

# Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar–hemlock forests of British Columbia

K. Dave Coates and Philip J. Burton

**Abstract:** Insights into field-planted conifer seedling growth were gained by fitting height and diameter growth to relative irradiance over the growing season using Michaelis–Menten functions. There was little difference among tree species (*Abies lasiocarpa* (Hook.) Nutt., *Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carr., *Pinus contorta* Dougl. ex Loud., *Thuja plicata* Donn ex D. Don, *Tsuga heterophylla* (Raf.) Sarg.) in response to ambient light. No significant differences in whole-plant compensation points were observed among species but the ranking of species' compensation points was consistent with their shade-tolerance ranking. Five years after planting, total size and recent growth rates varied little among species from low to high light, implying an absence of trade-offs in low- and high-light growth strategies. *Thuja plicata* had the greatest response to increased light under deep shade (<20% relative irradiance). All species increased growth above 40% relative irradiance, with no clear whole-plant light saturation point evident under field conditions. Growth rates at high light were broadly overlapping and varied considerably within species. As expected, *Pinus contorta* growth exceeded that of other species above 70% relative irradiance, but it also exhibited high growth rates at low light. Greatest variability among species was at intermediate light levels (30–70% relative irradiance) where careful matching of tree species to light environment can maximize growth rates.

**Résumé :** La croissance des semis de conifères plantés au champ a été mieux comprise en mettant en relation l'accroissement en hauteur et en diamètre avec l'irradiation relative durant la saison de croissance à l'aide des fonctions de Michaelis–Menten. Il y avait peu de différence quant à la réponse à la lumière ambiante entre les espèces arborescentes suivantes : *Abies lasiocarpa* (Hook.) Nutt., *Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carr., *Pinus contorta* Dougl. ex Loud., *Thuja plicata* Donn ex D. Don, et *Tsuga heterophylla* (Raf.) Sarg. On n'a pas observé, non plus, de différences significatives dans les points de compensation du plant entier entre les espèces. Cependant, l'ordination des points de compensation était en accord avec l'ordination de leur tolérance à l'ombre. Cinq ans après la plantation, la dimension totale et les taux d'accroissement récent variaient peu entre les espèces de la lumière faible à la lumière forte, ce qui impliquait qu'il n'y avait pas de substitution entre les stratégies de croissance à la lumière faible et à la lumière forte. Le *Thuja plicata* a eu la plus forte réponse à l'accroissement de la lumière, dans un milieu fortement ombragé (< 20% d'irradiation relative). Au champ, toutes les espèces ont augmenté leur croissance au-dessus de 40% d'irradiation relative, sans qu'on observe de points précis de saturation à la lumière pour le plant entier. Les taux d'accroissement, à la lumière forte, se chevauchaient largement et variaient considérablement au niveau de l'espèce. Tel qu'attendu, l'accroissement du *Pinus contorta* dépassait celui des autres espèces au-dessus de 70% d'irradiation relative; mais il montrait aussi des taux d'accroissement élevés à la lumière faible. La plus grande variabilité entre les espèces existait aux niveaux intermédiaires de lumière (30–70% d'irradiation relative) où un appariement attentif des espèces arborescentes avec l'environnement lumineux peut maximiser les taux d'accroissement.

[Traduit par la Rédaction]

## Introduction

Predicting the effects of management on long-term forest dynamics involves a complex suite of factors, especially when partial cutting systems are employed that retain variable levels of canopy trees in time and space. Light is arguably the most important factor influencing tree growth in

tropical, temperate, and boreal forest biomes (Denslow and Hartshorn 1994; Pacala et al. 1996; Lieffers et al. 1999) and is certainly the factor most directly manipulated by forest-management actions. Therefore, understanding the response of individual seedlings and saplings to variation in light is fundamental to predicting the effects of partial cutting on future forest composition and growth (Marks 1975; Shugart 1984; Carter and Klinka 1992).

Ecophysiological studies of leaf-level responses have shown that individual tree species have characteristic photosynthetic responses to variation in incident light (e.g., Grossnickle and Arnott 1992; Sipe and Bazzaz 1994; Burton and Bazzaz 1995; Mitchell and Arnott 1995; Barker et al. 1997). Under field conditions, these differences in leaf-level responses are not necessarily reflected in whole-plant

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aboveground growth rates. Part of the explanation for this discrepancy is tree age and crown architecture (leaf density and age, within-crown differences in leaf structure and orientation, and self-shading within the crown). Tree age and crown architecture critically influence how effectively light energy is absorbed by the whole plant (e.g., Field 1983, 1988; Givnish 1988). Soil resources (water and nutrients) also interact with ambient light levels to affect whole tree carbon balance (Klinka et al. 1992; Walters et al. 1993; Canham et al. 1996; Chen et al. 1996; Walters and Reich 1997). With growing public demands for silvicultural alternatives to clear-cutting, it is important for forest scientists to understand the whole-plant response of young trees to a wide range of light levels when growing under field conditions.

For British Columbia (B.C.) tree species, available field data on aboveground whole-plant growth rates in response to ambient light levels are derived mostly from retrospective studies of natural-origin trees. The studies, which generally utilized either clearcut edges or prior natural disturbances to provide a range of light levels, had little control over location, tree age, or growth history (Carter and Klinka 1992; Klinka et al. 1992; Chen et al. 1996; Kayahara et al. 1996; Wright et al. 1998a). Use of planted seedlings can help minimize the confounding effects of site, age, and crown architecture when determining growth responses to light environment in the field (Wang et al. 1994; Chen 1997, 1998).

The Date Creek study, a large silvicultural systems experiment in northwestern B.C. (Coates et al. 1997), has created ideal conditions for determining seedling growth responses to a wide range of ambient light levels after forest canopy manipulation. At Date Creek, the distribution of light environments changes dramatically from small single-tree openings to openings of 110–120 m diameter (0.8–1.1 ha), after which the distribution of light environments within openings is more uniformly high (Coates and Burton 1997). The maximum diversity of ambient light conditions is found in gaps of 0.05–0.4 ha (Coates and Burton 1997). An understanding of how tree species differ in their growth responses to the diverse light environments created after partial cutting is essential for prescribing species composition and predicting growth and yield in forests where alternatives to clear-cutting are being practiced.

This study was designed to characterize variation in height and radial growth in response to ambient light levels for the five most commonly planted tree species in northwestern B.C.: lodgepole pine (*Pinus contorta* var *latifolia* Dougl. ex Loud.), hybrid spruce (*Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). This research addresses four questions. (i) How do both the magnitude of seedling response to light, and the shapes of the light-response curves (i.e., the functional forms of light response), vary among the individual tree species under field conditions? (ii) Are there trade-offs among tree species in aboveground growth at low versus high light? (iii) Is ambient light level a good predictor of whole-tree growth in the field? (iv) Which species are best suited to different gap sizes or gap positions based on their light response characteristics?

## Methods

The research was a component of the Date Creek silvicultural systems study (Coates et al. 1997), located near Hazelton, B.C., Canada (55°22'N, 127°50'W; 370–665 m elevation). The study area lies within the moist cold subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmc) (Pojar et al. 1987; Banner et al. 1993), a transitional area between the coastal and interior forests of northwestern B.C.

Mature forests in the study area originated from a fire in 1855. They are dominated by western hemlock but are intimately mixed with western redcedar, subalpine fir, lodgepole pine, hybrid spruce, paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray). Subalpine fir is commonly replaced by amabilis fir (*Abies amabilis* Dougl. ex Forbes) at higher elevations. Detailed descriptions of these ICH forests can be found in Banner et al. (1993).

The replicated treatments applied in the Date Creek silvicultural systems study created a range of overstory canopy structure that included undisturbed forest, two levels of partial cutting, and clearcut forests (Coates et al. 1997). In the light partial-cutting treatment, approximately 30% of the stand volume was removed by cutting either single stems or small groups (3–10 trees). In the heavy partial-cutting treatment, approximately 60% of stand volume was removed via large gaps (0.1–0.5 ha in size) evenly distributed across the treatment units and either single tree or small gaps in the forest matrix between the large gaps.

Within this experimental framework, seedlings of five species (western redcedar, western hemlock, subalpine fir, hybrid spruce, and lodgepole pine) were planted in early May 1993. All planting stock was PSB 1+0 415 (1-year-old container stock, the root plug measuring 4 cm across and 15 cm long) except for subalpine fir seedlings which were PSB 1+0 313 (with 3 × 13 cm root plugs). Stock was grown in peat- and perlite-filled styroblocks in greenhouses and open compounds at Kalamalka Nursery in the summer of 1992 and stored at –5°C over winter. Initial sizes (height and basal diameter) were very consistent within each species; however, subalpine fir were shorter and redcedar taller than the other three species (Table 1).

Seedlings were planted in the understory of each of the four undisturbed forest treatment units, into 110 canopy gaps ranging in size from 20 to 5000 m<sup>2</sup> distributed within the partially cut treatment units, and in each of the four clearcut treatment units. In clearcuts, seedlings were planted at least three tree heights (~90 m) from the forest edge. In canopy gaps, seedlings were planted in five single-species rows oriented north–south; planting rows were spaced 2 m apart and trees within lines were spaced 1.5 m apart. In larger gaps, east–west planting lines for each species were also established. Tree species were randomly assigned to planting lines. Where conditions allowed, up to 10 seedlings were planted in each cardinal direction from the edge of the gap into the understory of the forest matrix.

To determine tree seedling growth responses to light environment, planted sample trees were selected in the undisturbed forest, within the partially cut forest matrix adjacent to gaps, in small to large gaps (and at different positions within those gaps) and in the full open (clearcuts). Approximately 75–95 planted seedlings per species were selected (Table 1). At each sampling location (e.g., south end of a large gap), sample seedlings of each of the five species were selected (in most cases). At each location, the best growing individual was selected if there was a choice among seedlings of the same species. Thus, the growth data represent the best performance that can be expected at any given light level.

Seedling growth is a function of light environment and soil resources (Latham 1992; Canham et al. 1996; Walters and Reich 1996). To minimize the effect of soil resource variability, all sample

**Table 1.** Provenance descriptions of planted seedlings, seedling size at outplanting, and seedling sample sizes by general canopy conditions that formed the light gradient from closed canopies to full sunlight.

	Western redcedar	Western hemlock	Subalpine fir	Hybrid spruce	Lodgepole pine
<b>Provenance description</b>					
Seedlot No.	35033	03437	35005	14577	27792
Subzone	ICHmc	ICHmc	ICHvc	ICHmc	ICHmc
Location	Date Creek	Suskwa River	Bell II	Calvin Creek	Kitseguetla River
Latitude (N)	55°27'	55°17'	56°45'	55°30'	55°06'
Longitude (W)	127°50'	127°17'	129°50'	128°45'	127°50'
Elevation (m)	370	500	700	610	650
<b>Characteristics at planting<sup>a</sup></b>					
Height (cm)	41.2±0.8	24.5±0.8	13.4±0.4	27.4±0.6	21.8±0.8
Diameter (mm)	3.3±0.1	3.3±0.1	3.9±0.1	3.7±0.1	4.2±0.1
<b>Sample size</b>					
Under closed canopies	28	20	8	22	12
In gaps <300 m <sup>2</sup>	24	17	32	30	28
In gaps 301–1500 m <sup>2</sup>	18	19	11	15	19
In gaps 1501–5000 m <sup>2</sup>	12	11	11	13	12
In full open conditions	12	12	12	12	12
Total	94	79	74	92	83

<sup>a</sup>Forty-five trees randomly selected per species prior to outplanting. All seedlings were planted in spring 1993. Values are mean ± SE.

locations were on mesic, hemlock – step moss ecosystems (ICHmc2, site series 01; see Banner et al. 1993). Soils on mesic sites are typically Eluviated or Orthic Dystric Brunisols (Agriculture Canada Expert Committee on Soil Survey 1987) that have developed on morainal parent materials, ranging in texture from loamy sand to clay loam (Coates et al. 1997). They exhibit no pronounced limitations to plant growth.

One hemispherical photograph was taken of the canopy directly above each planted sample tree to quantify the light environment experienced by that seedling. Photographs were taken in late summer 1996 at the end of the fourth growing season. All photographs were taken with a tripod-mounted Nikon camera equipped with a Nikkor 8-mm true fisheye lens and Fujichrome Sensia 400 ASA colour slide film. The camera was levelled and was equipped with coloured light emitting diodes mounted within the frame of the circular image to orient the image on an east–west axis. The processed slides were scanned in colour with a Polaroid Sprintsan 35 slide scanner. The digitized images were then analyzed using GLI/C software following Canham (1988) to derive an index of growing season light availability. The index, in units of percent full sunlight for a predefined growing season (from April 15 to September 15) and latitude (55.37°N), is calculated by combining the relative contribution of diffuse and direct radiation at a given microsite. All planted sample trees were free of overtopping shrubs or herbs and had no evidence of nearby windthrow that might have recently affected light levels. Because the camera lens was always oriented perfectly vertically, any slight topographic shading or exposure was treated by the GLI/C model in a manner that increased or decreased beam irradiance accordingly.

Seedlings selected for this study were measured for height increment and total height at the end of the first growing season, and basal diameter and total height at the end of the second, third, fourth, and fifth growing seasons. Canopy crown filling into openings is very slow in these forests (D. Coates, personal observation) and was not thought to have significantly altered light levels over the 5 years.

### Data analysis

Nonlinear regression was used to model growth as a function of light environment for each of the five tree species. Four growth re-

sponse variables were selected: fifth-year height, fifth-year basal diameter, and mean annual height and radial increments over years 3, 4, and 5. Our analysis used absolute size and growth rates for each tree species rather than fifth-year size relative to initial planting size or relative growth rates. Initial height and basal diameter within species was very uniform, and our data exhibited no size-dependent relationships. Transformations of the data were not required to stabilize variances. Residuals for all growth variables were well balanced.

We selected the Michaelis–Menten function to model the growth variables. This equation has been used in previous studies examining growth responses of tree seedlings and saplings to light environment (Pacala et al. 1996; Wright et al. 1998a; Kobe 1999). The Michaelis–Menten equation provided consistently reliable fits for the four growth variables, its parameters are easily interpreted, and the parameter values allow statistical testing of interspecific differences in growth response at high and low light. We used two forms of the Michaelis–Menten equation:

$$[1] \quad Y = \{(aL)/[(a/s) + L]\} + \epsilon$$

$$[2] \quad Y = \{[a(L - c)]/[(a/s) + (L - c)]\} + \epsilon$$

where  $Y$  is a measured growth variable,  $a$  and  $s$  are the estimated parameter values,  $L$  is the percentage of full sunlight determined from the hemispherical photograph for each seedling, and the error term,  $\epsilon$ , is assumed to be normally distributed. The parameter value  $a$  is the asymptote of the growth function at high light. The parameter can be considered a measure of the amplitude of potential growth at high light. Species with high  $a$  values are generally shade-intolerant species that perform well in open conditions. The  $s$  parameter is a measure of the slope of the relationship at low light levels. Shade-tolerant species are generally thought to have high  $s$  values compared with shade-intolerant species. The trade-off between asymptotic growth at high light versus the slope of the growth response at low light can be thought of a measure of a tree species shade tolerance (see Wright et al. 1998a). Equation 2 allows for tests of nonzero intercepts, where  $a$  and  $s$  are as previously described and  $c$  is the light level at which measured growth equals zero. This whole-plant aboveground growth light compensation

**Table 2.** Parameter estimates for fifth-year height (cm) and diameter (mm) using the equation  $Y = (aL)/[(a/s) + L]$  where  $L$  is the growing season percent full sunlight estimated from hemispherical photographs above each sample seedling.

	<i>a</i> parameter			<i>s</i> parameter			$R^2$	<i>N</i>
	Estimate	SE	95% CL	Estimate	SE	95% CL		
<b>Fifth-year height</b>								
Western redcedar	198.5	12.1	24.0	11.92	1.62	3.21	0.60	93
Western hemlock	260.6	23.3	46.3	7.56	1.04	2.07	0.68	77
Subalpine fir	125.7	16.0	31.9	2.77	0.44	0.87	0.55	72
Hybrid spruce	279.0	28.6	56.9	4.39	0.42	0.83	0.76	91
Lodgepole pine	506.8	71.1	141.5	4.55	0.37	0.73	0.81	80
<b>Fifth-year diameter</b>								
Western redcedar	50.4	6.3	12.5	0.89	0.11	0.22	0.69	93
Western hemlock	80.6	20.2	40.3	0.65	0.09	0.18	0.70	77
Subalpine fir	30.9	3.6	7.1	0.60	0.08	0.16	0.64	72
Hybrid spruce	107.3	20.0	39.7	0.57	0.04	0.08	0.89	90
Lodgepole pine	930.8	1390.9	2769.7	0.57	0.04	0.08	0.88	79

**Note:** The  $P$  values of all regression models were  $<0.0005$ .  $a$  and  $s$ , parameters of model; 95% CL, 95% confidence limits; SE, standard error of estimated parameter values.

**Table 3.** Parameter estimates for (A) height (cm) and (B) diameter (mm) growth rates (average growth increment per year in years 3, 4, and 5 after outplanting) using the equation  $Y = a(L - c)/[(a/s) + (L - c)]$ , where  $L$  is the growing season percent full sunlight estimated from hemispherical photographs above each sample seedling.

(A) Average height increment (cm).											
	<i>a</i> parameter			<i>s</i> parameter			<i>c</i> parameter			$R^2$	<i>N</i>
	Estimate	SE	95% CL	Estimate	SE	95% CL	Estimate	SE	95% CL		
Western redcedar	39.9	5.4	10.8	1.48	0.39	0.78	4.9	1.75	3.47	0.57	93
Western hemlock	64.7	10.0	10.0	1.56	0.37	0.74	6.5	2.09	4.16	0.68	76
Subalpine fir	27.8	5.8	11.6	0.69	0.23	0.47	10.7	2.94	5.86	0.57	72
Hybrid spruce	111.8	38.1	75.7	0.70	0.12	0.24	7.4	2.06	4.09	0.82	91
Lodgepole pine	132.8	34.8	69.4	1.16	0.21	0.43	8.8	2.53	5.04	0.82	79
(B) Average diameter increment (mm).											
	<i>a</i> parameter			<i>s</i> parameter			<i>c</i> parameter			$R^2$	<i>N</i>
	Estimate	SE	95% CL	Estimate	SE	95% CL	Estimate	SE	95% CL		
Western redcedar	14.2	4.2	8.4	0.162	0.04	0.08	3.2	3.16	6.27	0.63	93
Western hemlock	38.0	30.6	61.1	0.136	0.04	0.07	5.1	4.17	8.31	0.72	75
Subalpine fir	6.2	1.7	3.5	0.118	0.05	0.09	8.7	4.27	8.51	0.53	72
Hybrid spruce	35.0	17.6	35.0	0.124	0.02	4.11	6.6	2.07	4.11	0.87	90
Lodgepole pine	49.9	24.1	48.0	0.200	0.03	0.06	13.2	2.03	4.04	0.85	79

**Note:** The  $P$  values of all regression models were  $<0.0005$ .  $a$ ,  $s$ , and  $c$ , parameters of model; 95% CL, 95% confidence limits; SE, 1 standard error of estimated parameter values.

point is analogous to the leaf-level compensation point and could be more simply called a "field compensation point." We used eq. 1, which is forced through the origin, to develop functions for fifth-year height and basal diameter. Functions for recent growth rates (average height and radial growth increments in years 3, 4, and 5) were tested with eqs. 1 and 2.

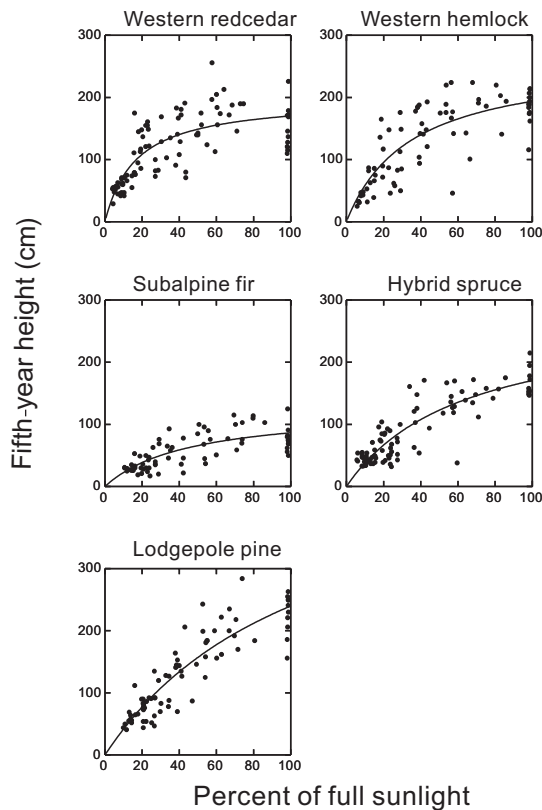
Model parameters ( $a$ ,  $s$ ,  $c$ ) were estimated for each species using the NONLIN procedure in SYSTAT version 6.0 with the simplex estimation method to minimize the loss function (SYSTAT, Inc. 1996). The 95% confidence limits for derived values of  $a$  and  $s$  were used as a basis for conservative pairwise comparisons among species at high and low light, respectively. We also used the 95% confidence limits to test for nonzero growth intercepts (the  $c$  parameter) for each species and to make pairwise comparisons between species to test for differences in field compensation points.

If the 95% confidence limits for two species did not overlap then the parameter estimates were deemed significantly different.

## Results

Ambient light levels proved to be a good predictor of tree size and growth rates under field conditions. Goodness-of-fit ( $R^2$ ) of the eq. 1 regression functions for fifth-year height and basal diameter of seedlings in the field ranged from 0.55 to 0.89 (Table 2). Equation 2 provided better functions for height and radial increments averaged over years 3, 4, and 5 than eq. 1. There was evidence among the tree species of nonzero intercepts for whole-plant aboveground growth rates ( $c$  parameter). The 95% confidence limits for growth

**Fig. 1.** Observed values and fitted regression lines of seedling height 5 years after planting versus percent of full sunlight for the tree species using eq. 1 and parameter values in Table 2.

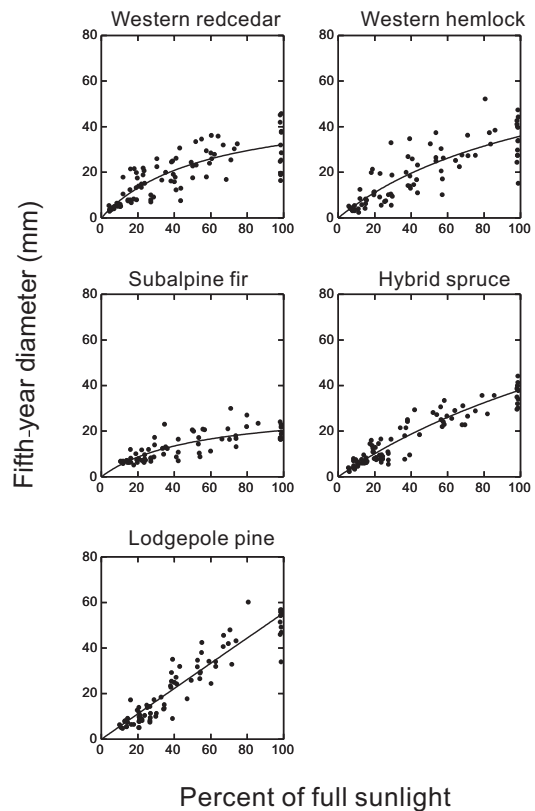


rates overlapped with zero in only two cases, for western redcedar and western hemlock diameter growth (Table 3). In all other cases, the whole-plant aboveground growth light compensation points were significantly greater than zero. The goodness-of-fit for eq. 2 regression functions were also good for field data ( $R^2 = 0.53\text{--}0.87$ ; Table 3).

The whole-plant aboveground growth light compensation points, or field compensation points (parameter  $c$  in Table 3), were consistent with the shade-tolerance ranking of the tree species. Western redcedar and western hemlock, the most shade tolerant of the five species (Krajina 1969; Krajina et al. 1982; Kobe and Coates 1997), had no detectable field compensation point; that is, their  $c$  parameter values were not significantly different from zero. Field compensation points of the three less shade-tolerant species were significantly greater than zero. Pairwise comparisons of field compensation points among all species revealed no significant differences for either height or diameter growth suggesting that, under field conditions, there is no meaningful variation in the light level at which growth ceases among the species.

Subalpine fir seedlings were not planted in the undisturbed forest understory because of stock shortages. The field compensation point estimates for subalpine fir were derived from data that did not include trees planted under completely closed canopies. However, extra care was taken to sample subalpine fir in the understory off the shady south end of gaps to obtain data at low light levels. Although we do not think it to be the case, the absence of subalpine fir

**Fig. 2.** Observed values and fitted regression lines of seedling diameter 5 years after planting versus percent of full sunlight for the tree species using eq. 1 and parameter values in Table 2.

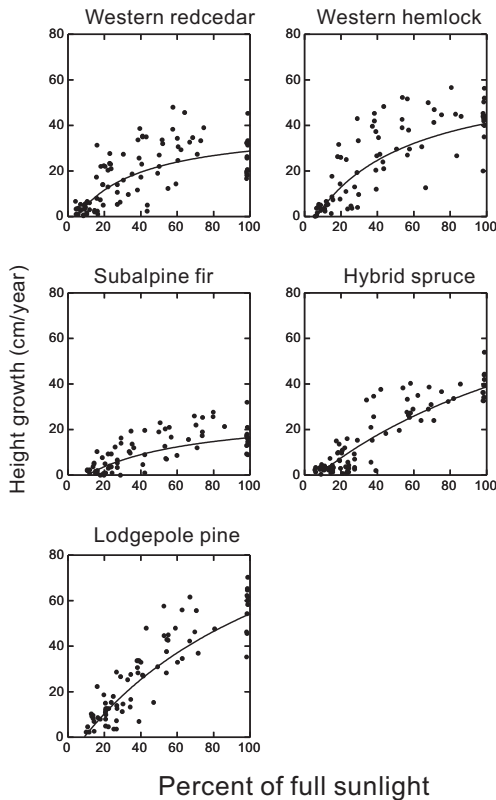


measurements at very low light levels may have artificially increased the  $c$  parameter estimates for this species.

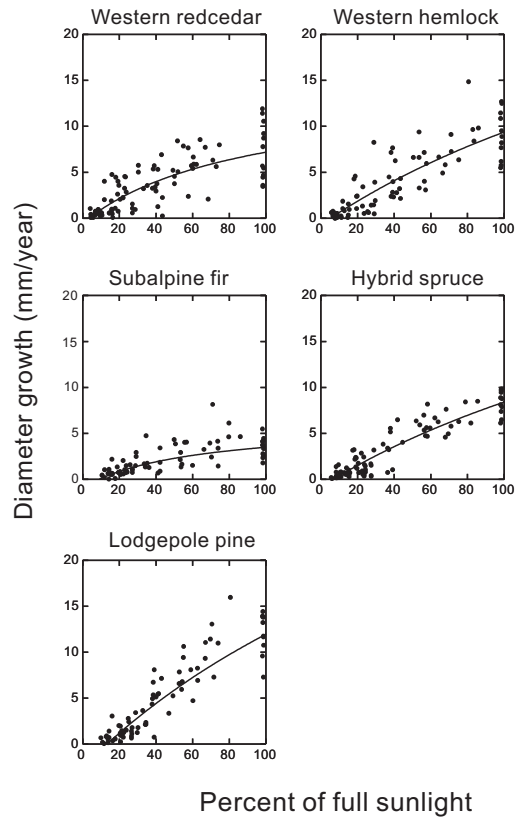
The shape of each species' light response curve (Figs. 1–4) was generally consistent with expectations based on physiological studies and the shade tolerance ranking of the species, with a few notable exceptions. First, total size and growth rates of all species in the field increased with increasing irradiance to full sunlight, unlike expectations from leaf-level physiological studies that suggest saturation points well below full sunlight. Hence, no clear growth “field saturation points” were observed for the study species. Second, there were no clear trade-offs in low versus high light growth among the species as might be expected based on shade-tolerance rankings. The slope of the relationship as light levels increase above 0% full sunlight ( $s$  parameter value) did not correlate well with traditional shade tolerance rankings. The most shade-tolerant species (western redcedar and western hemlock) did have the greatest increase in height growth at low light; however, lodgepole pine, the most shade intolerant of the species (Krajina 1969; Kobe and Coates 1997), was next in rank order (Table 3). At low light, lodgepole pine had the greatest increase in diameter growth of all five species. The 95% pairwise comparisons at low light indicated no significant differences between any of the species pairs (Table 3). At high light, lodgepole pine outgrew all other species, as expected based on shade tolerance (Table 3, Fig. 5).

Subalpine fir performed the poorest of the five species across the light gradient. This result may reflect poor planting

**Fig. 3.** Observed values and fitted regression lines of height growth rates (cm, average increment per year for years 3, 4, and 5 after outplanting) versus percentage of full sunlight for the five tree species using eq. 2 and parameter values in Table 3.



**Fig. 4.** Observed values and fitted regression lines of diameter growth rates (mm, average increment per year for years 3, 4, and 5 after outplanting) versus percentage of full sunlight for the five tree species using eq. 2 and parameter values in Table 3.



stock quality rather than an inherent characteristic of the species. At planting, subalpine fir was the smallest of the five species (Table 1). This species has a history of poor outplanting performance. After planting, terminal buds often do not flush, resulting in poor apical dominance for the first few years (Pinkerton 1994), a phenomenon observed in this experiment. Many of the stock problems with subalpine fir have recently been resolved (G. Pinkerton, personal communication).

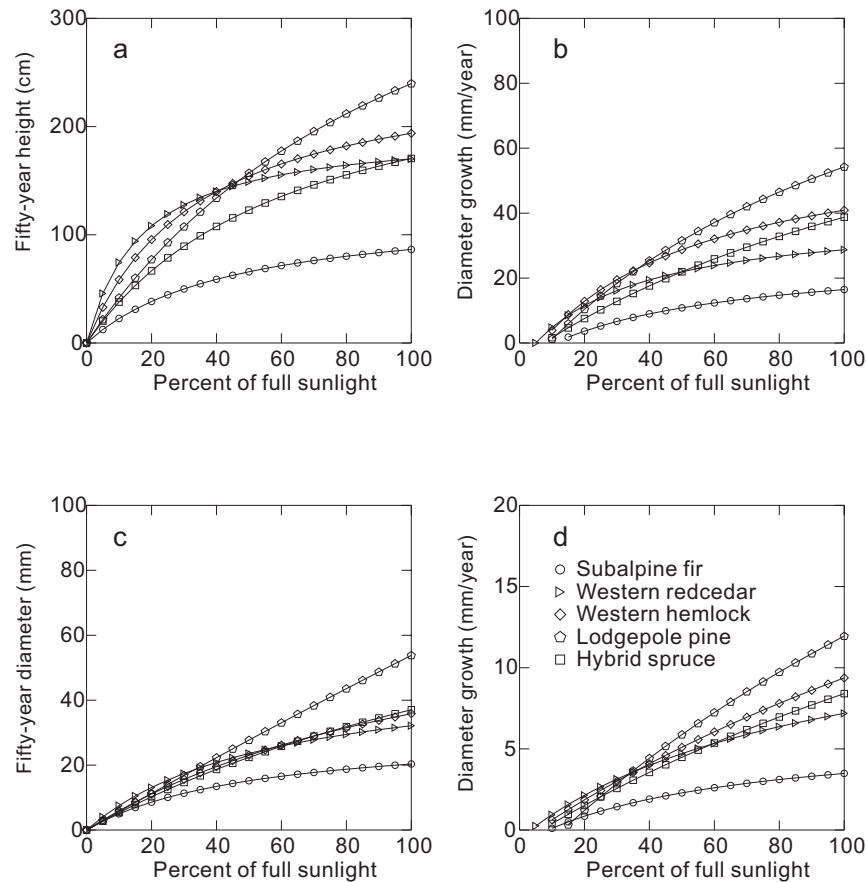
## Discussion

Partial cutting of forests presents new problems for foresters selecting tree species to plant after logging. In the open conditions of clearcuts, concern centred around stock quality, site preparation, and vegetation-management techniques to enhance early survival and promote rapid growth rates after outplanting (Walstad and Kuch 1987; Lavender et al. 1990). Because all trees were planted in open conditions, little attention was paid to a species' light response characteristics. Until recently, information on tree species light response came from leaf-level, controlled environment studies where light levels were manipulated alone or in combination with other resources or abiotic conditions. Basing species selection criteria on physiological data assumes that the relationships between leaf-level responses and whole-plant growth are strong and consistent. In fact, there are very few data comparing leaf-level and whole-plant responses

across light gradients (Sipe 1990; Barker et al. 1997). Studies that have examined growth as a function of light environment in the field often have had different results than leaf-level studies, especially at low light (Kitajima 1994; Pacala et al. 1994; Barker et al. 1997; Wright et al. 1998a; but see Burton and Bazzaz 1995).

Our field study was designed to test whether tree seedlings established across a light gradient created by partial cutting respond in a manner consistent with expectations based on leaf-level light response studies. We found no meaningful variation in whole-plant, aboveground-growth, light-compensation points (or field compensation points) among the five tree species. Nor were tree species growth rates at low light what we expected based on shade-tolerance ranking. Low-light diameter growth of lodgepole pine was similar to or better than that of the other species, which contrasts with expectations that shade-intolerant species grow at a slower rate than tolerant species at low light. Leaf-level experiments for our study species indicate that maximum photosynthesis (the light saturation point) is reached at 30–40% of full sunlight (Dykstra 1974; Bassman 1985; Smith 1985; Lavender 1990; Major 1990; Grossnickle and Arnott 1992; Koppelaar et al. 1995; Mitchell and Arnott 1995). This was not the case for measures of field saturation point. Diameter and height growth continued to increase steadily with increasing irradiance all the way to full sunlight, especially for the two most shade-intolerant species, lodgepole pine and hybrid spruce. Contrary to expectations

**Fig. 5.** Fitted regression lines for fifth-year height (*a*), height growth rates (*b*), fifth-year diameter (*c*), and diameter growth rates (*d*) in response to percent full sunlight.



from leaf-level studies, growth responses among the species varied considerably above 40% full sunlight.

Following partial cutting, we found ambient light levels to be a good predictor of total seedling size and current growth rates, even though other resources such as soil moisture (Wright et al. 1998*b*; M.B. Walters and K.D. Coates, unpublished data), nutrients (M.B. Walters and K.D. Coates, unpublished data), and abiotic conditions such as soil temperature (Coates 1998) also varied with the levels of canopy retention applied in this study.

The growth functions derived from our study are in general agreement with those of other field studies that have examined growth responses to variation in light of our study species (Carter and Klinka 1992; Klinka et al. 1992; Wang et al. 1994; Chen et al. 1996; Kayahara et al. 1996; Chen 1997; Wright et al. 1998*a*); however, our goodness-of-fit for the regression functions were often much higher than those previously reported. There are two likely reasons for this outcome. First, our planting stock was very uniform, thus minimizing the influences of differences in tree age and crown architecture (Field 1983, 1988; Givnish 1988) on growth response to light environment. Use of planting stock improved our goodness-of-fits for height growth by 15–35% (except for redcedar, 5%) compared with natural origin trees in a companion study that used the same method to quantify light environment (Wright et al. 1998*a*). Second, hemispherical photographs provide a better estimation of growing-season light environment in partial canopy forests than the

single-day measurement technique used by others (e.g., Carter and Klinka 1992).

In general, our study confirms the expectation that tree species traditionally classified as shade tolerant have the greatest response to an increase in light at low light levels (i.e., high *s* parameter values) but have relatively low growth rates at high light (i.e., low *a* parameter values) (e.g., Klinka et al. 1992; Walters et al. 1993; Pacala et al. 1994; Walters and Reich 1996). The two species traditionally classified as more shade intolerant (hybrid spruce and lodgepole pine) had the greatest growth rates at high light levels. There was one exception to the low light versus high light trade-offs. This was the very good growth of lodgepole pine at low light. Other recent studies have also reported high growth rates of shade-intolerant species at low light (e.g., Walters and Reich 1996).

Comparing absolute growth rates among tree species at low light may not be a good method for quantifying shade tolerance. A better characteristic for quantifying shade tolerance is the probability of survival at a given growth rate (Kobe et al. 1995; Kobe and Coates 1997). At a radial growth rate of 0.5 mm per year (a growth rate similar to that observed for all species at low light), approximately 38% of lodgepole pine seedlings are expected to die over a 3-year period compared with 1.3 and 0.2% for western hemlock and western redcedar, respectively (Kobe and Coates 1997). Although lodgepole pine growth at low light was similar to the other more shade-tolerant species it may not be equally

acceptable for regeneration of partially cut forests. Light levels of 20–40% full sunlight may be required to achieve radial growth rates above 2–2.5 mm per year, rates at which the mortality risk for all interior cedar–hemlock tree species, including lodgepole pine, are quite low (Kobe and Coates 1997).

Growth of the interior cedar–hemlock tree species increased gradually with increasing light and continued to increase even at very high light levels, albeit slowly for the most shade-tolerant species. Although the five tree species are commonly thought to have a wide range of shade tolerances, their growth rates were broadly overlapping from low to high light. The greatest variability in growth rates was at intermediate light levels (30–70% full sunlight) where careful matching of tree species to light environment can maximize growth rates.

Logging disturbance alters resource availability and physical conditions in forests. Our study confirms that one of the most important resources for predicting tree performance is light availability (Denslow and Hartshorn 1994; Pacala et al. 1996; Lieffers et al. 1999), and it is the one resource that silviculturists can easily manipulate through the spatial and temporal extent of canopy tree removal. Tree responses to changing light environment is of interest to forest managers concerned with future growth rates after partial cutting and to those trying to better understand community dynamics and succession following disturbance. Our study has shown that whole-plant aboveground growth rates in the field are not consistent with expectations from leaf-level physiological studies. Physiological studies should be viewed with caution as a basis for predicting community dynamics, succession, and growth rates in the field.

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