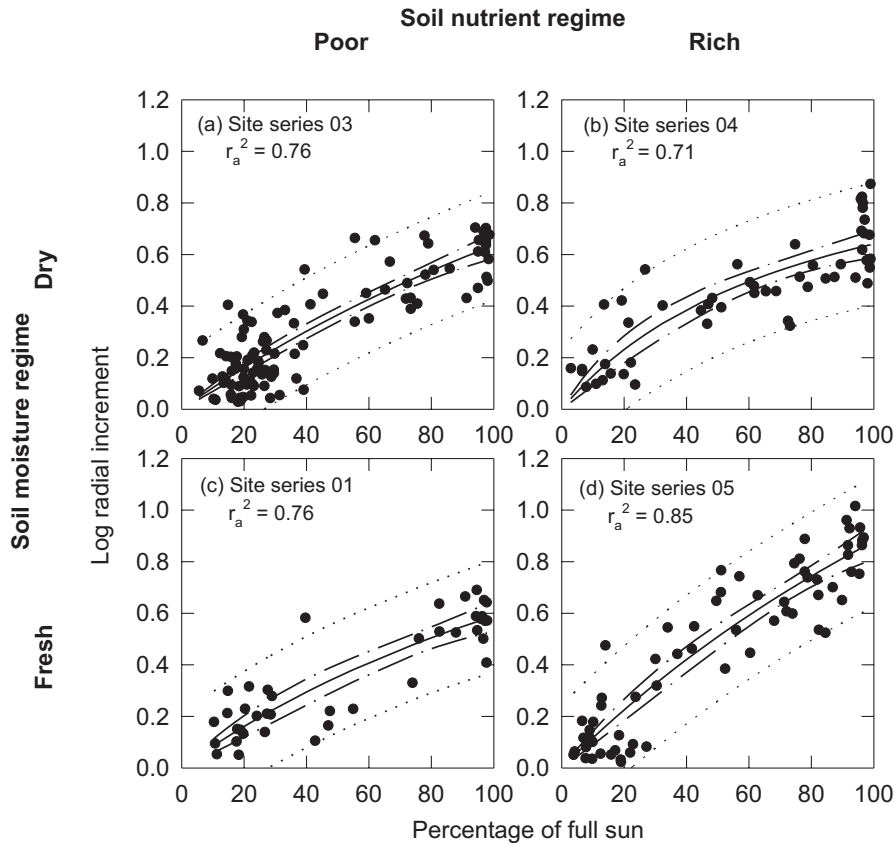
growth. We detected no significant differences in the response of height growth among the different site series below approximately 43% full sun. At light levels above 43% full sun, the 95% CI of the population means of Douglas-fir saplings growing in fresh, rich sites diverge from all site series examined (Fig. 2). This suggests that at light levels lower than approximately 43% full sun, light is the primary determinant of growth rate and soil moisture and nutrient regime are secondary. Above approximately 43% full sun, variation in height growth increases among different sites at similar light levels, leading to differences in height growth for Douglas-fir saplings among sites of different regimes of soil moisture and nutrients (Fig. 2). 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).

Above approximately 43% full sun, Douglas-fir saplings may have the resources to optimize crown architecture, leaf morphology, and other aspects of their ecophysiology to better utilize available soil resources (Meziane and Shipley 1999; Chen et al. 1996; Mailly and Kimmins 1997). Such optimization is apparent within Douglas-fir canopies, where net rate of CO_2 assimilation at the light saturation point increases with ambient light (Bond et al. 1999). Below the

light level where the light-growth response curves diverge, saplings may be preferentially allocating carbohydrate resources to belowground growth to allow survival and growth during times of nutrient or moisture stress (Kobe 1997; Canham et al. 1999).

The responses of aboveground growth to light we observed for Douglas-fir showed no clear plateau of growth at high light. Rather, the growth of Douglas-fir saplings increased steadily with increasing light, especially in fresh, rich sites, where a nearly linear response was apparent. This is inconsistent with studies of leaf-level photosynthesis, which indicate that Douglas-fir and other conifers reach a light saturation point between 30 and 40% full sun (Horn 1971; Leverenz 1981; Lavender 1990). This inconsistency highlights the caution necessary when making inferences from leaf-level studies to tree- and stand-level phenomena, such as shade tolerance (Coates and Burton 1999; Kobe and Coates 1997).

The role of soil moisture and nutrient regime

We 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 (Tables 2 and 3). Furthermore, the height and radial growth response to light of Douglas-fir did not change

with increasing soil moisture (Figs. 1 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 that shade tolerance of Douglas-fir decreases with soil moisture (Carter and Klinka 1992). The contrary conclusions regarding the relationship between shade tolerance and soil moisture may be the result of differences in the definition of shade tolerance, in study methods, and in the range of soil moisture analyzed (Carter and Klinka 1992). Alternatively, the divergence in shade tolerance may be a result of ecophysiological and morphological differences between the populations sampled in these studies, which in turn arise from climatic influences on sapling growth and development that determine the capacity of saplings to grow at low light (Wright et al. 1998). Therefore, intraspecific variation in shade tolerance of coastal Douglas-fir may develop not from microsite-scale factors but rather as a response to larger scale, regional factors, such as climate. Such variation in shade tolerance is well recognized between the coastal and interior varieties of Douglas-fir (Pojar and Mackinnon 1994; Lester et al. 1990).

Radial growth response to light of Douglas-fir saplings is not as responsive as height growth to differences in site quality. Statistically significant differences among site series occurred only above 60% full sun, where the growth response on fresh, rich sites differed from the response on other site series (Fig. 2). 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 to reach the forest canopy more quickly (Tilman 1988, pp. 98–135; Chen 1997; Chen and Klinka 1998).

Interspecific differences in growth response

The interspecific differences we detected in growth response are comparable with 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, which rank western redcedar as more shade tolerant than Douglas-fir. Shade-tolerant species typically grow faster at low levels of light, and shade-intolerant species typically grow faster at high light levels (Kobe and Coates 1997; Mailly and Kimmins 1997). This was the pattern we observed for height growth and radial growth at low light for Douglas-fir and western redcedar. These results indicate 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; Messier et al. 1999).

Variation in growth 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; St. Clair and Snieko 1999), mycorrhizal associations (Simard et al. 1997), previous periods of suppression (Wright et al. 2000), 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. Our data on sapling growth are likely influenced by all these factors. It is important for managers to bear this variation in mind when setting regeneration objectives and predicting growth and yield for partial-cutting treatments, even if the harvesting treatment creates a stand of evenly dispersed homogenous light environments (e.g., regular shelterwood or clearcut), especially if advance regeneration is incorporated into the stocking target. It is possible to mitigate some of this variation by appropriate stocking practices (Lester et al. 1990), as planted stock shows considerably less variation in growth response to light than trees of natural origin (Coates and Burton 1999).

Implications for forest management

Our data suggest multiple silvicultural opportunities are possible that allow vigorous regeneration of Douglas-fir in nonclearcut environments, particularly for partial-cutting treatments that provide substantial area with light environments brighter than 40% full sun. For example, Douglas-fir saplings show mean leader increments of 45 cm/year under 60% full sun on fresh, rich sites, as compared with 80 cm/year in full sun on similar sites (Fig. 3). Such growth rates should be encouraging for forest managers seeking to efficiently regenerate an area following timber harvesting while addressing other ecological objectives for the stand, e.g., retention of large live trees and snags. Light environments greater than 40% full sun can be created by various partial-cutting treatments, including commercial thinning, regular shelterwood, and green tree retention (Drever 1999). Moreover, retained forest structure in partial-cutting treatments can reach up to 350 stems/ha or 200 m^3/ha while still allowing light environments in excess of 40% full sun (Drever 1999).

Alternatively, silvicultural treatments that create light environments lower than approximately 40% full sun will result in a substantial reduction in potential growth rates for Douglas-fir, especially in fresh, rich sites. Our data indicate that a range in light level exists, between 40 and 45% full sun, beyond which regenerating Douglas-fir growth reflects primarily differences in site quality. Given that Douglas-fir regeneration requires at least 40% full sun to ensure survival and the development of morphological adjustments that increase its photosynthetic capacity (Mailly and Kimmins 1997), regeneration harvests for Douglas-fir should create light environments brighter than this.

The shade tolerance of western redcedar allows a wide range of silvicultural options that result in growth rates similar to those expected in clearcuts. Western redcedar approaches its maximum growth rate at approximately 30% full sun (Fig. 3). Therefore, partial-cutting treatments that create relatively low-light environments may be considered without compromising growth rates of regenerating redcedar. Even the light environment created by an individual tree selection treatment (median light environment of less than 10% full sun) may be associated with growth rates of regenerating redcedar that approximate 50% of the growth rates expected in clearcuts (Drever 1999). This shade tolerance allows great flexibility for forest managers in choosing the amount and distribution of retained structure

necessary to meet the complicated and varied management objectives characteristic of modern forestry.

While we have discussed these results primarily in terms of the potential growth expected from the average light conditions in a treatment, it is clear that the light environments provided by partial-cutting treatments are variable. This is especially true for the irregular patterns of retained forest provided by variable-retention treatments (Franklin et al. 1997; Drever 1999). Where shade-intolerant species, such as Douglas-fir are desired, we recommend that managers focus on such aggregated spatial distributions of retained forest, rather than more traditional regular patterns (e.g., regular shelterwoods), because they are more likely to provide high light levels for a given level of retention. The distribution of light environments created by a given treatment should be the key focus of managers wishing to understand silvicultural options for regeneration in partial-cutting treatments.

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