

# Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height

Yves Claveau, Christian Messier, Philip G. Comeau, and K. Dave Coates

**Abstract:** The effects of gradients in light levels and tree height on growth and crown attributes of six conifer species were studied in eastern and western Canada. Three conifers were studied in British Columbia (*Abies lasiocarpa* (Hook.) Nutt., *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm., and *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), and three in Quebec (*Abies balsamea* (L.) Mill., *Picea glauca*, and *Pinus banksiana* Lamb.). For several growth and morphological parameters, conifers reacted strongly to both an increase in light and tree height. Significant or nearly significant interactions between light classes and height were found for height and diameter growth of most species as well as for many crown attributes for both *Abies* and *Picea*. These interactions usually indicated that growth or morphological changes occurred with increasing height from a certain light level. Within a single genus, both eastern and western tree species showed the same overall acclimation to light and height. As generally reported, *Pinus* species showed less variation in growth and morphological responses to light than *Abies* and *Picea* species.

**Résumé :** Les effets de gradients d'intensité lumineuse et de hauteur des arbres sur la croissance et les attributs du houppier de six espèces de conifères ont été étudiés dans l'est et l'ouest du Canada. Trois espèces de conifères ont été étudiées en Colombie-Britannique (*Abies lasiocarpa* (Hook.) Nutt., *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm. et *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) et trois autres au Québec (*Abies balsamea* (L.) Mill., *Picea glauca* et *Pinus banksiana* Lamb.). Pour plusieurs paramètres liés à la croissance et à la morphologie, les conifères réagissent fortement à la fois à une augmentation de la lumière et de la hauteur des arbres. Des interactions significatives ou presque significatives entre les classes de lumière et de hauteur ont été trouvées pour la croissance en hauteur et en diamètre de la plupart des espèces ainsi que pour de nombreux attributs du houppier dans le cas d'*Abies* et de *Picea*. Ces interactions signifient habituellement que les changements dans la croissance ou la morphologie apparaissent avec une augmentation de la hauteur à partir d'un certain niveau de lumière. À l'intérieur d'un genre, les espèces de l'Ouest et de l'Est montrent la même acclimatation globale à la lumière et à la hauteur. Tel que rapporté généralement, les espèces de *Pinus* montrent moins de variation dans leurs réponses à la lumière, dans le cas de la croissance et de la morphologie, que les espèces d'*Abies* et de *Picea*.

[Traduit par la Rédaction]

## Introduction

Boreal forests are regularly subjected to various types of large- and small-scale disturbances that open up the canopy (Bergeron and Dubuc 1989; Antos et al. 2000). In these forests, both shade-intolerant and -tolerant tree species can establish in openings created by disturbance (Kneeshaw and

Bergeron 1998), but their long-term survival is dependent on the interplay between available light and growth rates (i.e., Kobe and Coates 1997; Barnes et al. 1998).

Differences among tree species in their response to light availability are related to various acclimations that influence their ability to capture light. For example, as light intensity declines, *Abies* species typically produce a flatter and shorter crown to capture light more efficiently (Kohyama 1980; O'Connell and Kely 1994) and to decrease self-shading within the crown (Kohyama 1991). Less shade-tolerant species such as *Picea* and *Pinus* also show similar acclimation but not as clearly as *Abies*, and this trend decreases with shade intolerance (Fabijanowski et al. 1975; O'Connell and Kely 1994; Williams et al. 1999). *Abies*, and to a lesser extent *Picea*, can drastically reduce their height and diameter growth without dying, which is not the case for less shade-tolerant *Pinus* species (Kobe and Coates 1997). Shade-tolerant species can also retain their foliage longer, hence requiring a lower production rate to maintain a constant foliage area (King 1994).

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**Table 1.** Description of study sites.

	British Columbia			Quebec		
	Lodgepole pine	Interior spruce	Subalpine fir	Jack pine	White spruce (site 1, site 2)	Balsam fir (site 1, site 2, site 3)
Latitude (N)	52°30'	54°07'	52°29'	48°30'	48°27', 48°26'	48°31', 48°26', 48°27'
Longitude (W)	121°46'	122°04'	121°40'	79°08'	79°26', 79°18'	79°24', 79°18', 79°15'
Mean annual precipitation (mm)	722 <sup>a</sup>	930.9 <sup>b</sup>	722 <sup>a</sup>	857 <sup>c</sup>	857 <sup>c</sup>	857 <sup>c</sup>
Mean annual temperature (°C)	4.2 <sup>a</sup>	2.6 <sup>b</sup>	4.2 <sup>a</sup>	0.8 <sup>c</sup>	0.8 <sup>c</sup>	0.8 <sup>c</sup>
Ecological classification <sup>d</sup>	ICHmk3	SBSwk1	ICHmk3	5a-T MS26	5a-T MS26	5a-T MS26
Drainage <sup>e</sup>	Mesic	Subhydric	Mesic	Submesic	Mesic	Mesic
Slope (%)	10	4	<20	5	8, 6	10, 6, 6
Frost-free period (days)	166 <sup>a</sup>	na <sup>f</sup>	166 <sup>a</sup>	64 <sup>c</sup>	64 <sup>c</sup>	64 <sup>c</sup>

<sup>a</sup>Steen and Coupé (1997).

<sup>b</sup>British Columbia Ministry of Forests (1996).

<sup>c</sup>Environment Canada (1993).

<sup>d</sup>ICHmk3, Interior Cedar-Hemlock, moist cool subzone, Horsefly variant (Steen and Coupé 1997); SBSwk1, Sub-Boreal Spruce, willow wet cool subzone (British Columbia Ministry of Forests 1996); 5a-T MS26, boreal balsam fir and white birch domain, balsam fir and white birch type on sub-hydric and fine-textured soil (Grondin et al. 1998).

<sup>e</sup>Following Saucier (1994).

<sup>f</sup>na, information not available.

While the influence of light availability on various measures of seedling and sapling performance has received considerable study (Logan 1969; Klinka et al. 1992; Parent and Messier 1995; Wright et al. 1998; Coates and Burton 1999), how these responses vary with tree height is not well understood. Tree height influences the ability of trees to survive under shaded conditions (Messier et al. 1999). Larger trees have a better capability to capture resources, but since the ratio of respiring nonphotosynthetic to photosynthetic tissues increases with increasing size (Givnish 1988), larger trees will require more light to survive and to achieve a positive net carbon gain and grow. Understory trees growing in constant low light might not be able to survive as they continue to increase in height, since more resources are required to support nonphotosynthetic tissues (Messier et al. 1999). Givnish (1988) illustrates such a situation where a yellow-poplar (*Liriodendron tulipifera* L.) of 1 m needs 12% of full light for its construction and respiration costs, 25% when 10 m tall and 75% of full light when it reaches 30 m in height.

A greater diversity of cutting practices are now being applied in the northern forests of Canada because of social pressure against traditional clear-cutting, a broader range of management objectives, and the emerging concepts of ecosystem management (Christensen et al. 1996). Efforts to reconcile ecosystem sustainability and cost-effective wood production have led to the development of partial-cutting practices that mimic the natural processes of these forests (Liefers et al. 1996a; Bergeron and Harvey 1997; Bergeron et al. 1999). As these practices increase in the northern forests of Canada we require a better understanding of how northern tree species respond to variable light conditions.

The primary objective of this study was to examine how ambient light conditions and tree height interact to influence growth and crown morphological acclimation of representative boreal and sub-boreal tree species with contrasting shade tolerance. We had two specific objectives: (i) to investigate how tree height (from 30 to 400 cm tall) affects seedling and sapling growth and crown morphological acclimations across a light gradient and (ii) to determine if such acclima-

tions are consistent between eastern and western genera of *Abies*, *Picea*, and *Pinus* species.

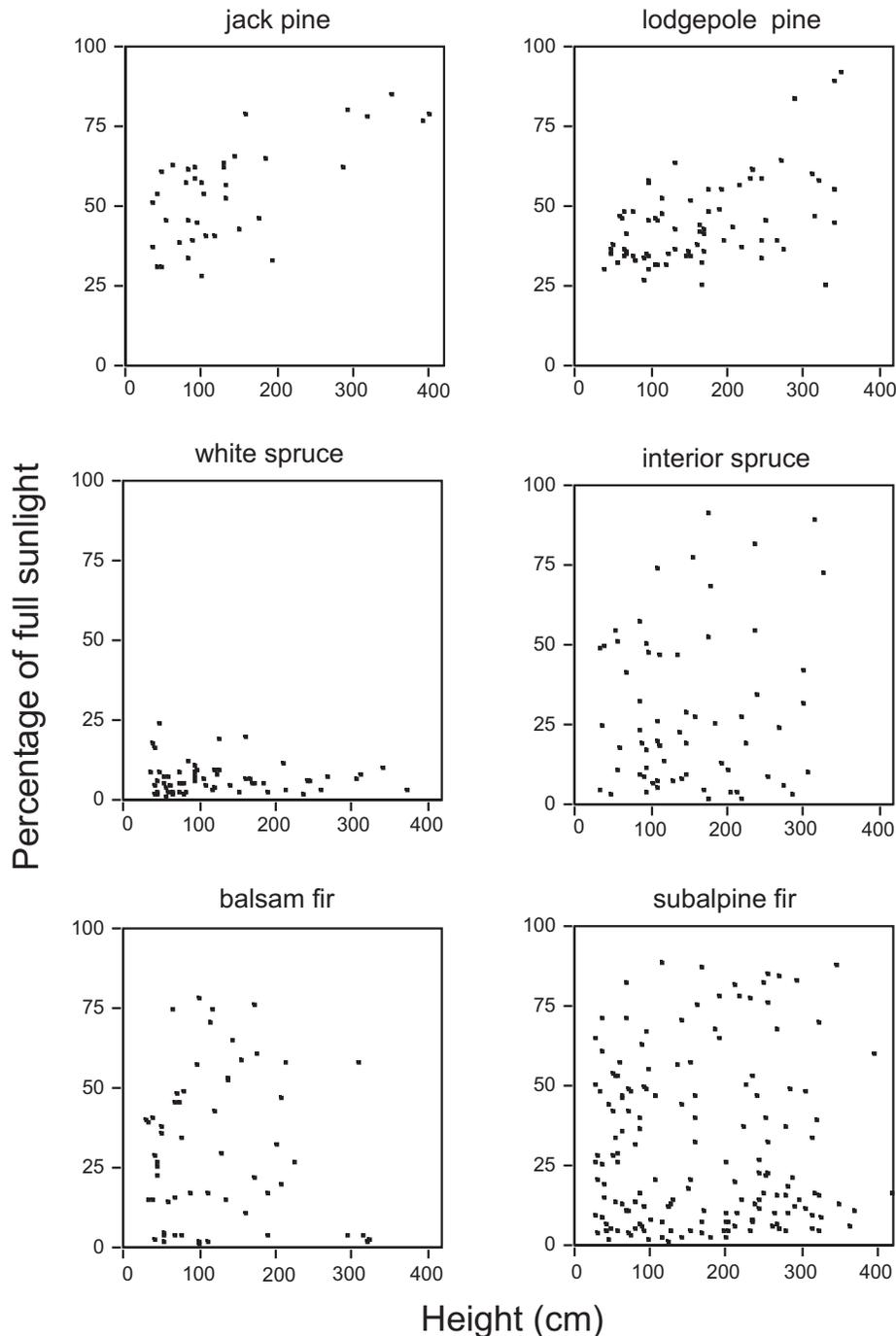
## Materials and methods

### Study sites and sample trees

Tree species were sampled in two major geographic areas: subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), interior spruce (a complex of white spruce (*Picea glauca* (Moench.) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in central British Columbia and balsam fir (*Abies balsamea* (L.) Mill.), white spruce, and jack pine (*Pinus banksiana* Lamb.) in northwestern Quebec. The shade-tolerance ranking of these species, from the most to the least tolerant, is as follows: balsam fir = subalpine fir > white spruce = interior spruce > lodgepole pine = jack pine (Klinka et al. 1990; Sims et al. 1990; Kobe and Coates 1997).

Three study sites in British Columbia and six in Quebec were selected (Table 1). They were selected to ensure that trees of each species could be sampled across a full light gradient (Fig. 1). For each species, care was taken to select stands within the same soil drainage and soil texture classes. Stands with multicanopied structure were preferred, because they offered better opportunities for finding a range of sample tree heights across light gradients. Areas disturbed within the last 10 years (e.g., harvesting, blowdown, insect-related attack) were avoided. Study trees were sampled along 5 m wide transects established along gradients of stand density. Study trees were straight, healthy, without a fork influencing the first node and free of competition. Sample trees varied in height from 0.3 to 4.0 m but could vary widely in age (Fig. 1). White spruce in Quebec was not sampled across the full light gradient (Fig. 1) because of difficulties in finding white spruce in the studied area. We were unable to find jack pine or lodgepole pine over 2 m at the lowest light levels. Sample trees were measured and harvested at the beginning or the end of the growing season during 1996, 1997, and 1998.

**Fig. 1.** Scatterplots of percentage of full sunlight in function of height for jack pine (mean age 17 years,  $n = 37$  trees), lodgepole pine (mean age 40 years,  $n = 74$  trees), white spruce (mean age 33 years,  $n = 42$  trees), interior spruce (mean age 22 years,  $n = 66$  trees), balsam fir (mean age 25 years,  $n = 96$  trees), and subalpine fir (mean age 38 years,  $n = 98$  trees).



### Light measurements

The light environment of each sample tree was measured at the top of the tree using hand-held sensors. Two methods were used to measure light intensity: (i) quantum sensors on overcast days and (ii) LAI-2000 units (LI-COR, Inc., Lincoln, Nebr.) following Gendron et al. (1998). The LAI-2000 method was used from the second field season, because it provides consistent estimates of light availability under various sky conditions. Readings from these two methods are

highly correlated and are closely related to growing season light measurements (Comeau et al. 1998; Gendron et al. 1998).

For the overcast day method, sample tree light measurements were obtained using a LI-189 and a LI-190SA quantum sensor (LI-COR, Inc., Lincoln, Nebr.). Open sky readings were taken in a nearby opening with a LI-190SA quantum sensor linked to a LI-1000 datalogger (LI-COR, Inc., Lincoln, Nebr.). The datalogger recorded measurements

every 5 s and stored 1-min averages. With the LAI-2000 method, the procedure was similar except that when measurements were taken under clear or variable sky conditions. In such a case, a 180° view restrictor was first placed over each sensor. Two readings, one in the morning and one in the afternoon, were taken so direct sunlight could not reach the sensors. Readings were in opposite directions to have a complete coverage of tree's environment. Values from sample tree and open conditions were used to convert all sample tree readings to percent of full sunlight (PFS) where data from the LAI-2000 were compiled for all rings.

### Sample tree measurements and variables

Various attributes of tree performance were measured in the field and laboratory: maximum needle age (the number of years where more than 50% of the needles still remain on the bole); crown length; mean crown diameter (crown diameters measured along north-south and east-west axes); tree height; mean yearly height increment for the last 4 years; number of branches at the upper node; length of the longest first-order lateral at the upper node; and root collar diameter. The following variables were calculated: live crown ratio (LCR; (crown length/tree height) × 100); crown profile (CP; (crown length/mean crown diameter) × 100); leader/lateral branch ratio (current height growth/longest first-order lateral); and height/diameter ratio.

In the laboratory, a disk was cut above butt swell and sanded to have an estimate of sample tree age and to determine diameter growth in the last 4 years. Ring width was measured using a micrometer (Velmex Unislide TA, New York) on four perpendicular radii offset by 22.5° from the largest diameter (Siostrzonek 1958, in Zarnovican 1985). Diameter growth was averaged for each year over the 4-year period.

### Analyses

ANCOVA was used for the following reasons: it represents the pattern of observations, it considers the height gradient within each class (Sokal and Rohlf 1995; Underwood 1997), and it can determine the presence of interactions between the categorical variable and the covariate.

Our exploratory data analyses revealed novel patterns in our data, and we sought a statistical approach that would best illustrate our findings. For instance, graphs of height growth against height showed distinct groups of seedlings, particularly where light levels were between 10 and 50% of full sunlight, and these groups were consistent for many morphological characteristics within the same species. The statistical analyses needed to be able to consider these patterns if we wanted to confirm our observations. Multiple linear regression failed to adequately represent these patterns. Hence, light measurements were divided into four classes of percent of full sunlight: 0–10, 10.1–25, 25.1–50, and 50.1–100%. These four light classes were also meant to represent very closed, closed, patchy, and very patchy to open canopy conditions, respectively.

The presence of interaction between light classes and height was investigated following the model:

$$[1] \quad \text{Variable} = \mu + \text{PFSC} + H + \text{PFSC} \times H + \varepsilon$$

where  $\mu$  is the overall mean, PFSC is the percentage of full sunlight class,  $H$  is the tree height as a covariate, and  $\varepsilon$  is the error term. Data were transformed when needed. Significance level was set at  $p = 0.05$ . The analyses were performed with the general linear models procedure of SYSTAT version 8.03.

## Results

### Interaction between light classes and height

The general linear model (Table 2) indicated significant or nearly significant interactions between light classes and height for many variables and species, so that many single factors could not be interpreted alone. Nevertheless, tree height and light class alone were important factors. Height and diameter growth were the only variables where most species showed a significant interactive term, while firs presented significant interaction terms for most of their crown parameters.

For height and diameter growth, the interactions indicated that growth increased with both height and light class above a given minimum light class (Figs. 2 and 3). These minimum light classes were 10, 10, and 25% of full sunlight for interior spruce, balsam fir, and subalpine fir, respectively. Below these light classes, growth was unaffected by tree height.

The significant interaction term for live crown ratio indicated that the crowns became thinner as height increased below 10 or 25% light classes for balsam fir and subalpine fir, respectively, (Fig. 4). Similarly, the significant interaction term for crown profile indicated that crowns became slender (higher crown profile values) as height increased above 10 or 25% of full sunlight for balsam fir and subalpine fir, respectively (Fig. 5). A similar trend was also found for the leader-to-branch ratio for both subalpine and balsam fir (Table 2, data not shown). The results for spruces followed the general pattern observed with firs, but the interactive terms were not significant (Table 2, Figs. 4 and 5).

### Comparison among species and between regions

Morphological variables of pines did not generally vary with light classes or height except for the number of nodal branches where values increased with height (Table 2, Figs. 4 and 5; data not shown for number of nodal branches). Pines had higher crown profile values (slender crowns) (Fig. 5) and higher height/diameter ratios (data not shown) than spruces and firs. Maximum needle age was lower for the most shade-intolerant species (jack pine (mean 2.9 years) < lodgepole pine (5 years) = balsam fir (5.4 years) < subalpine fir (6.6 years) = interior spruce (6.8 years)), and it tended to decrease with height for balsam fir (data not shown).

Firs and pines in eastern and western Canada were, overall, equally affected by light classes, height, and the interaction between these two factors. However, differences were observed between spruces but are likely related to the different number of light classes used for each species.

**Table 2.** General linear model results (*F* values and probabilities) of height and diameter growth, height/diameter ratio, live crown ratio, crown profile, leader/branch ratio, number of nodal branches, and needle age for each study species.

Source of variation	Lodgepole pine		Jack pine		Interior spruce		White spruce		Subalpine fir		Balsam fir	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
<b>Height growth</b>												
Light class (L)	3.522	0.071	4.474	0.042	2.057	0.116	0.532	0.470	3.126	0.031	1.892	0.139
Height (H)	120.7	<0.001	84.36	<0.001	65.45	<0.001	5.879	0.020	69.73	<0.001	26.10	<0.001
L × H	3.068	0.091	9.024	0.005	6.418	0.001	0.458	0.503	25.21	<0.001	2.941	0.039
df error		27		34		56		41		75		72
<b>Diameter growth</b>												
L	0.569	0.457	1.739	0.196	3.242	0.028	0.690	0.417	0.185	0.906	1.861	0.147
H	51.76	<0.001	21.41	<0.001	34.84	<0.001	25.38	<0.001	61.83	<0.001	25.34	<0.001
L × H	1.582	0.219	1.510	0.228	2.937	0.041	8.661	0.009	18.79	<0.001	3.689	0.017
df error		27		33		58		18		72		53
<b>Height/diameter ratio</b>												
L	4.378	0.046	0.781	0.383	0.524	0.667	0.095	0.760	0.137	0.938	1.175	0.324
H	0.328	0.572	0.628	0.433	1.141	0.290	0.389	0.538	4.198	0.045	9.476	0.003
L × H	4.745	0.039	0.037	0.849	2.366	0.080	0.093	0.762	1.804	0.155	0.247	0.863
df error		26		34		58		28		64		89
<b>Live crown ratio</b>												
L	0.807	0.372	0.156	0.696	1.704	0.177	0.100	0.753	18.54	<0.001	1.637	0.187
H	4.293	0.042	0.075	0.786	4.298	0.043	0.029	0.866	4.930	0.003	0.000	0.988
L × H	2.497	0.119	0.000	0.983	2.288	0.088	0.058	0.811	8.960	<0.001	10.73	<0.001
df error		68		34		56		40		121		89
<b>Crown profile</b>												
L	0.673	0.415	0.787	0.381	5.391	0.002	0.000	0.994	4.354	0.006	0.574	0.634
H	0.000	0.986	0.272	0.605	7.474	0.008	0.002	0.969	7.890	0.006	5.064	0.027
L × H	1.684	0.199	0.326	0.572	1.175	0.327	0.324	0.573	7.313	<0.001	4.973	0.003
df error		68		34		56		40		115		89
<b>Leader/branch ratio</b>												
L	0.453	0.508	4.750	0.037	4.063	0.012	2.380	0.135	2.827	0.048	4.673	0.005
H	1.000	0.328	2.259	0.143	1.552	0.219	0.004	0.950	25.26	<0.001	17.99	<0.001
L × H	0.018	0.895	4.898	0.034	0.622	0.604	0.015	0.903	6.226	0.001	2.691	0.053
df error		22		31		49		25		51		67
<b>No. of nodal branches</b>												
L	1.716	0.202	0.246	0.623	2.643	0.058	2.076	0.161	0.523	0.668	3.977	0.011
H	6.797	0.015	16.64	<0.001	0.189	0.666	0.938	0.342	0.754	0.388	1.694	0.197
L × H	0.562	0.460	1.751	0.195	1.366	0.262	0.255	0.618	1.834	0.150	1.427	0.241
df error		26		34		57		27		63		76
<b>Needle age</b>												
L	0.040	0.842	3.940	0.055	3.085	0.034	0.278	0.601	2.114	0.103	1.208	0.312
H	1.886	0.174	1.046	0.314	5.427	0.023	1.387	0.247	0.176	0.676	7.912	0.006
L × H	0.045	0.832	2.019	0.164	1.775	0.162	0.079	0.780	1.831	0.146	1.370	0.258
df error		68		34		56		35		113		83

Note: Pines and white spruce have two light classes, and the remaining species have four.

## Discussion

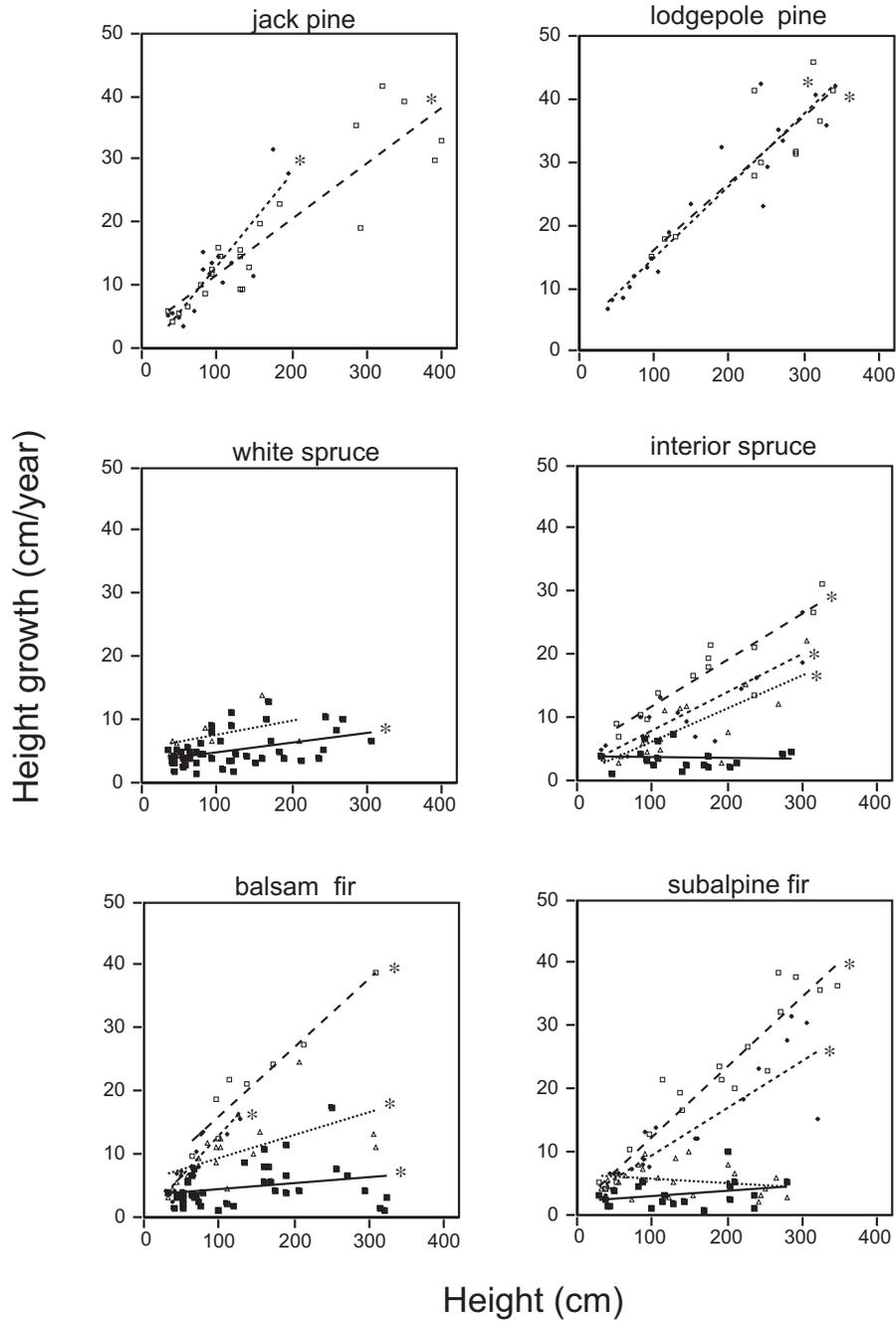
### Interacting effects of light and height

This study examined the growth and crown morphological response of conifers of three different genera growing in two geographical areas of northern and boreal forests to a wide range of overstory canopy openings and tree height. Previous studies of plant acclimation to changing light environment rarely considered the influence of height on the observed responses. Our study clearly demonstrates that tree growth and crown morphology varied as a function of light availability and tree species shade-tolerance ranking as has been observed elsewhere (e.g., Logan 1969; Kohyama 1980;

Chen et al. 1996; Wright et al. 1998). However, the observed responses often varied considerably as a function of tree height, and there were, in many cases, strong interactions between light intensity and tree height. These results show the importance of considering both plant size (height) and light environment when predicting growth rates or morphological variables.

Our study reveals that the typical increase in growth rate with age (height) found in young even-aged stands (e.g., Assmann 1970) under full light conditions also occurs under partial shading. Loeffers et al. (1996b) studied white spruce growth under a uniform trembling aspen (*Populus tremuloides* Michx.) canopy and also noted a marked rise in

**Fig. 2.** Scatterplots of height growth versus height for all light classes. Light classes are as follows: 0–10% of full sunlight (solid line and solid squares); 10.1–25% of full sunlight (dotted line and triangles); 25.1–50% of full sunlight (short dash line and crosses); and 50.1–100% of full sunlight (large dash line and open squares). Asterisk shows a significant slope ( $p \leq 0.05$ ).

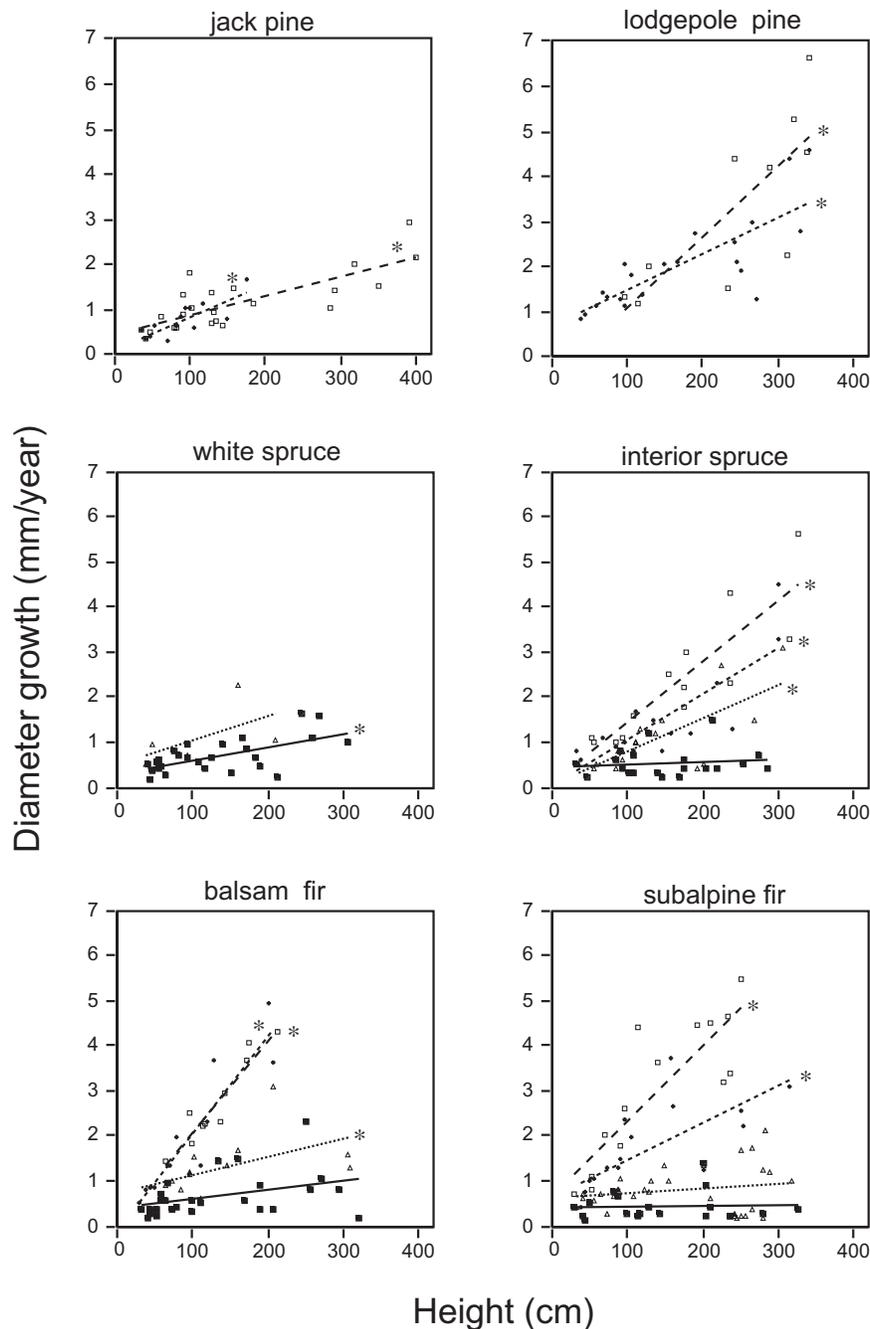


height increment as individual saplings increased in height. Similar results were also found by Williams et al. (1999) who observed increasing differences in growth across a light gradient as height increased for understory Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). While the interaction between tree height and light continues through the tallest trees from our study (about 4 m), it is unclear whether this interaction will continue with larger trees. Analysis of unpublished data from Wright et al. (1998) suggest that the influence of height may diminish as trees approach 6 m in height. This suggests that conifers require a certain amount of crown before they can maximize their growth rate, and

that the “optimum” crown volume may be attained at around 5–6 m height for the conifer species that were examined.

Under the darkest light conditions, height did not influence growth of interior spruce or the firs. These results are consistent with those obtained by Kubota et al. (1994) who found that height growth of deeply shaded *Abies sachalinensis* Masters was constant regardless of the diameter class. The lack of growth response in low light could be associated with a decrease in the ratio of photosynthetic to nonphotosynthetic tissue as tree height increases (Waring 1987; Givnish 1988; Messier and Nikinmaa 2000; Y. Claveau, C. Messier, and P.G. Comeau, in preparation). A

**Fig. 3.** Scatterplots of diameter growth versus height for all light classes. See Fig. 2 for explanations of symbols.

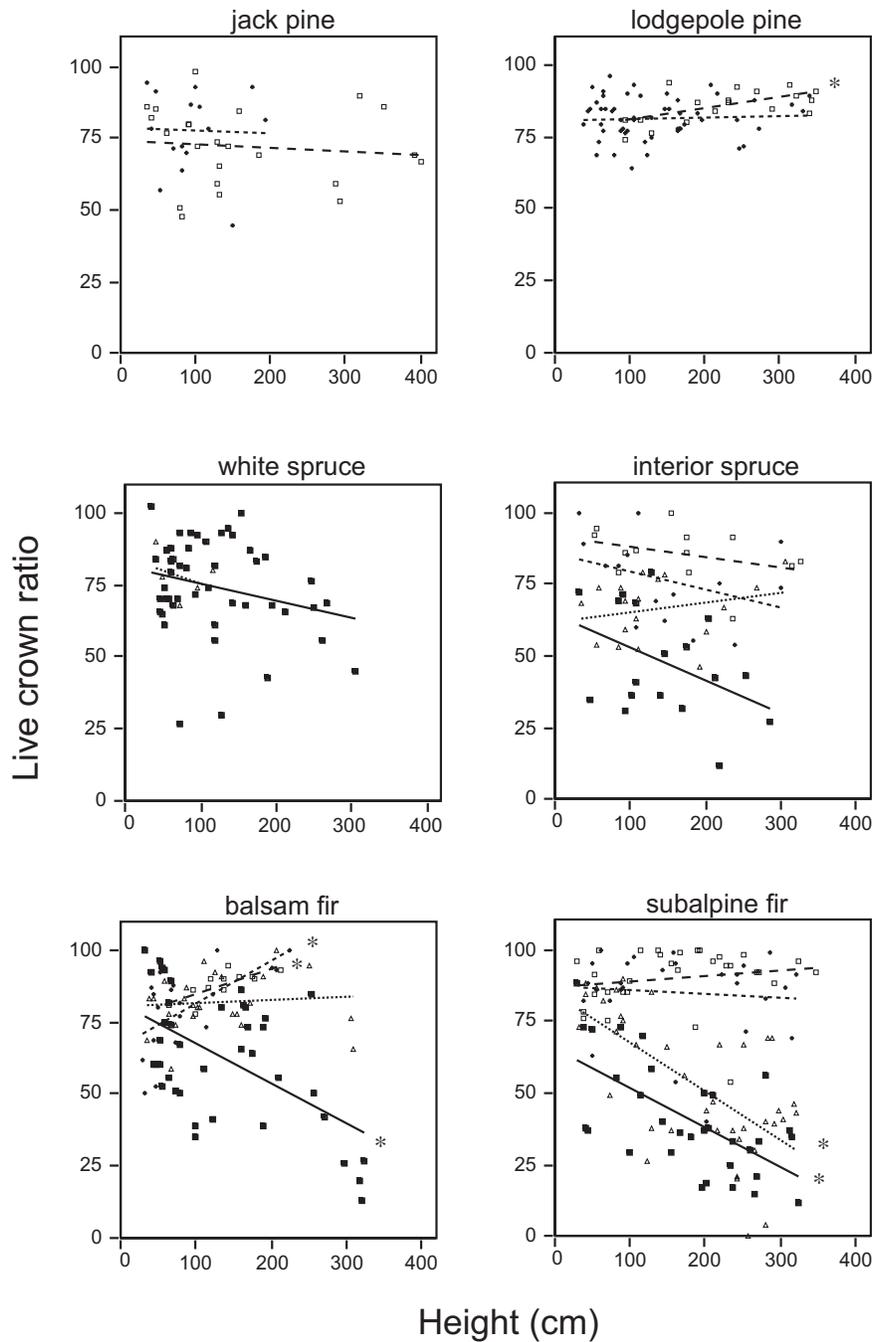


change in this ratio is believed to be the reason why trees require an increasingly greater amount of light for normal growth and survival as they become taller (Givnish 1988; Messier and Nikinmaa 2000). Gerrish (1990) used the term “carbon starvation” to explain the trend of higher mortality with increasing tree height. Messier et al. (1999) further suggested that the ability of shade-tolerant trees to reduce their growth when experiencing light limitation can be seen as an adaptation for maintaining a balance between photosynthetic and nonphotosynthetic tissues.

Many traits in trees are directly or indirectly related to tree height. For example, tree crown (Lieffers et al. 1996b) and root system volume (Cavender-Bares and Bazzaz 2000)

are directly related to tree height, and as a result, taller trees can capture more resources to sustain increasing growth. On the other hand, the yearly additions of branches with any increase in tree height can shade lower branches, and so light conditions at the bottom part of the crown may become so low that trees cannot maintain their lower branches (Givnish 1988), which may lead to a decrease in live crown ratio under the lowest light conditions. The effect of height on many of our measured crown morphological parameters presented here was not attributed to a correlation with light intensity (or light classes), since both variables were found to be independent for *Abies* and *Picea* ( $r = 0.08\text{--}0.19$ ;  $p = 0.08\text{--}0.45$ ). In conclusion, variation of traits with height can follow an

**Fig. 4.** Scatterplots of live crown ratio versus height for all light classes. See Fig. 2 for explanations of symbols.



allometric relationship or result from a dynamic interplay between light intensity, tree traits, and size as shown in this study.

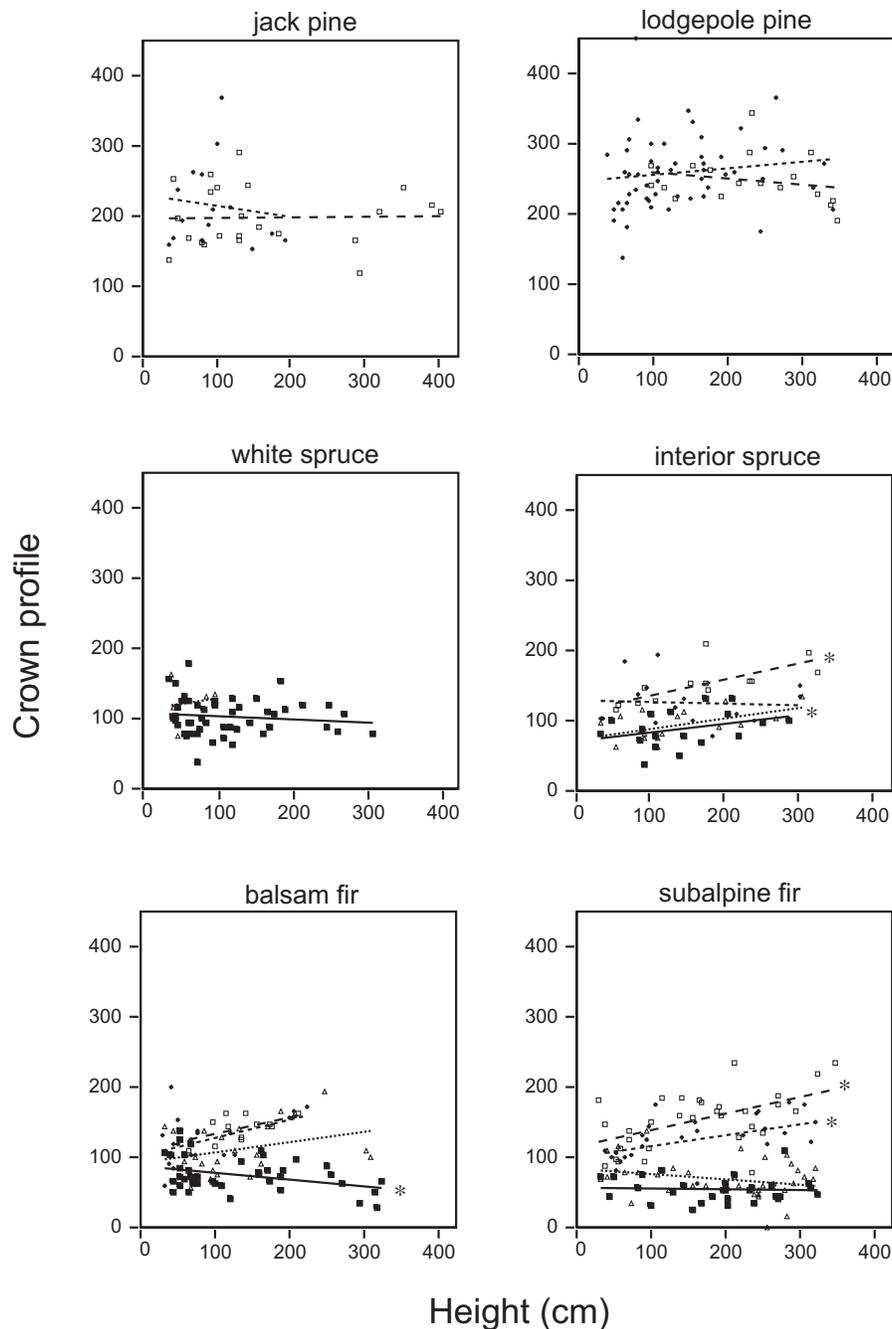
**Differences among species and between regions**

The *Pinus*, *Abies*, and *Picea* species in our study are close relatives based on morphological, genetic, or ecological characteristics (Mirov 1967; Robson et al. 1993; Sigurgeirsson and Szmidt 1993). Their genetic differences are relatively low, since they can form viable hybrids (Pielou 1988). Within a genus, growth and crown morphological responses in Quebec and British Columbia followed the same general pattern along light classes and the height gradient.

There were, however, some subtle differences between geographic regions in crown responses for the most shade-tolerant tree species under closed to very closed canopy conditions. At <10% full sunlight, the eastern fir and spruce species carried a higher live crown ratio, thus had larger crowns per unit of height, than the western species of the same genera. We think these differences could be related to canopy tree composition, where eastern and western species were under hardwood and conifer canopy species, respectively.

As observed in other regions of the world, our study supports the expectation that the more shade-tolerant *Abies* and *Picea* species show the most plasticity in their crown mor-

**Fig. 5.** Scatterplots of crown profile versus height for all light classes. See Fig. 2 for explanations of symbols.



phological responses to a strong gradient of light compared with the more light demanding *Pinus* species (e.g., Fabijanowski et al. 1974, 1975; Brunner 1993; Takahashi 1996). Overall, our broad geographical study confirms other, and often methodologically varied, studies that indicate that conifer species of the same genus tend to have similar strategies for acclimating to the various understory light environments found in northern and boreal forests.

#### **Ecological and silvicultural implications**

Understory seedling and sapling dynamics depend not only on species-specific regeneration and mortality rates but also on growth rates (Kato and Yamamoto 2001). Growth

drives the ascent of trees into the main canopy, and individuals showing greater growth rate will have the best chance of reaching the main canopy (Orwig and Abrams 1994). Our study suggests that there exists a subtle interplay between understory tree height and light availability that can affect understory tree dynamics. Taller individuals should have a competitive advantage in terms of growth and survival above a given light level, but may be at a disadvantage at lower light levels compared with shorter individuals. These findings could affect silvicultural decisions. For example, whether to protect short or tall residual trees during partial cutting should to some extent depend on the degree of canopy openness prescribed and the resultant understory light levels.

As forest management becomes more complex, there is an increasing reliance on simulation models to develop and test alternative management strategies. A critical element for any model is the prediction of tree growth rates across environmental gradients and under different stand compositions. Our study clearly has shown that simulation models that simulate the growth of understory trees should incorporate both height and light as important parameters.

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