Species variability in growth response to light across climatic regions in northwestern British Columbia

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Abstract: We characterize variation in radial and height growth of saplings of 11 tree species across a range of light levels in boreal, sub-boreal, subalpine, and temperate forests of northwestern British Columbia. Shade-tolerant species had the greatest response to an increase in light at low-light levels but had low asymptotic growth at high light. Shade-intolerant species had weaker responses to increases at low light but had the highest growth rates at high light. The effects of climate on intraspecific variation in sapling response to light were also related to shade tolerance: across different climatic regions, the most shade-tolerant species varied in their response to low light but not high light, while shade-intolerant species varied only in their high-light growth. Species with intermediate shade tolerance varied both their amplitude of growth at high light and the slope of the growth response at low light. Despite the interspecific trade-offs between high- and low-light growth, there was a striking degree of overlap in the light response curves for the component species in virtually all of the climatic regions. Successional dynamics in these forests appear to be more strongly governed by interspecific variation in sapling survival than growth.

Résumé : Les auteurs ont déterminé la variation de la croissance en hauteur et en diamètre des gaules de 11 espèces arborescentes soumises à différents niveaux d'intensité lumineuse dans des forêts boréale, sub-boréale, subalpine et tempérée, du nord-ouest de la Colombie-Britannique. Les espèces sciaphiles en situation de faible luminosité présentaient la plus forte réponse à l'augmentation de la lumière, mais avaient une faible croissance asymptotique en situation de forte luminosité. Les espèces héliophiles réagissaient moins bien à l'augmentation de la lumière en faible luminosité, mais avaient les taux de croissance les plus élevés en situation de forte luminosité. Les effets du climat sur la variation intraspécifique, quant à la réponse des gaules à la lumière, étaient aussi reliés à la tolérance à l'ombre. C'est-à-dire, qu'à travers les différentes régions climatiques, la réponse des espèces les plus sciaphiles variait en situation de faible luminosité, mais non de forte luminosité, alors que l'accroissement des espèces héliophiles variait seulement en situation de forte luminosité. Chez les espèces intermédiaires, à la fois l'amplitude de l'accroissement en situation de forte luminosité et la pente de la réponse en accroissement en situation de faible luminosité variaient. En dépit des compromis interspécifiques entre la croissance en situation de forte luminosité et celle en faible luminosité, il y avait un recouvrement frappant des courbes de réponse à la lumière des espèces composant pratiquement toutes les régions climatiques. La dynamique successionnelle des forêts étudiées semble davantage régie par la variation interspécifique dans la survie des gaules que par la variation de leur croissance.

[Traduit par la Rédaction]

Introduction

Knowledge of the effects of variation in light on seedling and sapling growth has long been considered fundamental to an understanding of forest community dynamics (Marks 1975; Shugart 1984; Carter and Klinka 1992; Klinka et al. 1992). Studies of leaf-level photosynthetic responses have frequently documented a trade-off among species in instantaneous rates of leaf-level carbon gain under low versus high light (e.g., Logan 1965; Loach 1970; Wallace and Dunn 1980). Shade-intolerant, early successional species typically have a broad suite of morphological and ecophysiological traits that support high rates of leaf-level carbon gain under high light, while shade-tolerant, late-successional species are characterized by traits that allow positive leaf-level carbon gain at much lower light levels, but that limit their ability to maximize carbon gain under high light (Bazzaz 1979).

Evidence of this interspecific trade-off has led to both conceptual and quantitative models of forest dynamics in which whole-plant variation in growth at low versus high light plays a pivotal role in determining the successional status of a species (e.g., Marks 1975; Shugart 1984; Canham and Marks 1985). Recent field studies indicate that differences among species in the shape of the functional relationship between ambient, integrated light levels and whole-plant, aboveground growth rates are much weaker than suggested by leaf-level studies (e.g., Pacala et al. 1994).

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For example, interspecific variation in leaf-level compensation points (i.e., light levels at which net carbon gain is zero) have traditionally been an important basis for differentiation among species in their light response curves. These differences may not be mirrored, however, in whole-plant, aboveground growth rates, where even early successional species often show measurable aboveground growth at even the lowest understory light levels (e.g., Pacala et al. 1994; Walters and Reich 1996). Weaker than expected discrimination among species in the response of whole-plant, aboveground growth rates to variation in light has led to recent debate over the importance of interspecific differences in growth for long-term community dynamics (e.g., Carter and Klinka 1992; Kobe 1996; Walters and Reich 1996).

Variation in species performance as a function of climate is generally assumed to be a major mechanism underlying geographic patterns of tree species distribution (e.g., Krajina 1969; Woodward 1987; Lenihan 1993; Pacala and Hurtt 1993; Loehle and LeBlanc 1996). Both the successional dynamics of species within a region, and differential success of species across regions, are likely to be more strongly influenced by variation in the performance of juveniles than adult trees (e.g., Kobe 1996). There are a number of reasons to expect that climatic variation will affect both the overall magnitude of sapling growth at a given light level and the shape of the light response curve and, thus, alter the effective shade tolerance of seedlings and saplings (e.g., Adams and Loucks 1971; Carter and Klinka 1992; Wang et al. 1994). This raises the potential for shifts in competitive hierarchies among tree species in different climates. These shifts will be increasingly important in efforts to predict changes in forest composition and dynamics under changing climates.

Logging in northern British Columbia is currently being transformed in response to two major pressures: (1) pressure (due to environmental concerns) to shift from reliance on clearcutting to use of partial cutting, and (2) pressure (from economic forces) to expand logging from the most productive forests in moderate climates to forests in harsher climates at higher latitudes and elevations. A quantitative understanding of interspecific variation in sapling response to light will be critical in the design of partial cutting regimes, particularly in regimes designed to produce the mix of light levels that will result in acceptable growth rates by a wide range of species. An understanding of variation in sapling response to light under different climates will be particularly useful in determining to what degree our understanding of species behavior and response to logging practices in forests of moderate climates can be extrapolated to forests in harsher climates.

This paper reports the results of research designed to characterize variation in height and radial growth of saplings of the major tree species of northern British Columbia in response to variation in ambient light levels, across the major forest zones in which the species typically occur. The research was specifically designed to address three basic questions. (1) Are there clear trade-offs among tree species in aboveground growth under low versus high light? (2) Are the interspecific differences in light response curves at the whole-plant level sufficient to play a dominant role in determining community dynamics within the forests in any given region? (3) How do both the magnitude and the shapes of light response curves vary among the major forest zones of the region? Shifts in the effective shade tolerance of species along climatic gradients could alter both competitive hierarchies of species in different forest zones and community response to different logging regimes.

Methods

Study areas and tree species

Our research was conducted in the four major forest zones of central to northwestern British Columbia: (1) high-latitude boreal forests, (2) lower latitude, interior, sub-boreal forests, (3) high-elevation subalpine forests, and (4) low-elevation northern temperate forests that are transitional between interior and coastal forests (Fig. 1). We used the British Columbia biogeoclimatic classification system (Pojar et al. 1987; Meidinger and Pojar 1991; Banner et al. 1993) to further subdivide these four major zones into nine regions with similar climate (Table 1). See Meidinger and Pojar (1991) for a full description of this system of biogeoclimatic classification.

The boreal forests within our study area occur in two distinct climates: the high latitude, Plains Boreal region has very short warm summers and long, very cold winters, while the Intermontane Boreal region has a more variable, montane climate characterized by drier and slightly cooler summers but warmer winters. Forests in both regions are dominated by white and black spruce (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) BSP), with lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) as codominant species. The sub-boreal zone is represented by a single climatic region (the Western Sub-boreal) with a continental climate (Table 1). The sub-boreal forests are dominated by interior spruce (a complex of white spruce and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), subalpine fir, and lodgepole pine.

The northern temperate zone is represented by three climatic regions (Wet, Snowy, and Moist Temperate) that vary in both temperature and precipitation (Table 1). Late-successional stands in this zone are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* (Donn ex D. Don), with mixtures of subalpine fir, hybrid spruce (a complex of interior and Sitka spruce (*Picea sitchensis* (Bong.) Carr.)), lodgepole pine, and three deciduous species: paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray).

The three subalpine regions (Continental, Transitional, and Coastal Subalpine) reflect a gradient from maritime to continental climates at elevations greater than 1000 m (Table 1). The Coastal Subalpine forests are characterized by short, cool growing seasons and long, cool wet winters, and are dominated by mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and amabilis fir (*Abies amabilis* Dougl. ex Forbes). The Continental Subalpine forests have a lower mean annual precipitation, a lower mean annual temperature, more months with snow and fewer growing degree-days > 5°C, and are dominated by subalpine fir and interior spruce (Table 1).

We sampled the major tree species of early- to late-successional forests in each climatic region (Table 2). Ranked from most shade tolerant to least shade tolerant (Krajina et al. 1982; Burns and Honkala 1990; Carter and Klinka 1992; Klinka et al. 1992; Wang et al. 1994; Kayahara et al. 1996; Kobe and Coates 1997), the species were ordered as follows: amabilis fir > western redcedar > western hemlock ≥ mountain hemlock = subalpine fir > black spruce ≥ white spruce > hybrid spruce = interior spruce > lodgepole pine > trembling aspen > black cottonwood = paper birch. Hybridization of spruces in the study area is complex (Szmidt et al.

Table 1. General location, sampling information, and climate data for each of the nine climatic regions in the study area.

Forested zone:	Boreal		Sub-boreal	Northern Temperate			Subalpine		
Climatic region:	Intermontane Boreal	Plains Boreal	Western Sub-boreal	Wet Temperate	Snowy Temperate	Moist Temperate	Continental Subalpine	Transitional Subalpine	Coastal Subalpine
Biogeoclimatic ecosystem classification[a]:	BWBSdk1	BWBSdk2	SBSmc2	ICHwc	ICHvc	ICHmc2	ESSFmc	ESSFwv	MHmm2
Area of biogeoclimatic unit (ha)	1 023 700	1 396 743	1 550 314	100 367	140 361	880 323	683 602	1 107 991	567 963
Longitude range of sampled trees (W)	128°30′–129°10′	128°53′–130°22′	126°31′–127°18′	130°11′–130°17′	129°16′–129°59′	127°15′–128°20′	126°18′–127°25′	127°28′–128°24′	127°51′–128°37′
Latitude range of sampled trees (N)	59°39′–59°57′	57°28′–59°03′	54°01′–54°52′	56°56′–57°08′	56°11′–56°51′	54°40′–55°30′	54°11′–55°06′	54°40′–55°40′	54°49′–55°24′
Elevation range (m)	690–950	810–990	800–990	610–800	290–970	100–750	1040–1450	1050–1255	1050–1200
Species sampled[b]	Bl, Pl, Sw	Pl, Sb, Sw	Bl, Pl, Si	Bl, Hw, Sx	Bl, Hw, Sx	At, Bl, Ct, Cw, Ep, Hw, Pl, Sx	Bl, Pl, Si	Bl, Hm, Hw, Pl, Sx	Ba, Hm
No. of sites	11	9	6	8	18	9	12	8	4
No. of saplings	200	245	237	141	228	549	441	514	66
Mean annual precipitation (mm)	445	355	575	620	nd	694	579	nd	1995
Mean growing season precipitation (mm)	207	170	226	258	250	276	290	nd	399
Mean annual snowfall (cm)	204	162	237	174	nd	207	249	nd	1041
Mean number of months with snow	11	9.7	9	9*	nd	8	10	nd	9
Mean annual temperature (°C)	–2.1	–1.4	1.5	3*	2	3.8	–0.7	nd	1.8
Mean temperature of coldest month (°C)	–22.5	–20.2	–12.6	–9.4	–12.6	–9.7	–12.6	nd	–9.1
Mean temperature of warmest month (°C)	14.7	12.2	12.3	14	13.8	14.9	9.5	nd	11.3
Growing degree-days >5°C	1006	678	947	979	nd	1469	147	nd	629
Frost free period	83	51	116	158	nd	117	nd	nd	56
Degree-days <0°C	2491	1938	1167	nd	nd	811	nd	nd	879

Note: Normalized climatic data from Environment Canada (1980) except for the Plains Boreal and Snowy Temperate regions, which are unnormalized short-term data. nd, no data available.

[a] Biogeoclimatic ecosystem classification (refer to Banner et al. 1993; Pojar et al. 1987; Meidinger and Pojar 1991): BWBSdk1, Boreal White and Black Spruce, dry cool subzone, Stikine variant; BWBSdk2, Boreal White and Black Spruce, dry cool subzone; SBSmc2, Sub-boreal Spruce, moist cold subzone, Babine variant; ICHwc, Interior Cedar–Hemlock, wet cold subzone; ICHvc, Interior Cedar–Hemlock, very wet cold subzone; ICHmc2, Interior Cedar–Hemlock, moist cold subzone, Hazelton variant; ESSFmc, Engelmann Spruce – Subalpine Fir, moist cold subzone; ESSFwv, Engelmann Spruce – Subalpine fir, wet very cold subzone; and MHmm2 (Mountain Hemlock, moist maritime subzone, leeward variant).

[b] Species codes: At, trembling aspen; Ba, amabilis fir; Bl, subalpine fir; Cw, western redcedar; Ep, paper birch; Hm, mountain hemlock; Hw, western hemlock; Pl, lodgepole pine; Sb, black spruce; Sx, hybrid spruce; Si, interior spruce; Sw, white spruce.

Table 2. Mean age, height, and diameter (at 1.3 m) of tree species sampled in each climatic region.

Species	Climatic region	Age (years)	Height (m)	Diameter (mm)
Amabilis fir	Coastal Subalpine	58 (10–151)	3.0 (0.8–8.4)	44 (6–118)
Western redcedar	Moist Temperate	31 (7–57)	3.5 (1.0–7.0)	42 (4–103)
Western hemlock	Transitional Subalpine	38 (12–98)	3.0 (1.0–5.8)	31 (3–86)
	Wet Temperate	29 (15–61)	3.4 (1.3–6.2)	35 (2–85)
	Snowy Temperate	49 (5–155)	3.7 (1.4–7.2)	44 (3–106)
	Moist Temperate	25 (6–83)	3.9 (1.2–7.7)	43 (3–100)
Mountain hemlock	Transitional Subalpine	53 (10–126)	3.0 (0.8–7.9)	40 (4–95)
	Coastal Subalpine	39 (9–115)	3.1 (1.4–6.0)	39 (6–115)
Subalpine fir	Intermontane Boreal	45 (10–121)	3.0 (0.6–10.5)	39 (4–112)
	Continental Subalpine	75 (8–208)	2.8 (0.6–7.1)	38 (2–124)
	Transitional Subalpine	45 (9–209)	2.8 (0.7–7.9)	40 (4–127)
	Western Sub-boreal	39 (16–103)	2.7 (1.0–9.3)	37 (4–165)
	Wet Temperate	34 (13–77)	2.5 (0.8–6.1)	31 (6–78)
	Snowy Temperate	65 (6–225)	3.0 (0.8–9.4)	46 (7–109)
	Moist Temperate	33 (8–165)	3.2 (0.6–7.6)	42 (8–109)
Black spruce	Plains Boreal	42 (15–93)	3.6 (1.1–7.6)	36 (6–69)
Hybrid spruce	Transitional Subalpine	39 (14–152)	2.8 (0.9–7.9)	38 (8–97)
	Wet Temperate	25 (9–51)	3.1 (0.6–6.7)	41 (15–94)
	Snowy Temperate	34 (9–116)	2.7 (0.8–8.7)	40 (7–111)
	Moist Temperate	19 (8–79)	3.4 (0.7–7.6)	43 (3–101)
Interior spruce	Continental Subalpine	45 (12–135)	3.1 (0.7–8.2)	44 (6–133)
	Western Sub-boreal	24 (13–51)	2.9 (0.9–6.0)	34 (1–92)
White spruce	Intermontane Boreal	48 (13–161)	3.5 (0.5–9.2)	42 (5–96)
	Plains Boreal	35 (10–79)	3.2 (0.9–7.6)	34 (7–69)
Lodgepole pine	Intermontane Boreal	21 (9–68)	3.1 (0.5–7.0)	40 (9–84)
	Plains Boreal	35 (6–77)	4.4 (1.0–9.7)	44 (5–114)
	Continental Subalpine	24 (6–69)	2.8 (0.6–7.8)	36 (7–88)
	Transitional Subalpine	22 (7–44)	2.6 (1.0–5.2)	31 (8–111)
	Western Sub-boreal	21 (7–58)	3.9 (0.9–8.6)	51 (8–146)
	Moist Temperate	15 (6–44)	3.6 (0.6–8.2)	46 (7–97)
Trembling aspen	Moist Temperate	12 (5–24)	6.4 (2.3–10.7)	47 (8–103)
Black cottonwood	Moist Temperate	12 (5–26)	5.8 (1.1–12.0)	50 (5–121)
Paper birch	Moist Temperate	15 (6–32)	5.7 (2.1–9.0)	43 (8–117)

Note: Data in parentheses are ranges.

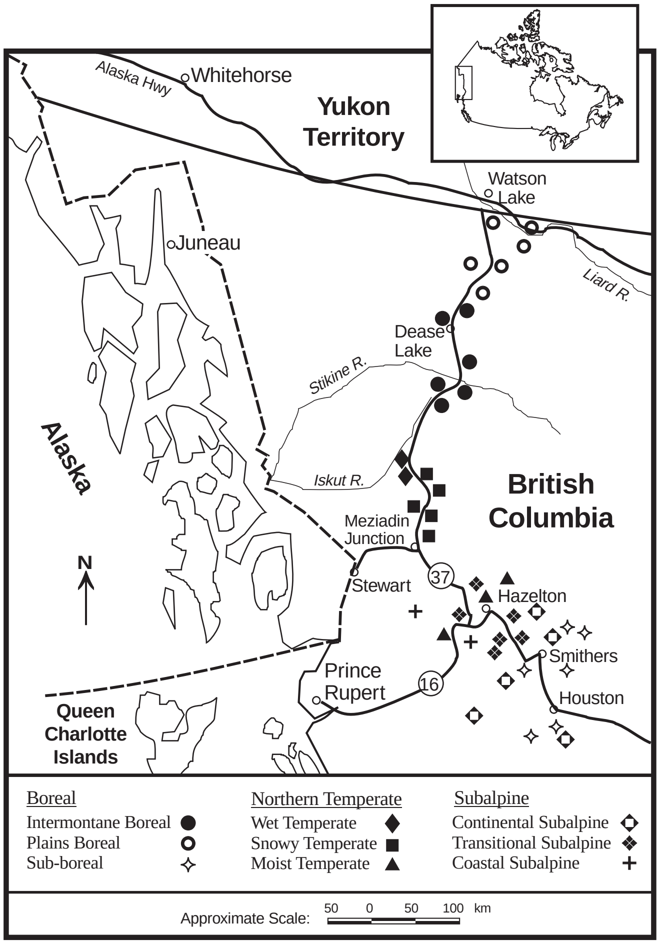
1988; Coates et al. 1994; Sutton et al. 1994; Grossnickle et al. 1996). The mixture is termed "hybrid spruce" in the temperate zone and in the Transitional Subalpine region and "interior spruce" in the Western Sub-boreal and Continental Subalpine regions. White and black spruce occur in the boreal zone.

Study sites and sampled trees

We sampled from a range of sites within each climatic region (Fig. 1, Table 1). Each site was uniform in topography and soils and represented mesic conditions (average soil moisture and nutrients for the region). The sites were located in mature stands (> 140 years old), in canopy gaps, along edges of old road or trail cuts, in regenerating burns (30+ years old) and associated mature remnants, and in partially cut and clearcut areas. Areas disturbed within the last 5 years (e.g., blowdown, insect related attack, new road cuts) were carefully avoided.

We sampled 25–216 trees per species and region across a light gradient from low to high light. Sampling occurred at the end of the 1995 growing season and throughout the 1996 growing season. Sample tree characteristics are found in Table 2. Sapling sizes were uniformly distributed across light levels within each climatic region. We always selected the best growing sample tree per species at a given light level. In this way, our data reflect "optimum" growth at a given light level for that site. Except for trembling aspen, a species that regenerates primarily by root suckers in our study area (Haeussler et al. 1990), all sample trees originated from seed. Layered black spruce, subalpine and amabilis fir, and western redcedar were avoided, as were paper birch stump sprouts. Field measurements taken on each sample tree included total height, diameter at 1.3 m (diameter at breast height; DBH), and leader length for each of the past 6 years (not including the current year in 1996). Each tree was cut 10 cm above the ground surface, and a disc was removed and numbered. In the laboratory, all growth rings were measured along a representative radius (the radius bisecting the angle formed by the longest and shortest radii of the cross-section) and tree age was determined. Growth rings were measured with a digital ring analyzer (0.025 mm resolution) using a high-resolution colour video camera connected to a 40× stereo microscope. The most recent growth ring was discarded for saplings

Fig. 1. Distribution of the sample sites within the study area by climatic region.



obtained in 1996 to ensure that the growth measurements were from a complete growing season.

Light measurements

Hemispherical canopy photos were taken at 1.0–2.0 m above the stump of each cut sample tree to quantify the light available for growth over the growing season. Sample trees were selected so that overstory canopy trees, rather than adjacent saplings, provided shading. Overstory canopies were always dominated by conifer species. GLI, an index of whole growing season light availability, was computed from each photograph using the GLI/C 2.0 software, following Canham (1988). This index integrates the seasonal and diurnal distribution of solar radiation transmitted through the canopy into a single index of available light in units of percentage of full sun for our selected growing season (mid-April through mid-September) (Canham et al. 1990).

Data analysis

Nonlinear regression was used to develop growth functions for each tree species. One-year ring increment (mm); 1-year leader length (cm); 2-, 3-, and 5-year mean ring increment (mm); and mean leader length (cm) were evaluated for use as response variables. The best fits were obtained for prediction of radial increment averaged over the five most recent years and the most recent year's leader length, and those models are presented below. We analysed absolute rather than relative growth. In our data growth did not show a consistent size-dependent relationship within any one species or across regions. Relative growth rates are often preferred for analysis to eliminate the potential for confounding by size when (1) relativizing by size removes any dependence of growth on size, and (2) plant size is not uniformly distributed across the light gradient. While there was evidence of a relationship between growth and size for some species in some climatic regions, the relationship was generally weak, and the traditional methods of controlling for size (i.e., dividing radial growth by radius) did not produce size-independent relative growth rates. Moreover, as mentioned above, sapling size was very uniformly distributed across the light gradient in all species and climatic regions. A log transformation of the absolute growth data was necessary to stabilize the variance.

Three nonlinear models were tested: the Weibull, Chapman–Richard's, and Michaelis–Menten functions. The Michaelis–Menten equation provided more consistently reliable fits for all growth variables across species and subzones and its parameters were more easily interpreted, allowing comparisons of growth response at high versus low light. The equation takes the form:

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

where Y is either $\log_{10}$(5-year average radial growth + 1) (radial growth was measured in millimeters) or $\log_{10}$(leader length) (leader length is expressed in centimeters), a is the asymptote of the function at high light, s is the slope of the relationship at zero light, L is GLI (in units of percent full light received over the growing season), and the error term is assumed to be normally distributed. In addition, we examined two additional equations to allow for tests of nonzero intercepts:

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

$$[3] \qquad Y = c + \{aL/[(a/s)+L]\} + \in$$

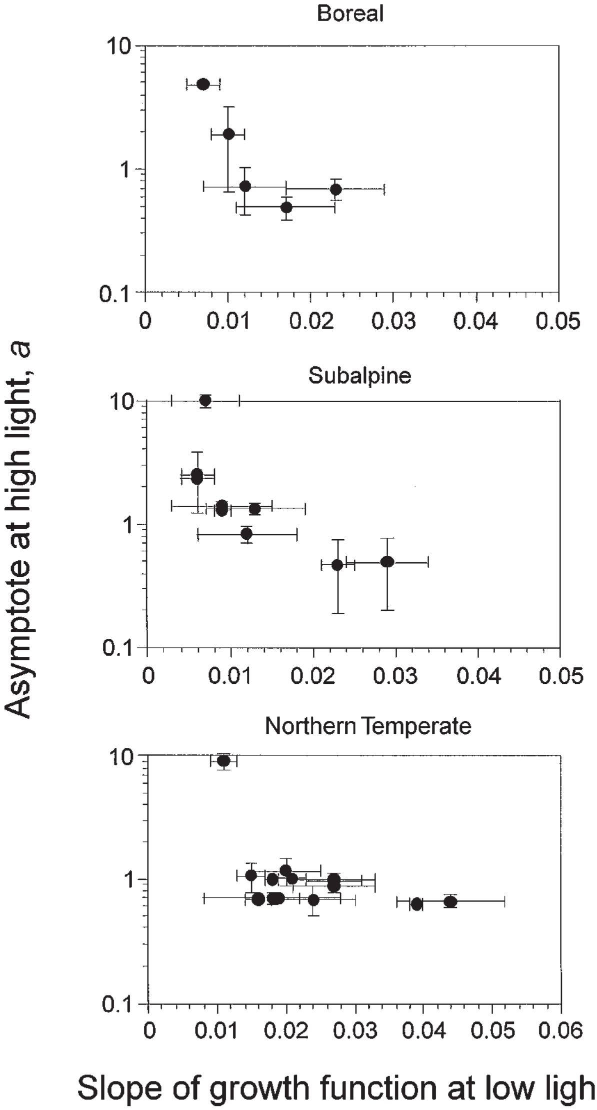
where c is the light level at which growth equals zero in eq. 2 (i.e., a whole-plant compensation point) and c is the growth (positive or negative) at zero light in eq. 3. We compared the results obtained from eq. 1 and these alternative models using the extra sums of squares principle (Bergerud 1991). Model parameters a and s were estimated for each species and climatic region using the NONLIN procedure in Systat 6.0 (Systat, Inc. 1996) and the simplex estimation method to minimize the loss function. We used 95% confidence limits for a and s as the basis for comparisons among species and regions of growth rates at high and low light, respectively.

Results

Light response curves did not cluster into distinct groups based on either shade tolerance or climatic regions. Overall, species that grew well at high light tended to grow slowly at low light; however, the strength of the trade-off and the range of variation in parameter estimates within species and climatic regions varied substantially (details below).

Saplings of all species had measurable radial and height growth rates even at the lowest light levels sampled in our study. Understory light levels in mature temperate and subalpine forests in our region rarely drop below 5% full light (E.F. Wright and K.D. Coates, unpublished data), unlike the much lower light levels (1–2% of full sun) often found in broadleaf forests of eastern North America or the tropics (Canham et al. 1990; Fetcher et al. 1994; Clark et al. 1996). Of the 54 models fit using eqs. 2 and 3, only 6 had intercepts that were significantly different than zero, and in all 6 of those models, the parameter value of c was very close to zero (< 0.24% of full sunlight). Thus, there was no meaningful

Fig. 2. Trade-off between asymptotic radial growth at high light (*a*) versus the slope of the growth response at low light (*s*) for tree species in the Boreal, Subalpine, and Northern Temperate forested zones using parameter values in Table 3 and log-transformed radial growth data. Each data point represents a growth function fit to an individual species in a specific climatic region within the forest zone (see Tables 1 and 2). Error bars are 1SE of the estimated parameter values.



variation in whole-plant compensation points for radial or height growth in our study species or regions.

Comparisons of species response to light gradients within climatic regions

Boreal forests

There was a strong trade-off between ability to grow at high versus low light among the boreal zone tree species (Fig. 2). The shapes of the light response curves for both radial and height growth of the four boreal species were consistent with expectations based on shade tolerance rankings (Fig. 3, Tables 3 and 4). For example, low-light radial growth of subalpine fir (the most shade-tolerant species) was higher than that of white spruce and lodgepole pine in the Intermontane Boreal region, while radial growth of lodgepole pine was significantly greater than that of white spruce and subalpine fir in high light (Table 3). In both boreal regions, the rank order of interspecific variation in height growth at both low and high light was the same as for radial growth, but the separation was smaller and differences in parameter estimates among species were generally not significant (Table 4).

Sub-boreal forests

Radial growth rates of the three sub-boreal species (subalpine fir, interior spruce, and lodgepole pine) were very similar at light levels < 20% full sun (Fig. 4). Growth diverged at progressively higher light levels, with the least shade-tolerant species (lodgepole pine) having the greatest radial and height growth in full sun (Fig. 4, Table 4). In contrast to radial growth, there was significant separation among the sub-boreal species in leader growth at low light (Table 4). The *s* estimates for height growth of interior spruce were significantly greater than for lodgepole pine (with predicted leader lengths of 13 cm for spruce versus 6 cm for lodgepole pine at 20% of full light).

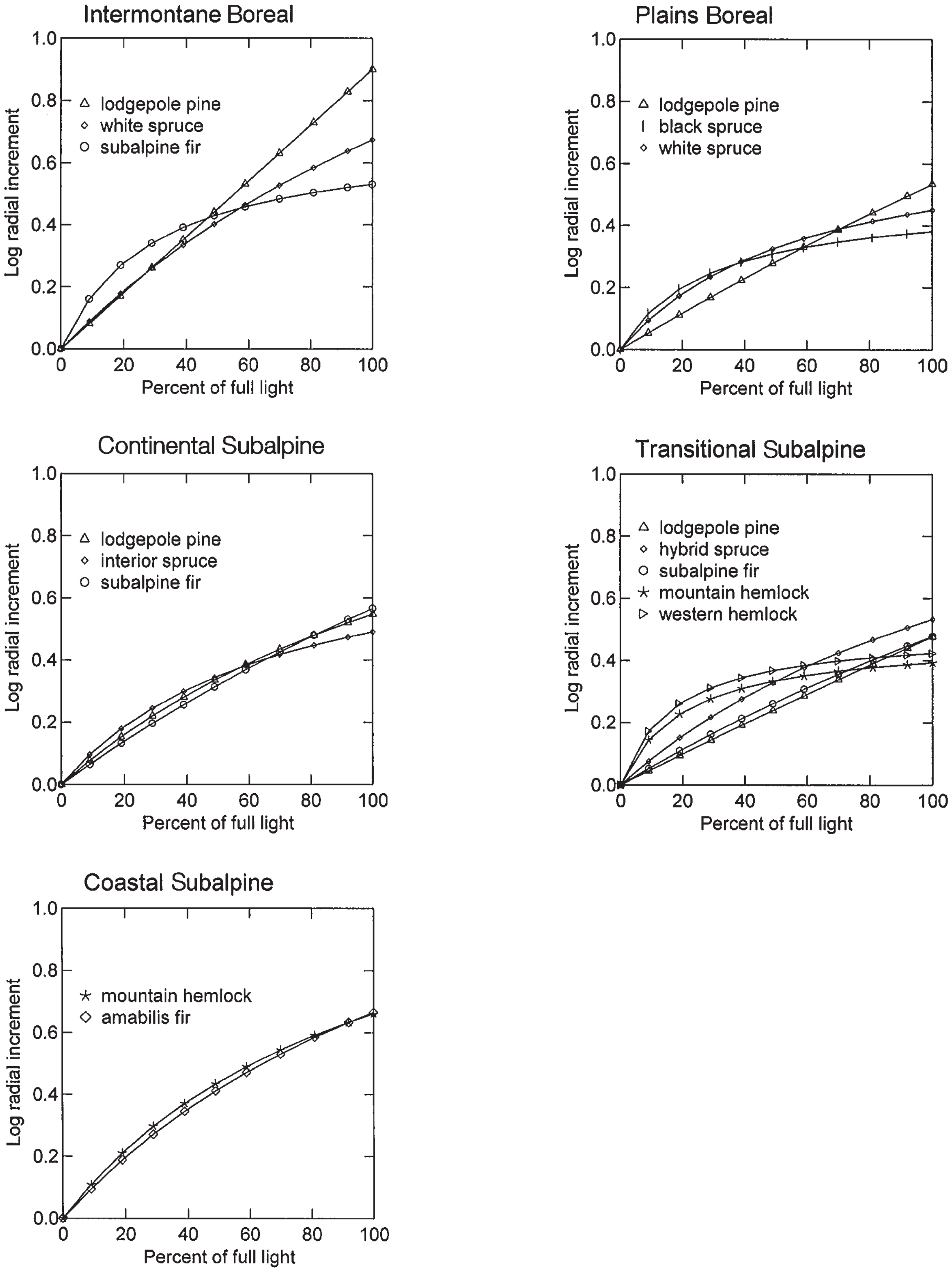
Subalpine forests

There was clear evidence of an interspecific trade-off in radial growth at high (*a*) versus low light (*s*) for the 10 species sampled in the three subalpine regions (Fig. 2), but the trade-off was largely restricted to the five species sampled in the Transitional Subalpine region (Fig. 3). Parameter estimates for those five species tended to cluster into two groups, with the two most shade-tolerant species (western and mountain hemlock) having high s and low *a* values as expected, while the reverse was true for the three less shade tolerant species (subalpine fir, hybrid spruce, and lodgepole pine) (Table 3, Fig. 3). While there were some significant pairwise differences among species in *a* and s parameter estimates for species in the Continental and Coastal Subalpine regions, the overall shapes of the radial growth responses were remarkably similar (Fig. 3). The goodness-of-fits of the regression models for leader length of species in the subalpine regions were generally quite poor. We suspect that the subalpine regions are characterized by particularly high climatic variability and that this may lead to high rates of leader dieback and generally high variance in height growth rates.

Northern Temperate forests

The temperate zone forests had the weakest evidence of a clear trade-off between high- and low-light radial growth (Fig. 2). With the exception of lodgepole pine in the Moist Temperate region, the shapes of the growth responses were strikingly parallel, and the species with the highest radial growth in low-light conditions also generally had the highest growth rates in high light (Figs. 4 and 5). This was particularly true for the Wet and Snowy Temperate regions, where the rankings of radial growth rates among species do not vary with light (although the absolute rankings among species do vary between the two regions; Fig. 4). Leader length was more sensitive to changes in light level than radial

Fig. 3. Predicted radial growth as a function of percentage of full light for the major tree species of the Intermontane Boreal (BWBSdk1), Plains Boreal (BWBSdk2), Continental Subalpine (ESSFmc), Transitional Subalpine (ESSFwv), and Coastal Subalpine (MHmm2) climatic regions using parameter values in Table 3. Vertical axis is $\log_{10}$(5-year average radial growth (mm) + 1).



growth, showing rapid increases in length between 5 and 20% of full sun (Fig. 6).

We sampled the greatest number of tree species (eight) in the Moist Temperate forests (the ICHmc subzone of the BC biogeoclimatic classification system). Again, with the exception of lodgepole pine, there was no clear trade-off among species in low- versus high-light radial growth (Table 3, Figs. 4 and 5). Moreover, the rank order of the *s* parameter

Table 3. Parameter estimates for predicted radial growth using the equation $Y = \{aL/[(a/s) + L]\}$ where L is the light level and radial growth is $\log_{10}$(5-year average radial growth (mm) + 1).

		Michaelis–Menten model parameters and goodness of fit			
Tree species	Climatic region	a ± 95% CL	s ± 95% CL	R^2	n
Amabilis fir	Coastal Subalpine	1.648±1.708	0.011±0.004	0.72	41
Western redcedar	Moist Temperate	0.799±0.299	0.019±0.007	0.48	52
Western hemlock	Transitional Subalpine	0.494±0.072	0.029±0.010	0.36	82
	Wet Temperate	0.688±0.195	0.019±0.008	0.51	40
	Snowy Temperate	0.659±0.078	0.044±0.010	0.66	82
	Moist Temperate	0.858±0.128	0.027±0.006	0.73	77
Mountain hemlock	Transitional Subalpine	0.473±0.080	0.023±0.008	0.47	73
	Coastal Subalpine	1.329±0.920	0.013±0.005	0.86	25
Subalpine fir	Intermontane Boreal	0.688±0.130	0.023±0.006	0.5	94
	Continental Subalpine	2.503±2.272	0.006±0.001	0.59	216
	Transitional Subalpine	2.324±2.767	0.006±0.001	0.43	152
	Western Sub-boreal	1.470±1.164	0.010±0.003	0.49	85
	Wet Temperate	0.683±0.212	0.016±0.006	0.5	54
	Snowy Temperate	0.696±0.176	0.018±0.005	0.56	83
	Moist Temperate	1.044±0.277	0.015±0.003	0.71	78
Black spruce	Plains Boreal	0.490±0.108	0.017±0.006	0.39	75
Hybrid spruce	Transitional Subalpine	1.297±0.821	0.009±0.003	0.42	117
	Wet Temperate	0.679±0.192	0.024±0.012	0.47	47
	Snowy Temperate	0.622±0.125	0.039±0.019	0.29	63
	Moist Temperate	1.001±0.263	0.021±0.006	0.61	74
Interior spruce	Continental Subalpine	0.829±0.280	0.012±0.002	0.39	153
	Western Sub-boreal	1.205±0.539	0.013±0.003	0.58	86
White spruce	Intermontane Boreal	1.921±1.262	0.010±0.002	0.57	80
	Plains Boreal	0.720±0.294	0.012±0.005	0.37	61
Lodgepole pine	Intermontane Boreal	$9.32 \times 10^9 \pm -8.39 \times 10^{10}$	0.009±0.002	0.77	71
	Plains Boreal	4.813±12.956	0.006±0.001	0.62	64
	Continental Subalpine	1.397±1.229	0.009±0.004	0.48	72
	Transitional Subalpine	9.952±49.222	0.005±0.001	0.58	90
	Western Sub-boreal	$1.87 \times 10^{10} \pm 0.000$	0.010±0.002	0.58	66
	Moist Temperate	11.099±38.913	0.010±0.002	0.81	68
Trembling aspen	Moist Temperate	0.987±0.180	0.027±0.006	0.68	59
Black cottonwood	Moist Temperate	0.963±0.305	0.027±0.012	0.39	73
Paper birch	Moist Temperate	1.157±0.352	0.020±0.006	0.59	68

Note: Radial growth is back transformed from eq. 1. a and s, parameters of model; CL, confidence limits.

values did not correlate well with traditional shade tolerance rankings (Krajina 1969; Kobe and Coates 1997) (Table 3). Two of the shade-intolerant hardwoods (aspen and cottonwood) had higher predicted radial growth at 10% full sun than the shade-tolerant species western red cedar and western hemlock (Fig. 5, Table 3). The confidence intervals for estimates of the asymptotic growth parameter (a) for the eight species were broadly overlapping; however, the rankings of radial growth rates among species at high light did generally follow expectations based on shade tolerance rankings (Table 3 and Fig. 4).

Intraspecific comparisons of light responses across climate regions

Western hemlock

There was no clear trade-off between high- (a) and low-light (s) radial growth of western hemlock across climatic regions. There was, however, a shift in the effective shade tolerance of western hemlock with regional climate, because of variation in the slope of the growth response at low light (Fig. 7). Under low light, radial growth was significantly faster in the cooler, Snowy Temperate forests than in the Moist or Wet Temperate forests (Table 3, Fig. 8). High-light radial growth was lowest in the harshest climate in which this species was sampled (the Transitional Subalpine region) (Fig. 8).

Subalpine fir

There was significant variation in both the amplitude of radial growth at high light (a parameter) and response to low light (s parameter) of subalpine fir (Table 3, Figs. 7 and 8), indicating significant shifts in the effective shade tolerance of subalpine fir across the seven climatic regions in which it was sampled. Radial growth in the subalpine forests was substantially lower than in all other regions (Fig. 8), even though this species reaches its greatest relative abundance in these forests. At high light, radial growth was highest in the moderate climates of the Moist Temperate and Sub-boreal forests, and lowest in the colder Transitional Subalpine and

Table 4. Parameter estimates for predicted leader length using the equation $Y = \{aL/[(a/s) + L]\}$ where L is light level and leader length is $\log_{10}$(1995 leader length (cm)).

		Michaelis–Menten model parameters and goodness of fit			
Species	Climatic region	a ± 95% CL	s ± 95% CL	R^2	n
Amabilis fir	Coastal Subalpine	1.636±0.207	0.306±0.176	0.38	41
Western redcedar	Moist Temperate	1.616±0.191	0.163±0.055	0.47	52
Western hemlock	Transitional Subalpine	1.413±0.073	0.763±0.570	0.09	82
	Wet Temperate	1.537±0.131	0.285±0.147	0.32	40
	Snowy Temperate	1.516±0.084	0.856±0.324	0.34	82
	Moist Temperate	1.783±0.125	0.323±0.108	0.38	77
Mountain hemlock	Transitional Subalpine	1.393±0.097	0.313±0.138	0.32	73
	Coastal Subalpine	1.771±0.240	0.128±0.056	0.72	25
Subalpine fir	Intermontane Boreal	1.573±0.100	0.247±0.072	0.41	94
	Continental Subalpine	1.359±0.130	0.131±0.040	0.18	216
	Transitional Subalpine	1.181±0.083	0.605±0.639	0.03	152
	Western Sub-boreal	2.086±0.452	0.074±0.024	0.44	85
	Wet Temperate	1.770±0.273	0.082±0.027	0.56	54
	Snowy Temperate	1.448±0.130	0.227±0.080	0.41	83
	Moist Temperate	1.735±0.151	0.192±0.059	0.42	78
Black spruce	Plains Boreal	1.583±0.154	0.247±0.142	0.18	75
Hybrid spruce	Transitional Subalpine	1.369±0.165	0.168±0.087	0.12	117
	Wet Temperate	1.944±0.301	0.100±0.036	0.59	47
	Snowy Temperate	1.578±0.154	0.302±0.148	0.27	63
	Moist Temperate	1.983±0.222	0.152±0.049	0.47	74
Interior spruce	Continental Subalpine	1.428±0.147	0.213±0.086	0.16	153
	Western Sub-boreal	1.756±0.177	0.153±0.051	0.37	86
White spruce	Intermontane Boreal	1.824±0.216	0.152±0.057	0.29	80
	Plains Boreal	1.678±0.177	0.154±0.065	0.26	61
Lodgepole pine	Intermontane Boreal	1.896±0.242	0.133±0.056	0.25	71
	Plains Boreal	1.881±0.253	0.134±0.056	0.29	64
	Continental Subalpine	1.428±0.154	0.503±0.507	0.06	72
	Transitional Subalpine	1.442±0.118	0.390±0.295	0.11	90
	Western Sub-boreal	2.808±0.938	0.056±0.022	0.32	66
	Moist Temperate	2.300±0.285	0.114±0.031	0.61	68
Trembling aspen	Moist Temperate	1.959±0.113	0.532±0.233	0.27	59
Black cottonwood	Moist Temperate	1.967±0.246	0.221±0.129	0.22	73
Paper birch	Moist Temperate	1.853±0.202	0.456±0.378	0.22	68

Note: Leader length is back transformed from eq. 1. a and s, parameters of model; CL, confidence limits.

Wet Temperate forests (Fig. 8), although the differences in a parameters were not significant (Table 3).

Hybrid, interior, and white spruce

There were shifts in both asymptotic growth (a) and response to low light (s) for the spruces across climatic regions (Fig. 7), with the greatest differences in response to low light. Hybrid spruces in the three temperate zone regions had greater low-light radial growth rates than hybrid, interior, or white spruces in the harsher climates of the subalpine, sub-boreal, and boreal zones (Fig. 8, Table 3).

Lodgepole pine

Large shifts in the asymptotic radial growth parameters (a) among climatic regions led to significant differences in radial growth at high light (Fig. 8). However, differences in s were relatively minor (Table 3). Thus, lodgepole pine responded to variation in regional climate by growing better at all light levels, without a shift in effective shade tolerance. As in other species, the best growth occurred in the more moderate climates of the Moist Temperate, Sub-boreal, and Intermontane Boreal forests, while the lowest radial growth rates occurred in the harsher climates of Plains Boreal and Continental and Transitional Subalpine forests (Table 3, Fig. 8).

Intraspecific comparisons across climatic regions within Northern Temperate forests

The three regions sampled within the northern temperate zone represent a gradient in moisture and temperature, ranging from the coldest, wettest, Snowy Temperate forests to the warmer, more mesic, Moist Temperate forests (Banner et al. 1993). While the radial growth responses of the three species that were sampled in each of the three temperate regions are not strikingly different, there were consistent patterns of variation in species response to climate for all

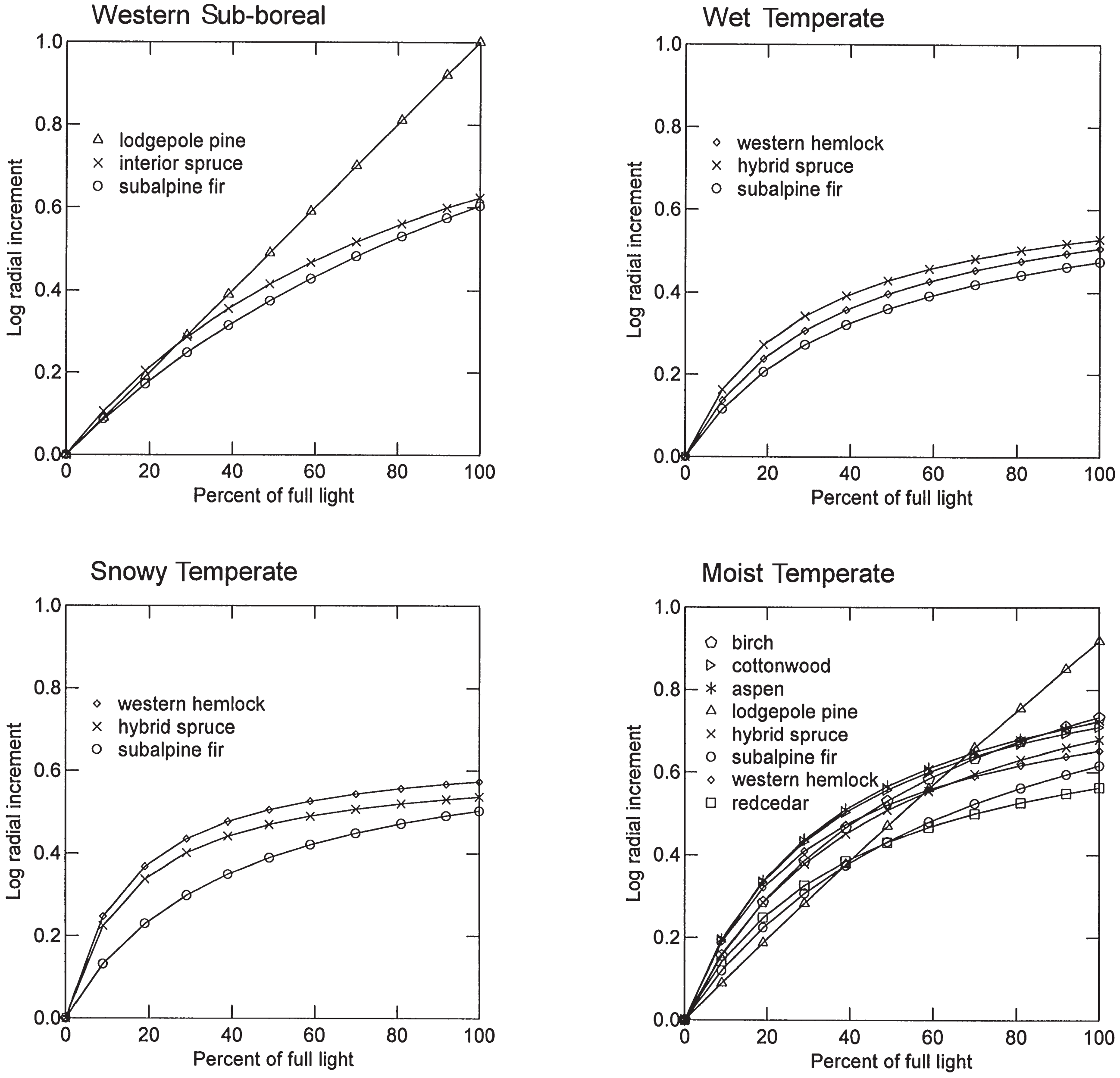


Fig. 4. Predicted radial growth as a function of percentage of full light for the major tree species of the Western Sub-boreal (SBSmc2), Wet Temperate (ICHwc2), Snowy Temperate (ICHvc), and Moist Temperate (ICHmc2) climatic regions using parameter values in Table 3.

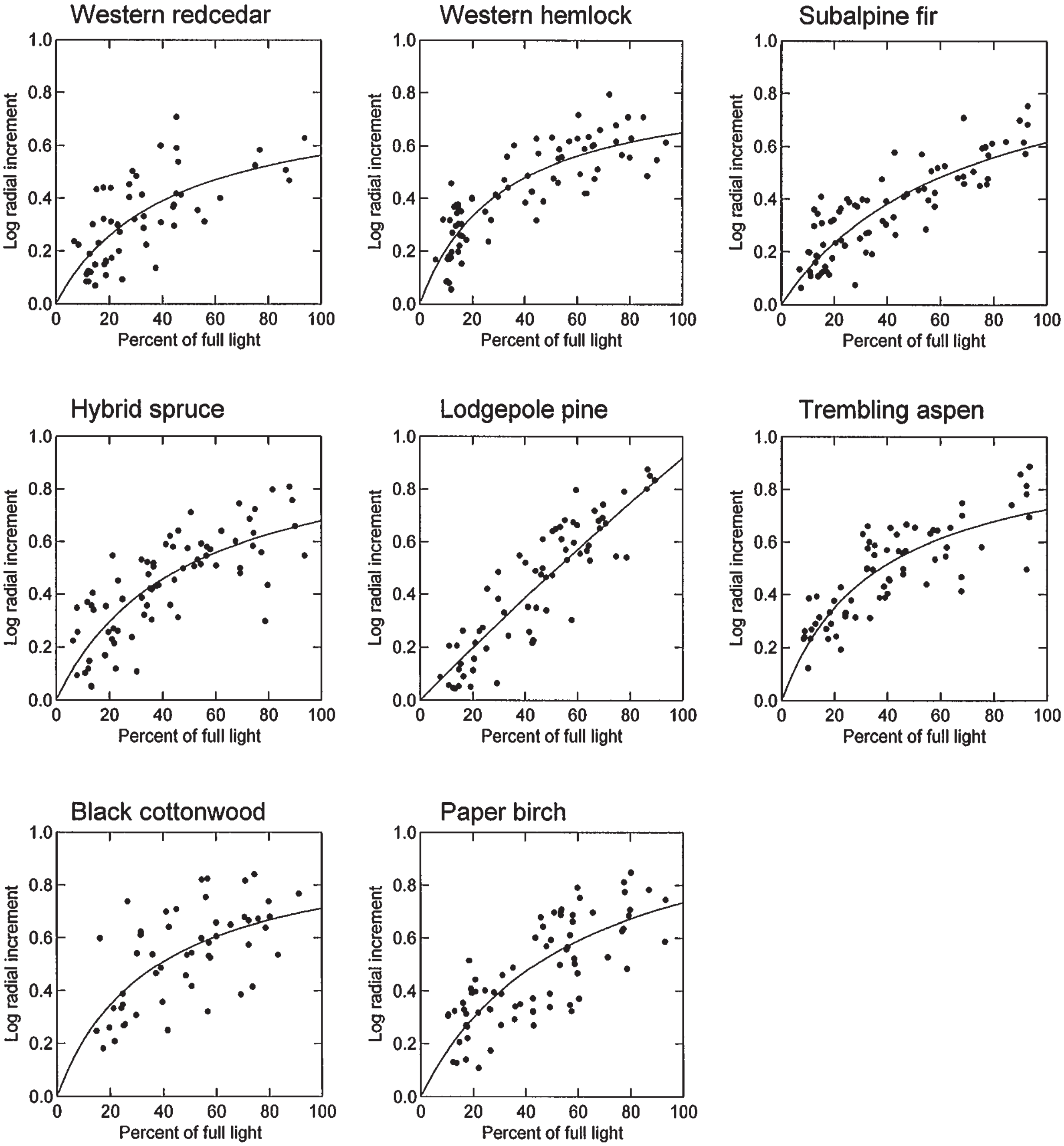
three species. Specifically, saplings in the coldest, wettest region (Snowy Temperate) had higher low-light growth and saplings in the warmest, driest region (Moist Temperate) had higher high-light growth, suggesting that all three species were slightly more shade tolerant on colder, wetter sites in these northern temperate forests (Fig. 4).

Discussion

Interspecific trade-offs between low-light and high-light growth

Our results confirm the expectation (e.g., Klinka et al. 1992; Walters et al. 1993; Pacala et al. 1994; Walters and Reich 1996) that species traditionally classified as shade tolerant had the greatest response to an increase in light at low-light levels (i.e., high *s* values), but had relatively low asymptotic growth at high light (i.e., low *a* parameter values). Conversely, species traditionally classified as shade intolerant tended to have weaker responses to increases in light at low light but had the highest growth (high *a* parameter values) at high-light levels. Radial growth of these conifer species in high-latitude temperate and boreal forests appear to have fundamentally different responses to light than deciduous species in tropical and lower latitude temperate forests (Fetcher et al. 1993; Pacala et al. 1994), where growth rates of most species sharply increase at very low light levels and can reach 50% of maximum growth at light

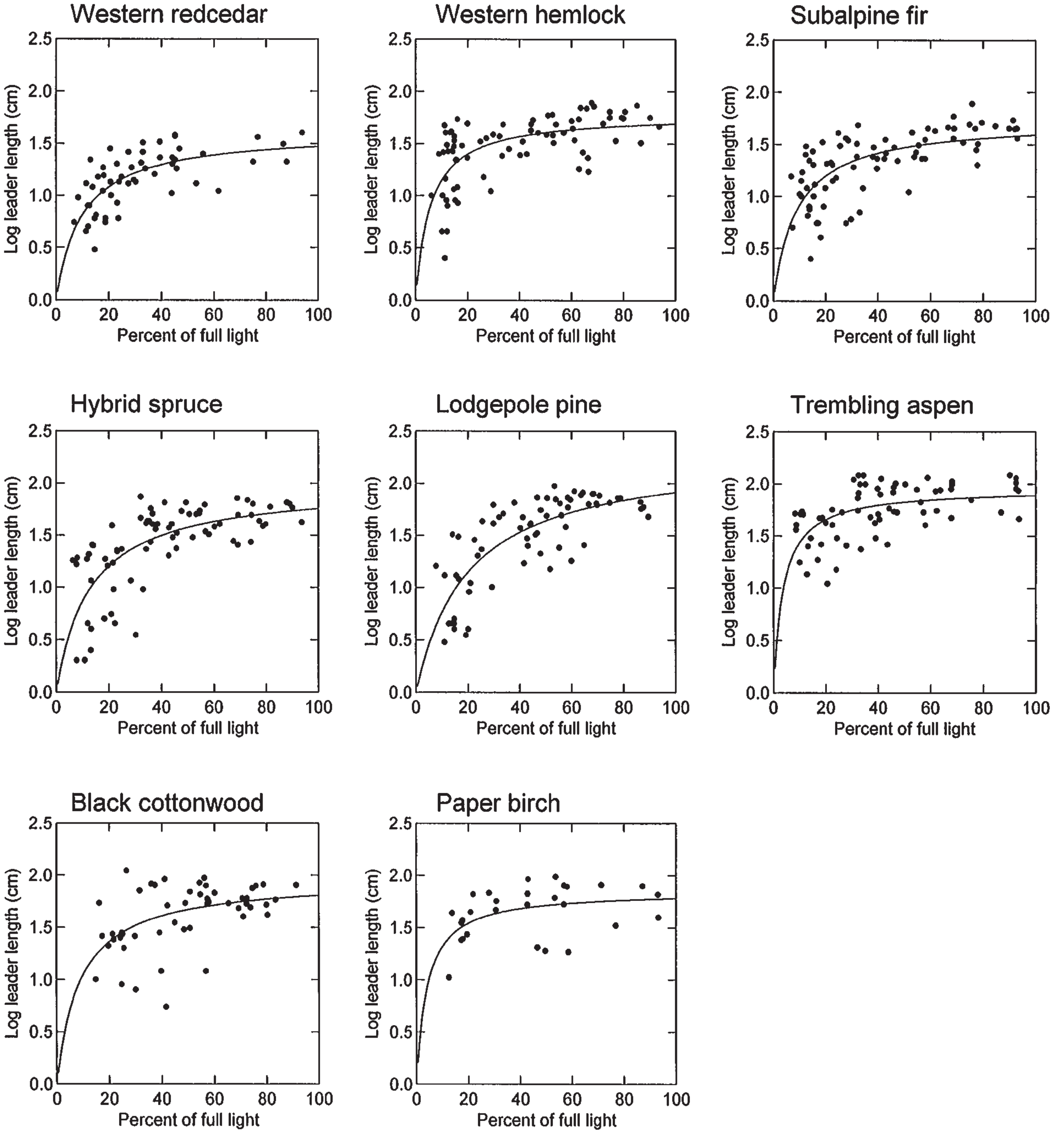
Fig. 5. Observed values and fitted regression lines of radial increment for western redcedar, western hemlock, subalpine fir, hybrid spruce, lodgepole pine, trembling aspen, black cottonwood, and paper birch in northern, Moist Temperate forests (ICHmc2) using parameter values in Table 3. Vertical axis is $\log_{10}$(5-year average radial growth (mm) + 1).



levels < 10% of full sun and near maximum growth at 20% full sun (Fetcher et al. 1993). In contrast, lodgepole pine in northern British Columbia requires 38–50% of full sun to reach 50% of maximum radial growth, and even the more shade tolerant species required 20–40% of full sun to reach 50% of maximum radial growth. Lower air temperatures and lower seasonal water deficits may reduce the temperature and drought stress commonly associated with exposure of saplings to full sunlight in lower latitudes. In contrast to radial growth, leader growth in all of our species increased rapidly, reaching at least 50% of maximum growth by 25% of full sunlight. Less than 5% of full sun was necessary for 50% of maximal leader growth of shade tolerant species such as western hemlock.

We only sampled the deciduous species (paper birch, black cottonwood, and trembling aspen) within the most moderate climate in our study area (the Moist Temperate region). Thus, we are unable to contrast growth trade-offs for these species across regional climate gradients. The three species had asymptotic growth rates that were similar to the conifers in the Moist Temperate region, but were not as high as might be expected for species traditionally considered very shade intolerant. Under low light, the deciduous species showed a faster increase in growth with increasing light than

Fig. 6. Observed values and fitted regression lines of leader length for western redcedar, western hemlock, subalpine fir, hybrid spruce, lodgepole pine, trembling aspen, black cottonwood, and paper birch in northern, Moist Temperate forests (ICHmc2) using parameter values in Table 4. Vertical axis is $\log_{10}$(leader length).

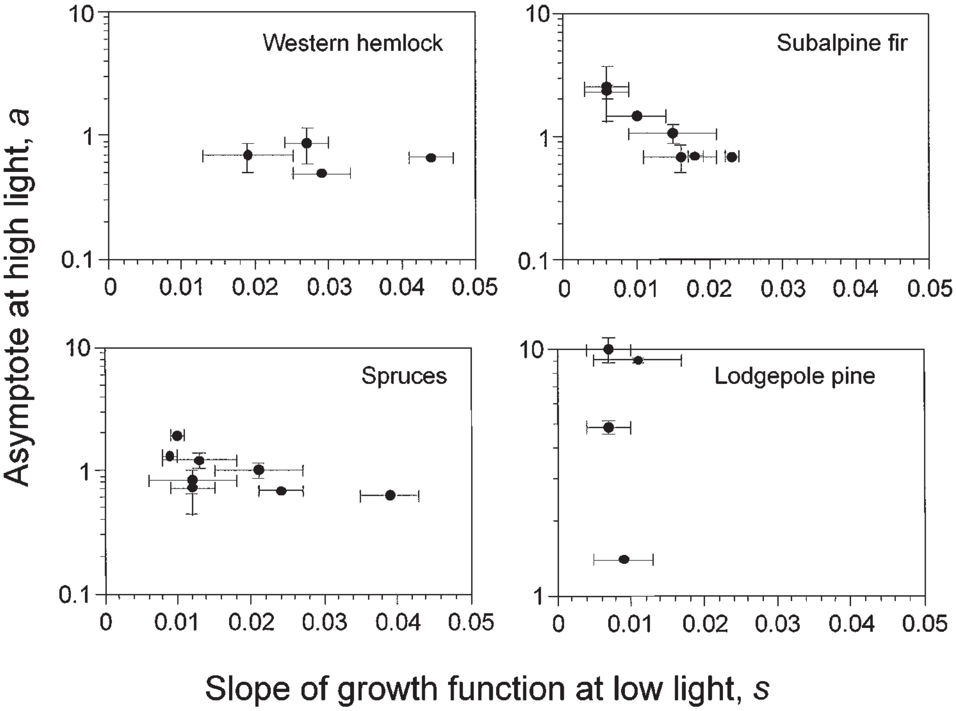


many of the conifers, again in conflict with our expectations for species that are traditionally considered the most shade intolerant in northwestern British Columbia but in agreement with other studies that have reported high low-light growth rates for shade-intolerant species (e.g., Loach 1970; McClendon and McMillen 1982; Walters et al. 1993; Kitajima 1994).

Intraspecific variation in response to light gradients in different climatic regions

Our results clearly demonstrate that there are shifts in the shapes of species-specific light response curves among the different climatic regions in northwestern British Columbia, rather than just proportionate increases in the amplitude of growth across all light levels (Fig. 8). Growth of lodgepole pine (the least shade tolerant of the conifer species) under low light was unrelated to regional climate, but its growth in high light varied considerably among the climatic regions, with the poorest growth in the harshest. High-light growth by hemlock (one of the most shade tolerant of the conifer species) was greatest in the most moderate region (Moist Temperate), but low-light growth was greatest in the coolest of the northern temperate regions (Snowy Temperate). Two species with moderate shade tolerance (hybrid spruce and

Fig. 7. Trade-off between growth at high light (*a*) versus the slope of the growth response at low light (*s*) for western hemlock, subalpine fir, spruce (includes hybrid spruce, interior spruce, and white spruce), and lodgepole pine across climatic regions using parameter values in Table 3. Each data point represents a growth function fit in a specific climatic region within the forest zone (see Tables 1 and 2). Error bars are 1SE of the estimated parameter values.



subalpine fir) varied both their asymptotic growth at high light and the slope of the light response curve under low light in different climates but maintained a clear trade-off among these two parameters in different climatic regions (Fig. 7). Both species had their greatest high-light growth in the most moderate climate (Moist Temperate region), but had the highest low-light growth in colder climates (the Snowy Temperate region for spruce and the Intermontane Boreal region for subalpine fir). This pattern of enhanced growth at low light in colder regions was inconsistent, notable exceptions being the very cold Subalpine and Plains Boreal regions. Interestingly both hybrid spruce and subalpine fir had their lowest growth across all light levels in the Continental and Transitional Subalpine regions, where they are the dominant species and reach their greatest relative abundance among all of the biogeoclimatic zones in the study area.

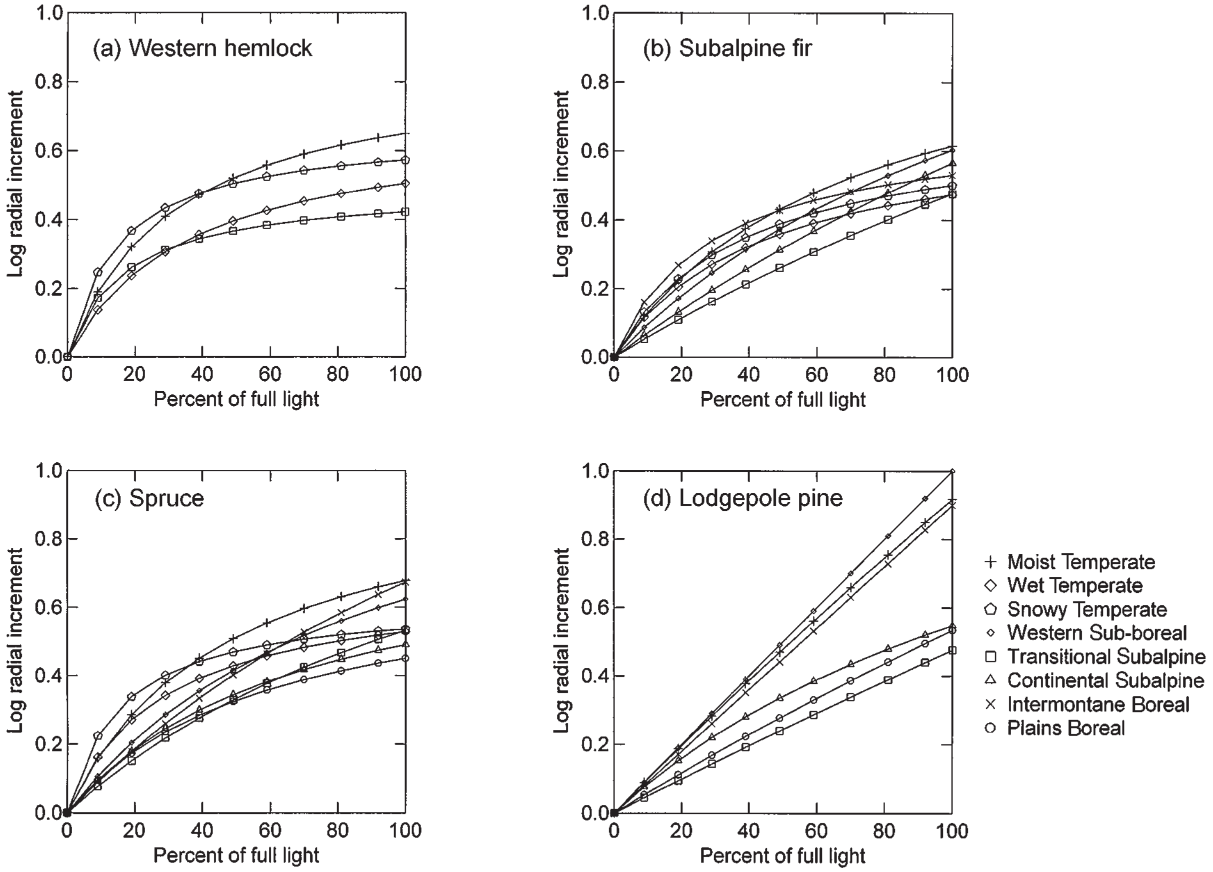
Thus, while high-light growth was consistently greatest in the most moderate climates, we also found some support for the hypothesis that low-light growth in conifers may be enhanced in colder climates (presumably because of lower maintenance respiration rates (Adams and Loucks 1971)). The overall magnitude of this effect was fairly small, varied among species, and was really only obvious in comparisons among the three temperate regions. The climates and physical environments of the nine climatic regions we sampled in this study differ in many ways, and it is possible that the observed pattern is correlated with temperature but causally related to some other environmental factor. For example, western hemlock, hybrid spruce, and subalpine fir all had higher growth rates at 5% full sun in the Snowy Temperate region with cool summers than in the Moist Temperate region with warmer summers. However, the warmer summers of the Moist Temperate region are also associated with more frequent drought stress than the Snowy Temperate region (Banner et al. 1993).

Our results clearly suggest that models that base predictions of community response to climate change on climate-dependent changes in optimal (i.e., high-light) growth, or that use simple multipliers that alter growth proportionately across light gradients (e.g., Soloman 1986, Pastor and Post 1988), will miss potentially important changes in low-light performance, particularly in shade-tolerant species (Pacala and Hurtt 1993). This is particularly critical in forests where gap-phase dynamics (and the resulting low to moderate light levels) represent the dominant natural disturbance regimes, and where partial cutting is or will be the dominant management practice.

Effects of interspecific variation in light-dependent growth rates on community dynamics

Despite the existence of interspecific trade-offs between high- and low-light growth in all four of the forest zones, the observed differences in both the shapes and the amplitudes of the whole-plant aboveground growth rates do not appear to be sufficient to play a dominant role in successional dynamics and competitive interactions in these forests. There is a striking degree of overlap in the light-response curves for the component species in virtually all of the regions (Figs. 3 and 4). The climatic region with the most diverse tree canopy (the interior cedar–hemlock (ICH) forests of the Moist Temperate region) had the weakest evidence of a low-light

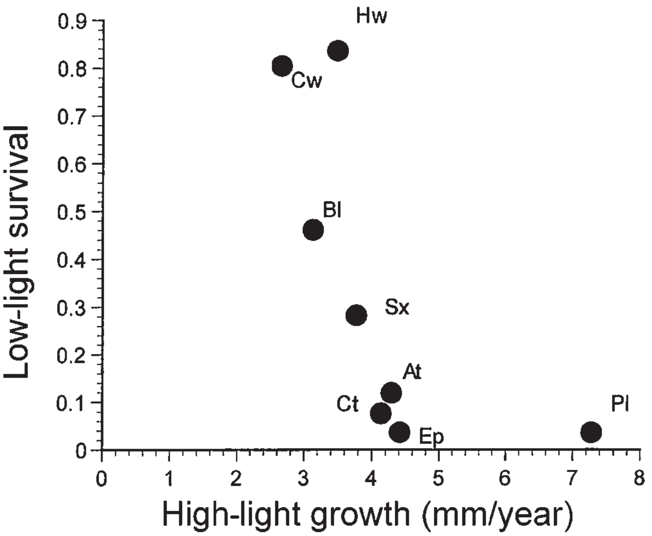
Fig. 8. Predicted radial growth as a function of percent of full light for western hemlock, subalpine fir, spruce, and lodgepole pine by climatic region using parameter values in Table 3. Vertical axis is $\log_{10}$(5-year average radial growth (mm) + 1).



versus high-light trade-off. With the exception of lodgepole pine, the light response curves for the remaining seven species show a striking degree of similarity (Figs. 4 and 5, Moist Temperate). Moreover, the scatterplots for both radial and height growth of species in the Moist Temperate forests show considerable within-species variability (Figs. 5 and 6). Some of that variability is undoubtedly due to measurement error, but some portion of the variability is certainly due to genetic and phenotypic variability among saplings. We recently completed the field work required to completely parameterize SORTIE, a spatially explicit model of forest dynamics (Pacala et al. 1996), for the ICH forests, and initial runs of the model (C.D. Canham, personal observation) indicate that interspecific variation in the shapes of light response curves would need to be far greater to be sufficient to generate the successional dynamics observed in ICH forests (Banner et al. 1993).

Pacala et al. (1996) present evidence that successional dynamics in a temperate forest in eastern North America were governed primarily by a trade-off between high-light growth and low-light survivorship (rather than growth) among species. Kobe and Coates (1997) have recently documented wide differences in mortality rates among ICH forest species as a function of recent growth, and found a wide range of low-light (i.e., low-growth) survivorship among species. The results reported here provide light response curves for the same species in the same sites as the species sampled by

Fig. 9. High-light growth (at 100% full sun, in millimeters per year) versus low-light survivorship (fraction surviving over 5 years at 5% full sun) for the eight tree species sampled in the Moist Temperate region. Survivorship was calculated from relationships presented in Kobe and Coates (1997) combined with relationships presented in this study. Species codes are given in Table 1.



Kobe and Coates (1997), and allow us to translate from their growth-dependent mortality rates to light-dependent mortality rates. A plot of high-light growth versus low-light survivorship (Fig. 9) shows both a trade-off and a very broad range of low-light survivorship. Initial runs with SORTIE for ICH forests (C.D. Canham, personal observation) confirm that the interspecific variation in low-light survivorship documented by Kobe and Coates (1997) is critical to successional dynamics in these forests. Thus, as was the case for the eastern temperate forests sampled by Pacala et al. (1996), we expect that successional dynamics in ICH forests will be more strongly governed by interspecific variation in sapling survival than growth in low-light conditions.

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