

Interacting influence of light and size on aboveground biomass distribution in sub-boreal conifer saplings with contrasting shade tolerance

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Summary Plant size often influences shade tolerance but relatively few studies have considered the functional response of taller plants to contrasting light environments. Several boreal and sub-boreal *Abies*, *Picea* and *Pinus* species were studied along a light (0–90% full sunlight) and size (30–400-cm high) gradient to examine the interactive influence of tree size and light availability on aboveground biomass distribution. Sampling was conducted in two regions of Canada: (A) British Columbia, for *Abies lasiocarpa* (Hook.) Nutt., the *Picea glauca* (Moench.) Voss × *P. engelmannii* Parry ex. Engelm. complex and *Pinus contorta* Dougl. var. *latifolia* Engelm.; and (B) Québec, for *Abies balsamea* (L.) Mill., *Picea glauca* (Moench. Voss) and *Pinus banksiana* (Lamb.).

All biomass distribution traits investigated varied with size, and most showed a significant interaction with both size and light, which resulted in increasing divergences among light classes as size increased. For example, the proportion of needle mass decreased as size increased but the rate of decrease was much greater in saplings growing at below 10% full sunlight. Needle area ratio (total needle area:aboveground mass) followed a similar pattern, but decreased more rapidly with increasing tree size for small trees up to 1 m tall. The proportion of needle biomass (needle mass ratio) was always lower in taller trees (i.e., > 1 m tall) than in small trees (< 1 m tall) and increasingly so at the lowest solar irradiances (0–10% full sunlight). Thus, extrapolating the functional response to light from small seedling to taller individuals is not always appropriate.

Keywords: conifer, light gradient, optimal allocation theory, shade tolerance, size gradient.

Introduction

Differences in intrinsic traits and plasticity among tree species can determine the presence, abundance and successional position of a species (Barnes et al. 1998). Much work has been done to associate specific traits with the growing conditions

occurring during forest succession, especially light availability. For example, traits such as photosynthetic capacity, needle biomass ratio and root/shoot ratio have been associated with shade tolerance (e.g., Givnish 1988, Reich et al. 1998, Messier et al. 1999, Delagrange et al. 2004).

The success or failure of a tree species to establish in different light conditions has been associated with optimum allocation theory. According to this theory, trees modify their allocation pattern to capture the resource that most limits growth (Poorter and Nagel 2000). For example, trees in low light conditions should favor foliage growth to improve light interception (King 1991). However, observed plasticity in biomass allocation among tree parts creates predictable biomass distribution patterns over time (Evans 1972, Coleman et al. 1994). These factors could result in significant differences in biomass distribution between trees in low- and high-light environments, whereas comparisons of similar sized trees would not (McConnaughay and Coleman 1999). Moreover, biomass distribution patterns of trees can be further modified by differences in foliage, branch and stem shedding rates (Niinemets 1998). Because shedding rate can also vary with light environment (Lusk 2002, Mori and Takeda 2004), sapling size and light are likely to interact, influencing the functional response of trees to different light environments.

Responses to light availabilities also differ among conifer genera. Under low light conditions, shade-intolerant *Pinus* allocate biomass preferentially to the stem (particularly to terminal shoot elongation) at the expense of branch and needle growth (Nilsson and Albrektson 1993), whereas mid-shade-tolerant *Picea* gives an equal priority to stem and needle growth (Nilsson and Hällgren 1993). Shade-tolerant species typically assign a higher priority to foliage growth to optimize light capture (Givnish 1988, King 1991). *Abies* species partially follow this pattern, allocating resources in comparable proportions to branches and foliage (King 1997), presumably to hold branches horizontally to favor light interception. However, comparisons of *Abies* and *Picea* saplings did not reveal differences in biomass distribution (Logan 1969). Further comparisons between these genera under natural conditions may

help identify the traits associated with the greater shade tolerance of *Abies* and indicate if these differences are related to allocation alone or if they are also influenced by tree size.

To investigate the interacting effects of light availability, tree size and conifer genera on the functional response of conifer saplings, we studied biomass distribution of boreal and sub-boreal *Abies*, *Picea* and *Pinus* species along a wide gradient of light availability and tree size. Specifically, we (1) tested the hypothesis that tree size and light interact in affecting biomass distribution in saplings, and (2) examined how these interacting effects vary among genera with contrasting shade tolerance.

Material and methods

Study sites and sample trees

Sample conifer trees were selected in two regions of Canada to broaden the applicability of our results. *Pinus contorta* Dougl. var. *latifolia* Engelm. (52°30' N, 121°46' W), the *Picea glauca* (Moench.) Voss × *P. engelmannii* Parry ex. Engelm. complex (54°07' N, 122°04' W) and *Abies lasiocarpa* (Hook.) Nutt. (52°29' N, 121°40' W) were sampled in central British Columbia, whereas *Pinus banksiana* Lamb. (48°30' N 79°08' W), *P. glauca* (48°27' N, 79°26' W and 48°26' N, 79°18' W) and *Abies balsamea* (L.) Mill. (48°31' N, 79°24' W, 48°27' N, 79°15' W and 48°26' N, 79°18' W) were sampled in north-western Québec. *Pinus contorta* and *A. lasiocarpa* grow in the interior cedar–hemlock moist cool subzone (Horsefly variant) (Steen and Coupé 1997) and *P. glauca* × *P. engelmannii* is

found in the sub-boreal spruce–willow wet cool subzone (British Columbia Ministry of Forest 1996). Québec species are found in the boreal balsam fir and white birch domain—balsam fir and white birch type on sub-hydric and fine-textured soil (Grondin et al. 1999).

Six stands were selected in Québec and three in British Columbia. These natural and unmanaged stands are on well-drained sites and had undergone no obvious disturbances during the last 10 years. Multi-canopied older stands were preferred over younger stands because they provided more opportunities to find trees along a gradient of size and light availability. Studied trees were sampled along equidistant transects in stands of varying density and canopy-gap sizes. Selected trees were not subjected to direct aboveground competition from neighboring vegetation and showed no signs of injury, disease or damage so as to obviate the potential effects of these factors. Care was taken to choose trees along broad size and light gradients, where size and light were independent for *Abies* and *Picea* (Figure 1, Table 1). However, we could find no *Pinus* trees less than 3 m tall under the highest light conditions, and we could find no *P. glauca* trees at irradiances exceeding 25% of full sunlight. Light and saplings measurements, as well as the harvest of aboveground parts, were generally done during the same growing season in the summers of 1996, 1997 and 1998. Because of difficulties in finding suitable stands, *Picea glauca* was measured and harvested in 1996 and 1998 only. We did not harvest the belowground parts of the selected trees. According to the literature, *Abies* is shade tolerant, *Picea* is mid-shade tolerant and *Pinus* is shade intolerant (Klinka et al. 1990, Sims et al. 1990).

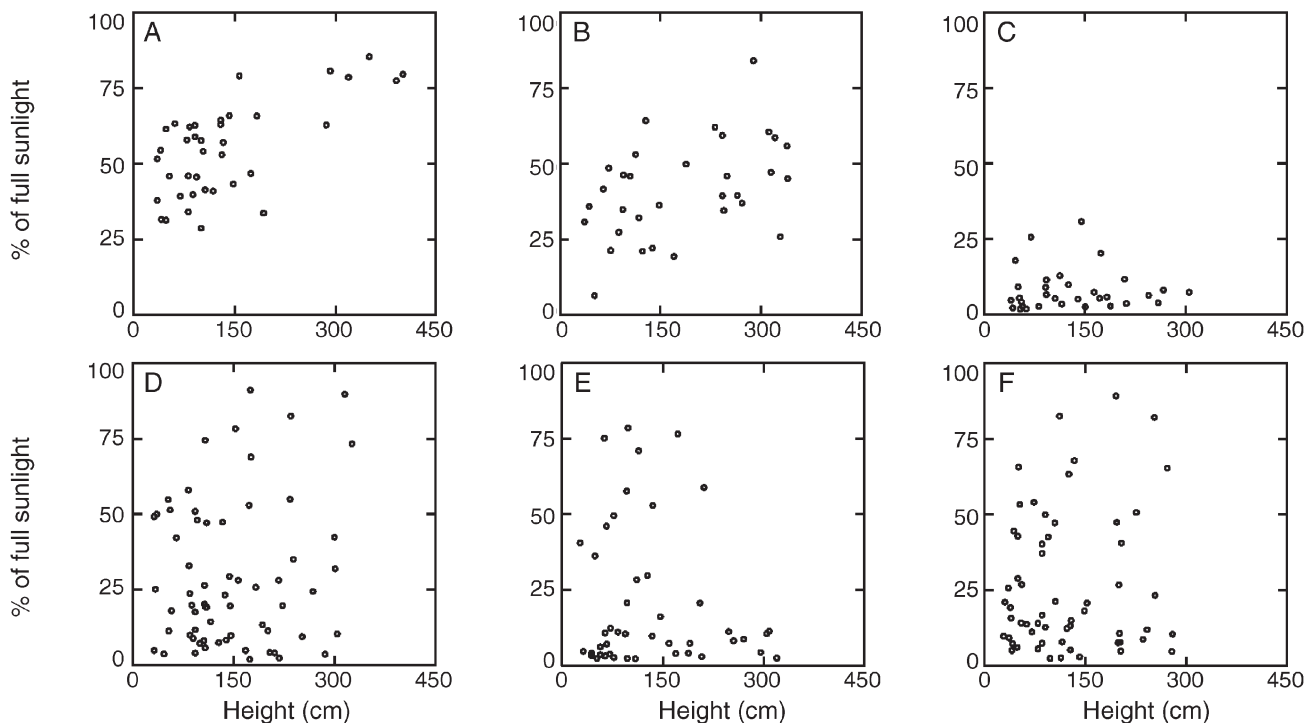


Figure 1. Relationships between percentage of full sunlight and tree height for: (A) *Pinus banksiana*; (B) *Pinus contorta*; (C) *Picea glauca*; (D) *Picea glauca* × *Picea engelmannii*; (E) *Abies balsamea*; and (F) *Abies lasiocarpa*.

Table 1. Mean and range of tree age and aboveground biomass of the studied species.

Species	Age	Aboveground biomass (g)	n
<i>Pinus contorta</i>	9.8 (6–12)	413.3 (6.1–1933.1)	32
<i>Pinus banksiana</i>	16.6 (10–25)	273.3 (7.0–2266.8)	38
<i>Picea glauca</i> × <i>Picea engelmannii</i>	22.3 (7–33)	550.4 (3.9–3247.8)	64
<i>Picea glauca</i>	32.7 (12–59)	568.4 (12.4–3047.0)	31
<i>Abies lasiocarpa</i>	35.0 (11–96)	524.5 (14.1–3635.9)	59
<i>Abies balsamea</i>	24.8 (10–53)	509.1 (10.8–1976.3)	43

Light measurements

Light measurements were used as an overall indicator of competition for resources (light, water and nutrients). In the first field season, one or two readings immediately above sample tree leaders were taken with quantum sensors (Li-Cor, Lincoln, NE) on overcast days as described by Claveau et al. (2002). Light measurements were made with a Li-Cor LAI-2000 in the second and third field seasons, because this instrument provides consistent estimates of light availability. Values from the two methods were highly correlated and were closely related to growing season light measurements (Comeau et al. 1998, Gendron et al. 1998).

Field and laboratory manipulations

In the field, crown diameter was measured along North–South and East–West axes. Sample trees were cut at ground level and brought to the laboratory. Tree age was estimated from a disk taken at ground level. Trees were separated into stem, branches and needles. To determine dry mass, needles, branches and small stems (< 1 cm in diameter) were dried in a forced-air oven for 48 h at 70 °C, whereas bigger stems were dried at 70 °C for 7 days. To estimate total needle area, needles of all species except *Picea* were separated into current-year, 1-year-old and older age classes; each class was measured separately and the class values summed (Coyea and Margolis 1992). In the case of *Picea*, needles could not be separated into age classes because they fell from the twigs into the paper bag before processing. To shorten the manipulation time, branches of *Abies* trees taller than 1 m were sub-sampled. Branches were first sorted into groups of both similar length and comparable ratios of foliage versus wood mass (visual estimation). One branch from each group was processed as previously described. Each group of the remaining branches was weighed to determine fresh mass. To determine dry mass, ratios of oven-dried mass to fresh mass of the processed branch from each group of branches were calculated and applied to the corresponding group. To determine the total dry mass of needle and branches of each tree, the estimated masses were summed.

Estimation of specific needle area was based on a sample of 30 needles for *Abies* and *Picea* and 15 fascicles for *Pinus*. One-sided needle area was measured with a MacSeedle 4.3b meter (Regent Instrument, Québec, QC, Canada) connected to a flatbed scanner (Scan Jet 3c/T, Hewlett-Packard, Palo Alto, CA). Values were multiplied by two to approximate total need-

le area. Although this approach has been used elsewhere (Jose et al. 2003), we are aware that it can underestimate needle area for species with non-flat needles as shown by Niinemets and Kull (1995) and Niinemets et al. (2001). After measurement of needle area, needles were then oven dried at 70 °C for 24 h and weighed (± 0.1 mg).

Variables and statistical analyses

Total needle area was estimated from specific needle area and needle mass of each needle-age class. We calculated the needle area index (NAI; (tree total needle area/(0.25 π)(mean crown diameter²)), needle area ratio (NAR; (total needle area/aboveground total mass)), needle mass per unit area (NMA; needle mass/total needle area), needle mass ratio (NMR; (needle mass/aboveground total mass)100), branch mass ratio (BMR; (branch mass/aboveground total mass)100) and stem mass ratio (SMR; (stem mass/aboveground total mass)100). It was impossible to calculate NAI, NAR, and NMA for *P. glauca* growing in > 10% of full sunlight because total needle area could not be determined.

Exploratory data analyses revealed novel patterns in our data. For instance, graphs of NMR against size showed distinct groups of saplings, particularly where irradiances were between 10 and 50% of full sunlight, and these groupings were consistent for many traits within a species. We first analyzed our data by multiple linear regression where the model included an interaction term between light availability and tree height. However, regression estimates failed to represent each group because of a nonlinear pattern in the data. We therefore used ANCOVA because: (1) it represents the pattern of observations; (2) it considers the full size gradient within each light class (Sokal and Rohlf 1995, Underwood 1997); and (3) it can determine the presence of interactions between the categorical variable and the covariate. Light measurements were divided into four classes of percent of full sunlight: (0–10, 10.1–25, 25.1–50 and 50.1–100) to represent dense, closed, patchy, and very patchy to open canopy conditions (Messier et al. 1998, Claveau 2002, MacDonald et al. 2004). Analyses were performed with the model:

$$\text{Variable} = \mu + \text{PFSC} + \text{H} + \text{PFSC}(\text{H}) + \varepsilon \quad (1)$$

where μ is the overall mean, PFSC is percentage of full sunlight class, H is tree height and ε the error term. The influence of height in each class was determined by a simple linear regression where height was the independent variable.

Species were compared with Equation 2:

$$\begin{aligned} \text{Variable} = & \mu + \text{PFSC} + \text{H} + \text{S} + \text{PFSC}(\text{H}) \\ & + \text{PFSC}(\text{S}) + \text{H}(\text{S}) + \text{PFSC}(\text{H})(\text{S}) + \varepsilon \end{aligned} \quad (2)$$

where S represents species. Light classes and sapling height were included in the model to increase the power of the test. To reduce the possible confounding effect between species and site, comparisons were performed within each region and only terms significant in both regions were considered during the interpretation of the results. *Abies* and *Pinus* were analysed for

Table 2. Summary of ANCOVA results (F -values) of the needle area, needle mass, stem mass and branch mass ratios, needle mass per unit area, and needle area index for each study species. Analyses involved two light classes for *Pinus* and *Picea glauca* and four light classes for the remaining species. Significant results ($P \leq 0.05$) are in bold; * indicates near-significant results ($P \leq 0.10$). Abbreviations: L = light classes; and H = height.

Source	<i>Pinus</i> sp.		<i>Picea</i> sp.		<i>Abies</i> sp.	
	<i>P. contorta</i>	<i>P. banksiana</i>	<i>P. glauca</i> × <i>P. engelmannii</i>	<i>P. glauca</i>	<i>A. lasiocarpa</i>	<i>A. balsamea</i>
<i>Needle area ratio</i>						
L ($F(P)$)	0.874 (0.359)	0.542 (0.467)	1.562 (0.209)	– ¹	4.425 (0.008)	2.155 (0.110)
H ($F(P)$)	94.11 (< 0.001)	98.81 (< 0.001)	54.89 (< 0.001)	–	62.88 (< 0.001)	36.63 (< 0.001)
L×H ($F(P)$)	1.009 (0.325)	0.499 (0.485)	2.279 (0.089 *)	–	5.245(0.003)	3.252 (0.033)
df error	24	34	56	–	50	36
R^2	0.93	0.81	0.59	–	0.70	0.82
Transformation ²	Log ₁₀	Log ₁₀	Log ₁₀	–	Log ₁₀	Log ₁₀
<i>Needle mass ratio</i>						
L ($F(P)$)	2.421 (0.133)	0.051 (0.822)	0.462 (0.710)	0.531 (0.472)	4.147(0.011)	1.327 (0.281)
H ($F(P)$)	36.15(< 0.001)	82.54 (< 0.001)	51.74 (< 0.001)	9.699 (0.004)	64.24 (< 0.001)	40.39 (< 0.001)
L×H ($F(P)$)	4.549 (0.044)	0.080 (0.777)	1.388 (0.256)	0.002 (0.963)	3.876 (0.014)	9.401 (< 0.001)
df error	23	34	56	28	51	36
R^2	0.79	0.80	0.61	0.49	0.77	0.87
Transformation	None	Log ₁₀	None	None	None	None
<i>Stem mass ratio</i>						
L ($F(P)$)	3.289 (0.083 *)	0.412 (0.525)	0.246 (0.864)	0.003 (0.956)	3.144 (0.033)	1.867 (0.153)
H ($F(P)$)	6.217 (0.020)	26.00 (< 0.001)	21.52 (< 0.001)	1.189 (0.285)	41.97 (< 0.001)	18.45 (< 0.001)
L×H ($F(P)$)	5.559 (0.027)	0.342 (0.563)	2.277 (0.090 *)	0.456 (0.505)	7.659 (< 0.001)	10.48 (< 0.001)
df error	23	34	56	28	51	36
R^2	0.55	0.56	0.51	0.24	0.73	0.85
Transformation	None	Log ₁₀	None	None	None	None
<i>Branch mass ratio</i>						
L ($F(P)$)	1.338 (0.259)	4.189 (0.049)	0.581 (0.630)	1.303 (0.263)	4.181 (0.010)	1.326 (0.281)
H ($F(P)$)	22.36 (< 0.001)	14.55 (0.001)	0.909 (0.345)	4.599 (0.041)	0.321 (0.574)	0.717 (0.403)
L×H ($F(P)$)	1.755 (0.198)	6.581 (0.015)	2.938 (0.041)	2.126 (0.156)	6.027 (0.001)	2.590 (0.068 *)
df error	23	34	56	28	51	36
R^2	0.56	0.32	0.30	0.15	0.31	0.45
Transformation	None	None	None	None	None	None
<i>Needle mass per unit area</i>						
L ($F(P)$)	0.744 (0.397)	2.338 (0.136)	2.640 (0.058 *)	– ¹	9.526 (< 0.001)	0.209 (0.890)
H ($F(P)$)	8.529 (0.008)	9.713 (0.004)	18.23 (< 0.001)	–	41.92 (< 0.001)	7.989 (0.008)
L×H ($F(P)$)	0.033 (0.859)	3.266 (0.080 *)	0.184 (0.907)	–	0.198 (0.897)	1.227 (0.314)
df error	23	34	56	–	51	37
R^2	0.56	0.26	0.48	–	0.76	0.41
Transformation	None	None	SQR	–	None	None
<i>Needle area index</i>						
L ($F(P)$)	1.685 (0.207)	0.025 (0.876)	1.304 (0.282)	– ¹	2.949 (0.041)	4.293 (0.011)
H ($F(P)$)	0.107 (0.747)	0.081 (0.777)	19.99 (< 0.001)	–	4.128 (0.047)	0.066 (0.799)
L×H ($F(P)$)	2.233 (0.149)	0.317 (0.577)	6.426 (0.001)	–	4.025 (0.012)	1.367 (0.268)
df error	23	34	56	–	51	37
R^2	0.16	0.03	0.67	–	0.65	0.66
Transformation	None	None	None	–	SQR	Log ₁₀

¹ Calculation was not possible for saplings growing at irradiances > 10% of full sunlight. See Materials and methods section for details.

² Transformations: None = no transformation; Log₁₀ = base 10 logarithm; and SQR = square root.

the 25.1–50% and 50.1–100% of full sunlight classes, *Abies* and *Picea* for the 0–10% and 10.1–25% of full sunlight classes, whereas for *A. balsamea* and *P. glauca* the < 10% of full sunlight classes were selected for variables involving needle area (NAR, NAI and NMA).

For both models, data were transformed by square root, logarithm (base 10) or rank when residuals were heteroscedastic

or not normal. These transformations also linearized the relationship between the dependent variable and the covariate, as required in ANCOVA (Sokal and Rohlf 1995). However, figures present untransformed variables and a line or a logarithmic curve was fitted in each light class to better illustrate the pattern of observation. The significance level was set at $P \leq 0.05$. The analyses were performed with the GLM procedure of

SYSTAT 10 software package (Systat, Point Richmond, CA).

Results

Interaction between light classes and the height gradient

The ANCOVA indicated significant ($P \leq 0.05$) or near-significant ($P \leq 0.10$) interactions between light classes and tree size for 17 of the 36 interaction terms reported in Table 2. For the three species (i.e., *P. glauca* \times *P. engelmannii*, *A. lasiocarpa* and *A. balsamea*) with full light and size gradients, 13 of the 18 interaction terms were significant or near-significant (Table 2). Overall, these interactions indicated that differences between light classes increased with increasing tree height.

Needle area ratio and NMR both decreased with tree size for all species, but the rate of decrease was highest when light was below 10 or 25% of full sunlight for those species showing a significant or near-significant interaction term (Figures 2 and 3; Table 2). Conversely, SMR increased with tree size for all species, but for *P. contorta*, *P. glauca* \times *P. engelmannii*, *A. balsamea* and *A. lasiocarpa*, the increase was greater at low irradiance (Figure 4; Table 2). There was no clear trend in BMR with tree size. For *P. glauca* \times *P. engelmannii*, *A. balsamea* and *A. lasiocarpa*, the significant interactions indicated that BMR tended to increase with tree size at high light (i.e., light classes $> 25\%$ of full sunlight), but tended to remain constant or decrease at low light (i.e., light classes $< 25\%$ of full sunlight) (Figure 5; Table 2). Needle mass per unit area increased with

tree height, but solar irradiance had a significant influence only on *A. lasiocarpa* where NMA values were higher at higher irradiances (Figure 6). Needle area index tended not to change with tree size for either of the *Pinus* species (Figure 7; Table 2). Needle area index also tended not to change with tree size at low irradiance for the *Picea* and *Abies* species. However, NAI increased with tree height at high irradiances for *P. glauca* \times *P. engelmannii* and *A. lasiocarpa* (Figure 7; Table 2). Inspection of the data indicates few differences among light classes for trees < 1 m tall, and the few observed differences are small compared with the large differences found for trees > 1 m tall. Analyses with sapling mass instead of sapling height as a covariate yielded the same trends (data not shown).

Comparison among and within genera

Two sets of ANCOVA were made among tree species within each geographical region to analyze the main differences among the various traits investigated, but only terms significant in both regions were considered. First, when comparing *Abies* and *Picea* in the lower light class (statistical data not shown), we found that the NAR and NMA tended to be higher and lower, respectively, in *Abies* (Figures 6 and 8). Second, when comparing *Pinus* and *Abies* in the two higher light classes (statistical data not shown), we found that SMR and NMA tended to be higher and BMR lower in *Pinus* (Figures 4–6). Although not statistically significant for either region, there was a clear trend for NAR to be lower in *Pinus* than in *Abies*. Overall, the magnitude of the responses of the sampled

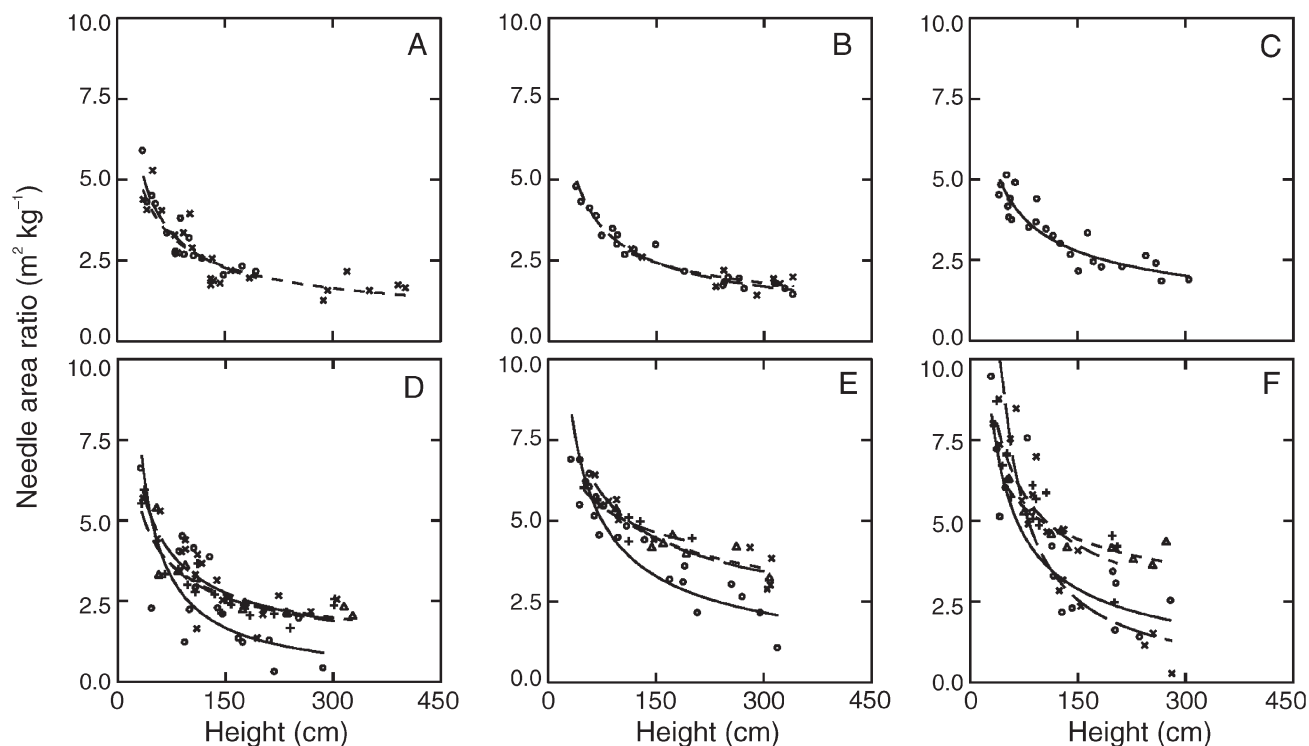


Figure 2. Interacting effects of light availability and tree height on needle area ratio. Values are presented for (A) *Pinus banksiana*, (B) *Pinus contorta*, (C) *Picea glauca*, (D) *Picea glauca* \times *Picea engelmannii*, (E) *Abies balsamea* and (F) *Abies lasiocarpa*, growing in four light classes: 0–10% of full sunlight (\circ , solid line); 10.1–25% of full sunlight (\times , long-dashed line); 25.1–50% of full sunlight ($+$, medium-dashed line); and 50.1–100% of full sunlight (\triangle , fine-dashed line). Slopes of the log-transformed data are significant ($P < 0.05$) with the exception of that for *P. glauca* (C) in the 10.1–25% of full sunlight class.

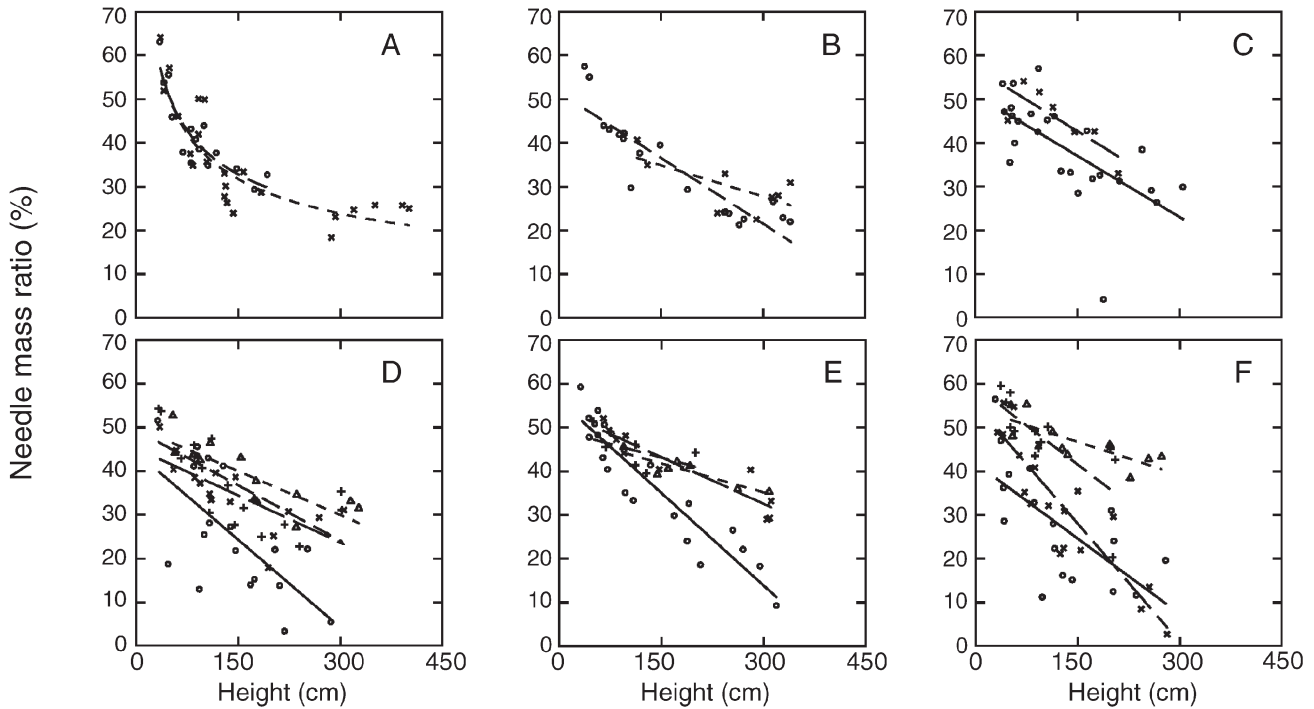


Figure 3. Interacting effects of light availability and tree height on needle mass ratio. Values are presented for (A) *Pinus banksiana*, (B) *Pinus contorta*, (C) *Picea glauca*, (D) *Picea glauca* × *Picea engelmannii*, (E) *Abies balsamea* and (F) *Abies lasiocarpa*, growing in four light classes: 0–10% of full sunlight (○, solid line); 10.1–25% of full sunlight (×, long-dashed line); 25.1–50% of full sunlight (+, medium-dashed line); and 50.1–100% of full sunlight (△, fine-dashed line). Slopes are significant ($P > 0.05$) with the exception of those for *P. contorta* (B) in the 50.1–100% class and for *A. balsamea* (E) in the 25.1–50 and 50.1–100% classes.

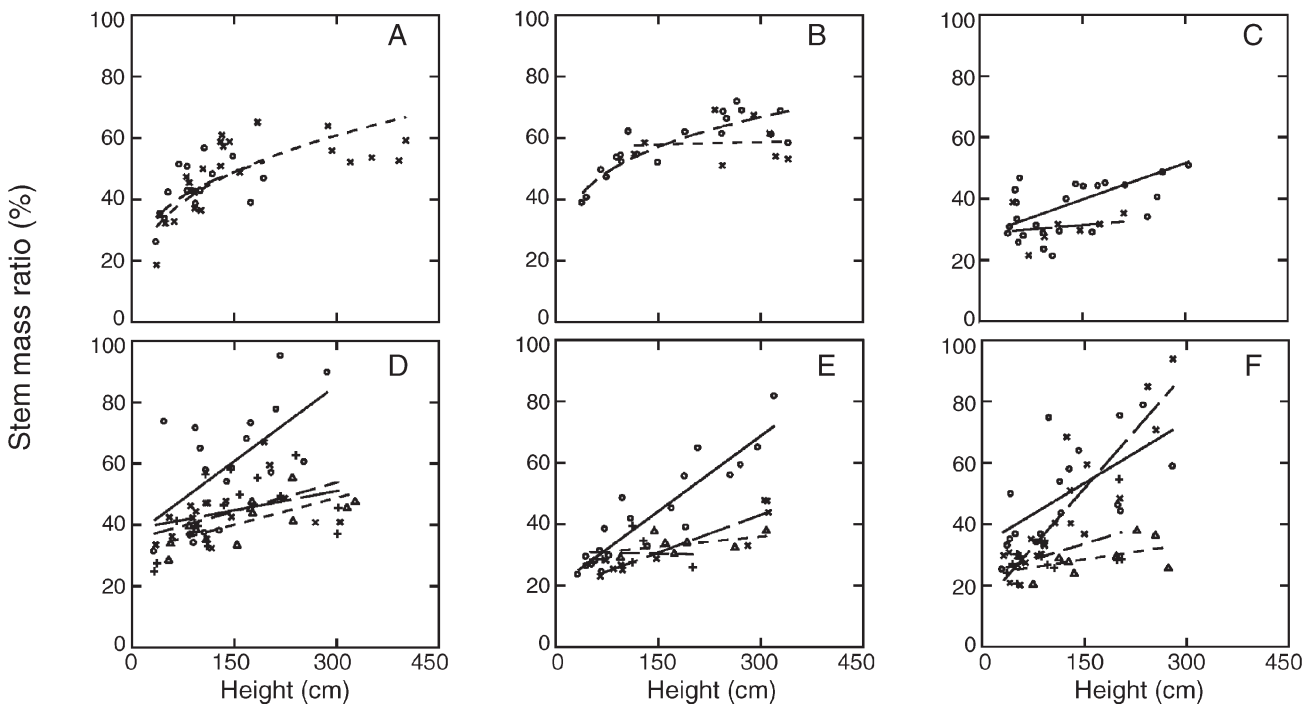


Figure 4. Interacting effects of light availability and tree height on stem mass ratio. Values are presented for (A) *Pinus banksiana*, (B) *Pinus contorta*, (C) *Picea glauca*, (D) *Picea glauca* × *Picea engelmannii*, (E) *Abies balsamea* and (F) *Abies lasiocarpa*, growing in four light classes: 0–10% of full sunlight (○, solid line); 10.1–25% of full sunlight (×, long-dashed line); 25.1–50% of full sunlight (+, medium-dashed line); and 50.1–100% of full sunlight (△, fine-dashed line). Slopes are significant ($P > 0.05$) with the exception of those for *P. contorta* (B) in the 25.1–50% class, for *P. glauca* (C) in the 10.1–25% class, for *P. glauca* × *P. engelmannii* (D) in the 10.1–25 and 25.1–50% classes, for *A. balsamea* (E) in the 10.1–25 and 25.1–50% classes and for *A. lasiocarpa* (F) in the 25.1–50 and 50.1–100% classes.

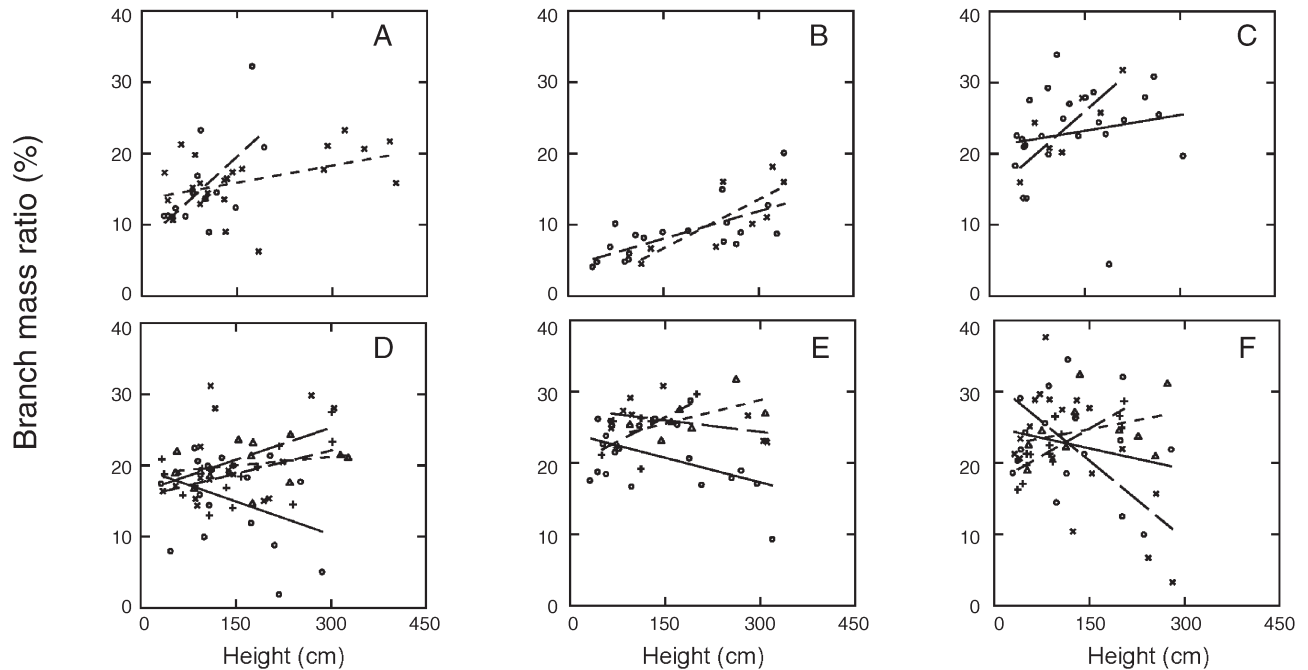


Figure 5. Interacting effects of light availability and tree height on branch mass ratio. Values are presented for (A) *Pinus banksiana*, (B) *Pinus contorta*, (C) *Picea glauca*, (D) *Picea glauca* × *Picea engelmannii*, (E) *Abies balsamea* and (F) *Abies lasiocarpa*, growing in four light classes: 0–10% of full sunlight (○, solid line); 10.1–25% of full sunlight (×, long-dashed line); 25.1–50% of full sunlight (+, medium-dashed line); and 50.1–100% of full sunlight (△, fine-dashed line). Slopes are significant ($P > 0.05$) with the exception of those for *P. glauca* (C) in the 0–10% class, for *P. glauca* × *P. engelmannii* (D) in all light classes, for *A. balsamea* (E) in all classes but 0–10% and for *A. lasiocarpa* (F) in the 10.1–25 and 50.1–100% classes.

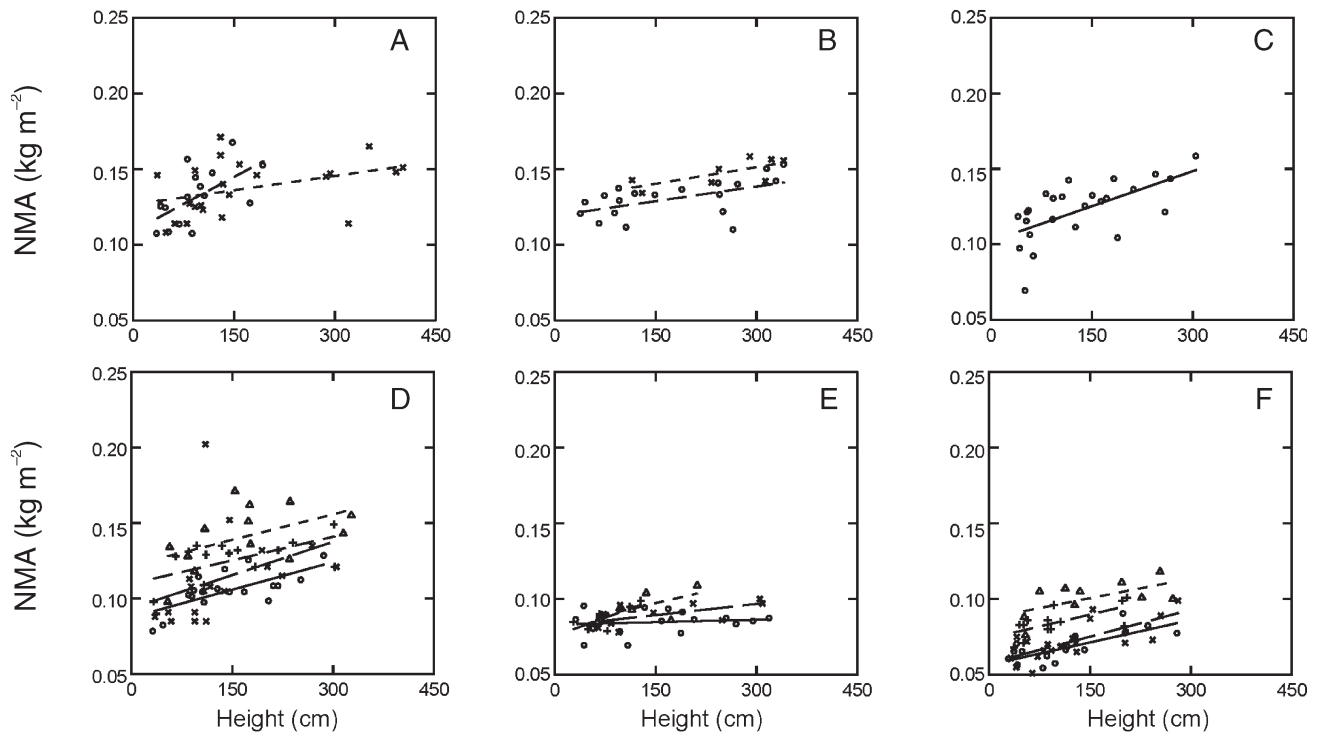


Figure 6. Interacting effects of light availability and tree height on needle mass per unit area (NMA). Values are presented for (A) *Pinus banksiana*, (B) *Pinus contorta*, (C) *Picea glauca*, (D) *Picea glauca* × *Picea engelmannii*, (E) *Abies balsamea* and (F) *Abies lasiocarpa*, growing in four light classes: 0–10% of full sunlight (○, solid line); 10.1–25% of full sunlight (×, long-dashed line); 25.1–50% of full sunlight (+, medium-dashed line); and 50.1–100% of full sunlight (△, fine-dashed line). Slopes are significant ($P > 0.05$) with the exception of those for *P. banksiana* (A) in the 50.1–100% class, for *P. glauca* (C) in the 10.1–25% class, for *P. glauca* × *P. engelmannii* (D) in the 50.1–100% class, for *A. balsamea* (E) in all classes but the 10.1–25% class and for *A. lasiocarpa* (F) in the 50.1–100% class.

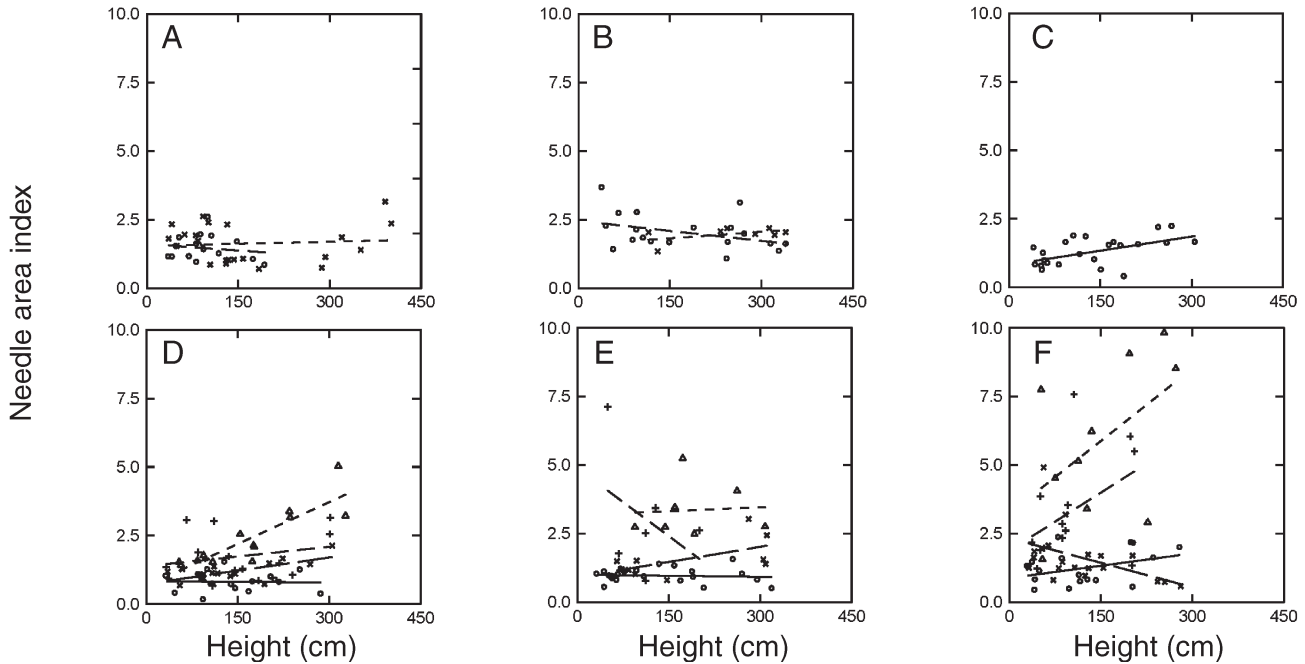


Figure 7. Interacting effects of light availability and tree height on needle area index. Values are presented for (A) *Pinus banksiana*, (B) *Pinus contorta*, (C) *Picea glauca*, (D) *Picea glauca* × *Picea engelmannii*, (E) *Abies balsamea* and (F) *Abies lasiocarpa*, growing in four light classes: 0–10% of full sunlight (○, solid line); 10.1–25% of full sunlight (×, long-dashed line); 25.1–50% of full sunlight (+, medium-dashed line); and 50.1–100% of full sunlight (△, fine-dashed line). Slopes are significant ($P > 0.05$) with the exception of those for *P. banksiana* (A), *P. contorta* (B), *P. glauca* (C), and *A. balsamea* (E) in all light classes, for *P. glauca* × *P. engelmannii* (D) in the 0–10 and 25.1–50% classes and for *A. lasiocarpa* (F) in all light classes but the 10–25.1% class.

trees along the size and light class gradients was similar within each genus.

Discussion

Tree species have different combinations of acclimation mechanisms and each combination can favor success in a specific light environment (Givnish 1988, Messier et al. 1999). We explored how the interplay between tree height and light availability affects aboveground biomass distribution of *Abies*, *Picea* and *Pinus* species in the boreal and sub-boreal forests of Canada. Because tree height and light availability were not correlated ($r = 0.002$ to 0.14 ; $P = 0.27$ to 0.99) for *Abies* and *Picea*, the effects of these variables can be evaluated sepa-

rately for these species; however, there was a slight correlation between light and tree height for *Pinus*, necessitating a more careful interpretation of the data.

Interacting effects of light and tree size

As a tree grows taller, differences in biomass allocation and shedding rates among tree parts result in biomass distribution patterns that can vary markedly from optimal allocation theory predictions (Ninemets 1998, McConnaughay and Coleman 1999) and from findings from small seedlings in short-term studies (e.g., Lambers and Poorter 1992, Walters et al. 1993, Kitajima 1994). For trees < 1 m tall, traits such as NMR and NAR were higher or not different at low irradiances compared with higher irradiances, but they declined at low irradiances in

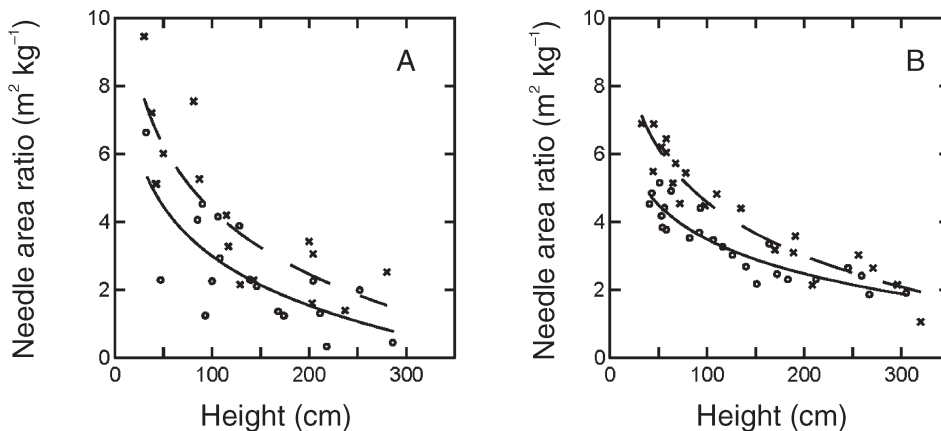


Figure 8. Comparison of the relationships between needle area ratio and tree height for (A) *Abies lasiocarpa* and *Picea glauca* × *Picea engelmannii* and (B) *Abies balsamea* and *Picea glauca*. Symbols: *Abies* (×, dashed line); *Picea* (○, solid line). Only trees below 10% of full sunlight were compared. See the Material and methods section for more details. All slopes are significant ($P > 0.05$).

larger trees. In addition, NMR and NAR decreased with increasing tree size regardless of the light environment, as found in other sapling studies (Britt et al. 1990, Messier and Nikinmaa 2000, Poorter 2001). These differences from the predictions of optimal allocation theory can lead to different interpretations of the functional response of saplings to light availability.

High NMRs and NARs found in small seedlings under low light conditions are interpreted as mechanisms to improve light capture (e.g., Poorter and Nagel 2000). Saplings can also allocate an important share of their growth to foliage (King 1991, Messier and Nikinmaa 2000, King 2003). However, the long life span of saplings in the understory, combined with biomass shedding and low production rates, can lead to low NMRs and NARs. Such low ratios can limit the ability of trees to acquire the necessary carbon to sustain their growth rates (Claveau et al. 2002) or defence mechanisms, which could ultimately lead to death (Gerrish 1990). Kohyama (1983) showed that *Abies* seedlings must maintain their foliage growth above a critical rate to maintain a viable NMR. Results from studies that included observations on root biomass (O'Connell and Kelty 1994, Naidu et al. 1998, Delagrangé et al. 2004) showed trends comparable to those we observed, suggesting that our conclusions would be similar if we had included root biomass in the study.

The optimal allocation theory is unclear regarding optimal allocation to branches. Following the rationale previously presented, allocation to branches should be higher under low light conditions because a branch can support a higher proportion of foliage mass than the stem (Kohyama 1980). This rationale is supported by the findings of Mori and Takeda (2004), as well as by studies on crown morphological plasticity showing that understory *Abies* and *Picea* have greater annual branch growth than leader growth (e.g., Greis and Kellomäki 1981, Parent and Messier 1995). Our results, however, suggest that the greater allocation to branches does not compensate for natural branch shedding observed under low light conditions. As a result, saplings growing in low light, especially the tallest saplings, have a lower BMR and a typical short and wide crown (Kohyama 1980, Claveau et al. 2002, Kato and Yamamoto 2002). Such a crown shape minimizes self-shading and in turn allows saplings to improve their light capture under shaded conditions (Kohyama 1991).

Several studies have shown that temperate deciduous tree saplings exhibit decreasing crown morphological plasticity in relation to light as they increase in size (Messier and Nikinmaa 2000, Delagrangé et al. 2004). This reflects the rapidly increasing physical constraint that restricts the ability of trees to modify crown morphology: because all species are subjected to gravitational forces, they may ultimately be constrained to adopt a similar biomass distribution strategy to support their increasing crown mass. In functional terms, this could mean that taller saplings need to rely on different strategies to tolerate shade than shorter saplings. Except for two traits (NMR and crown profile), our results and those of a companion study (Claveau et al. 2002) show no convergence in sapling traits, contrary to the findings reported for temperate deciduous trees (Messier and Nikinmaa 2000, Delagrangé et al. 2004). Although it is difficult to compare these studies with our study

because we did not measure the same traits, such differences suggest that angiosperm and gymnosperm tree species differ in mechanical constraints.

Differences among genera

Species that are similar in shade tolerance often show subtle differences in growth, morphological or physiological traits (Beaudet and Messier 1998, Messier and Nikinmaa 2000, Delagrangé et al. 2004). Comparisons of crown morphological (Claveau et al. 2002) and biomass distribution traits (present study) among genera revealed differences in only two traits, NMA and NAR. Among the genera studied, the higher NAR observed for *Abies* could be related to four distinct but not necessarily exclusive processes: (1) a greater allocation to foliage growth; (2) a longer needle life span that can result in the maintenance of a higher foliage area (Lusk 2002, Mori and Takeda 2004); (3) a limitation in non-photosynthetic biomass accumulation through a drastic decrease or a cessation of growth (Kohyama 1980, Van Pelt and Franklin 1999, Parent et al. 2002), as well as an enhanced ability to shed lower branches (Takahashi 1996); and (4) a lower NMA (NAR = NMR/NMA). The two latter processes are more likely to explain the difference between *Abies* and *Picea*, because NMA was lower for *Abies* than for *Picea*, whereas these genera did not differ in relative foliage mass (NMR). The high NAR for *Abies* is in accordance with its high shade tolerance (Klinka et al. 1990, Sims et al. 1990), because high NARs are related to high light-capture efficiency.

Several studies have shown that total needle areas of *Picea abies* (L.) Karst. and *Pinus sylvestris* L. trees estimated from direct measurements are higher than values based on projected areas (Niinemets and Kull 1995, Niinemets et al. 2001). To evaluate possible bias in our estimates of total needle area based on projected area, we corrected our total needle area values for the *Picea* and *Pinus* species based on ratios of total needle area to projected needle area published by Niinemets and Kull (1995) and Niinemets et al. (2001), and then performed statistical analyses on the corrected values. The corrected traits' values led to a similar interpretation of results except for the comparisons of NMA.

A framework for evaluating how various aboveground attributes vary with light and tree size

Few studies have compared how traits vary along a light gradient among species within a genus. Our findings in boreal and sub-boreal conifers complement those of Lei and Lechowicz (1998) who reported similar biomass distribution patterns along light gradients within the genus *Acer*. Our findings are also consistent with the general patterns observed in biomass distribution studies (Kimura 1963, Logan 1966, 1969, Eis 1970, Britt et al. 1990, Kubota et al. 1994, King 1997). Taken together, these studies suggest that a theoretical framework could be developed to draw useful generalizations from the published data (M.J. Lechowicz, pers. comm.). Such generalizations must be made with caution because distant common ancestry, differences in growing conditions or selective forces can modify traits (Ackerly and Donoghue 1995, Westoby et al. 1995) and the phenotypic plasticity of species. Balaguer et al. (2001) have presented an interesting example of the effects of

selective forces. *Quercus coccifera* L. seedlings from a forested environment showed greater differences in traits between light environments than seedlings of stands that have been growing for many generations in dry environments such as on rock outcrops or in the garrigue where such plasticity does not contribute to tree survival.

Ecological implications

Tall individuals have greater light requirements than short individuals because respiration and construction costs increase with size (Waring 1987, Givnish 1988); however, this increase in light requirement may not be constant. Givnish (1988) estimated that light requirements of *Liriodendron tulipifera* L. increase sharply as trees increase in size up to 1 m and thereafter increase more slowly. Our results and those of Messier and Nikinmaa (2000) suggest that this sharp increase in light requirement is associated with the marked decline in NAR (or leaf area ratio) observed in trees < 1 m tall. The greatest changes in leaf (needle) area ratio, which is a coarse indicator of photosynthesizing tissues to respiring tissues (Hunt 1990), occur as trees increase in size up to 1 m. Beyond a height of 1 m, the increasing respiratory burden (Lambers and Poorter 1992) becomes less important as trees increase their photosynthetic capacity by increasing foliage area and presumably start discarding respiring tissues as dead heartwood. We suggest that as trees increase in size to 1 m in height, they proceed through a critical stage where mortality related to carbon starvation is increasingly important.

This suggestion is supported by several recent studies. For example, Messier and Nikinmaa (2000) found that maximum height for *Betula alleghaniensis* Britton, *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. declined with decreasing light availability below 4% of full sunlight. Furthermore, limited height under dark understory conditions has also been reported for *Abies* species where individuals tend to be less than 1 m tall (Kato and Yamamoto 2001, Parent et al. 2002).

We found that tall saplings exhibited greater plasticity to variations in light than small saplings (cf. Claveau et al. 2002). Contrary to common belief, such plasticity does not necessarily provide a functional advantage because the lower NMRs and NARs found in taller individuals in low light resulted in trees that were less vigorous. Our results suggest a subtle interplay between tree size and light availability where a small decrease in light in shaded conditions could place taller individuals at a disadvantage (Claveau et al. 2002). Compared with small individuals, tall individuals are more likely to die from carbon starvation because light requirements increase with size (Messier et al. 1999). This could have an important impact on seedling and sapling dynamics under conditions of rapid canopy closure following gap formation because such an event can result in lower irradiances than under closed canopies (Beaudet and Messier 2002).

In conclusion, tree size and light availability interact in modifying several tree traits and responses, and these responses were consistent among three genera found in two broadly different geographical locations. This interaction has an important impact on the functional response of understory trees, because growth and survival can be favored or depressed

depending on the particular combination of light environment and tree size. Our results also indicate that the functional response of small seedlings cannot necessarily be extrapolated to taller individuals. As concluded by McConnaughay and Coleman (1999), there is need to account fully for the strong ontogenetic drift in biomass distribution and also for natural biomass loss in order both to better understand the sources of phenotypic plasticity in trees and to model tree growth and development accurately.

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