

Functional relationships between crown morphology and within-crown characteristics of understory saplings of three codominant conifers in a subalpine forest in central Japan

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Summary Light-related plasticity of crown morphology and within-crown characteristics were investigated in understory sun and shade saplings of three codominant subalpine conifers, *Abies mariesii* M.T. Mast., *Abies veitchii* Lindl. and *Picea jezoensis* var. *hondoensis* (Mayr) Rehd. Compared with those of sun saplings, current-year shoots of shade saplings allocated less biomass to needles, resulting in less dense needle packing and hence less mutual needle shading. The proportion of lateral branch biomass in foliage was either similar in sun and shade saplings or greater in shade saplings, depending on the species, suggesting that, over the lifetime of a branch, greater needle longevity in shade compensates for reduced biomass investment in needles of current-year shoots of shade saplings. Saplings with slower-growing branches tended to have greater needle life spans, suggesting that plasticity of branch growth rate and plasticity of needle life span are interdependent. Both *Abies* species showed greater light-related plasticity of needle life span and branch growth than *P. jezoensis*. The greater shade tolerance of the *Abies* species derives from their broad flattened crowns with slow-growing branches. This type of crown development incurs substantial support costs, but the long needle life span of shade saplings of the *Abies* species compensates, at least in part, for their low annual investment in foliage, especially in the case of *A. mariesii*, which has a longer needle life span and slower-growing and stouter branches than *A. veitchii*. Compared with the *Abies* species, *P. jezoensis* had a less plastic crown morphology, and less variability of needle life span and branch growth in response to light, resulting in lower shade tolerance. However, compared with the flattened crown of *Abies* shade saplings, the conical crown of *P. jezoensis* saplings imposes a smaller support cost, making this species better adapted to rapid height growth than to survival in shade.

Keywords: *Abies mariesii*, *Abies veitchii*, allocation, branch growth, light regime, needle life span, *Picea jezoensis* var. *hondoensis*, plasticity.

Introduction

Functional relationships between crown morphology and light

capture have been shown in many woody species (Horn 1971, Kohyama 1980, Canham 1988, Küppers 1989, Poorter and Werger 1999). Generally, shade-tolerant species invest more in lateral expansion of the crown, thus increasing light interception under shaded conditions, whereas light-demanding species invest more in height growth to avoid being shaded by neighbors. Thus, there is a trade-off in the forest understory between lateral crown expansion for present survival and height growth for future competitive advantage (Kohyama 1987, Kohyama and Hotta 1990).

In addition to crown morphology, leaf traits such as life span, nitrogen content, and structure also respond to light conditions (Reich et al. 1991, Kudo 1995a, 1995b, 1990, Sprugel et al. 1996, Stenberg et al. 1998, Niinemets and Lukjanova 2003). Leaf life span is often extended in the understory, thereby compensating for low productivity in shade; however, this can lead to increased self-shading, because older leaves may become shaded by younger shoots or leaves. Self-shading can be minimized by a flatter crown and a more planar leaf arrangement. Although a flattened crown greatly improves light interception in shade (Kohyama 1980, King 1997), it requires substantial investment in stem supporting tissues (Hunter 1997, King 1997, Poorter and Werger 1999), especially where snow places an additional load on the crown (King 1991, 1997). In *Abies amabilis* Dougl. ex J. Forbes saplings growing in a snowy Oregon forest, long needle life span compensated for relatively high allocation of biomass to supportive tissues and low allocation to foliage in shade (King 1997). In addition to leaf properties, shoot and branch traits associated with supportive functions have a close relationship with crown morphology (King 1997, Hunter 1997). Thus, the degree of response to changes in irradiance is linked to plasticity in a variety of crown morphology and within-crown characteristics.

In boreal and subalpine forests, where the dominating evergreen conifers have needles that often live more than 8–10 years (Kohyama 1980, King 1997, Balster and Marshall 2000), old needles tend to be shaded by their own crowns. So, if there is a linkage between crown morphology and within-crown characteristics such as needle life span, needle arrangement, and shoot/branch support, it should be evident in boreal

and subalpine conifers. Conifer saplings growing in different irradiances are known to show acclimation at the needle, shoot and branch levels. However, little is known about how the cost–benefit consequences of acclimation at these scales within conifer sapling crowns affect crown development and morphology, and consequently, performance at the whole-plant level.

To clarify the details of such linkages, we investigated crown morphology and within-crown characteristics in understory sun and shade saplings of the codominant evergreen conifers, *Abies mariesii* M.T. Mast., *Abies veitchii* Lindl., and *Picea jezoensis* var. *hondoensis* (Mayr) Rehd. growing in subalpine snowy forests in central Japan (Franklin et al. 1979, Kaji 1982, Yamamoto 1993, Mori and Takeda 2003). Previously, we demonstrated that changes in species-specific crown morphology in response to shade strongly affects the shade-tolerance of these species (Mori and Takeda 2003). Here we investigate the cost–benefit implications of interspecific differences in crown morphology.

Material and methods

Study site

The study site is located in a subalpine forest (altitude 2050 m, 35°56' N, 137°28' E) on Mt. Ontake (peak 3067 m high) in central Japan. The subalpine forest is dominated by *Abies mariesii*, *A. veitchii* and *Picea jezoensis* var. *hondoensis*, hereafter referred to simply as *P. jezoensis*. Mean annual precipitation is about 2500 mm and mean annual temperature is between 3 and 4 °C. The forest floor is snow-covered from mid-November or early December until late May or early June. Maximum snow depths from 1995 through 1999 in the study plot ranged from 175 to 230 cm. The forest understory mainly consists of herbs and mosses.

Light assessment within the plot

To measure spatial variation in the understory light regime, hemispherical fish-eye photographs were taken 2 m above ground at each corner of 2.5 × 2.5 m grids in September 1999. The photographs were taken under an overcast sky with a Coolpix 910 digital camera equipped with an FC-E8 fish-eye lens (Nikon, Tokyo, Japan), which was kept horizontal with a leveling device. From the photographs, the indirect site factor (ISF) was estimated using HEMIVIEW Canopy Analysis software Version 2.1 (Delta-T Devices, Cambridge, U.K.). Within the study plot, we chose two microsites, one a gap microsite (ISF > 0.40) and the other a closed-canopy microsite (ISF < 0.05). The gap microsite was about 50 m from the closed-canopy microsite.

Data collection

In early June 1999, for each study species (*A. mariesii*, *A. veitchii* and *P. jezoensis*), we harvested four sun saplings from the gap microsite and four shade saplings from the closed-canopy microsite. At harvest, none of the 24 saplings showed signs of bud break, which normally occurs in late June at this site.

We measured sapling height (H ; cm), main trunk length (L_T ; cm), trunk diameter at ground level (D_T ; cm), vertical crown length (L_C ; cm), greatest horizontal crown width (W_{Cmax} ; cm) and smallest horizontal crown width (W_{Cmin} ; cm), where horizontal crown shape was defined as an ellipse. We also estimated what the height would have been 5 years earlier (H_{p-5}) based on measurements of trunk elongation growth for each year. From these measurements, we calculated horizontally projected crown area (A_C ; cm²), crown volume (V_C ; cm³), trunk volume (V_T ; cm³) and relative height growth rate (R_{HG} ; year⁻¹). We estimated A_C as an ellipse ($(\pi/4)W_{Cmax}W_{Cmin}$) (Kubota and Hara 1996). We calculated V_C as $A_C L_C$ (Kubota and Hara 1996), V_T as $L_T D_T^2$ (Ogawa and Kira 1977), and R_{HG} for the previous 5 years as $(\ln H - \ln H_{p-5})/5$.

To investigate biomass allocation patterns, we measured shoot length (L_0), stem mass (M_{S0}) and needle mass per shoot (M_{N0}) of all current-year shoots of the harvested saplings. We then measured the age, branch length (L_B), stem mass (M_{SB}) and needle mass per branch (M_{NB}) of all lateral branches. Needle mass on the main trunk (M_{NT}) and trunk mass (M_T) of each harvested sapling were also measured. Here, stem was defined as shoot or branch after removal of needles. All tissues were dried for 96 h at 40 °C before weighing. From the biomass measurements of harvested saplings, total needle mass within each sapling (M_{NSAP} ; g) and aboveground sapling mass (M_{SAP} ; g) were obtained as:

$$M_{NSAP} = \sum_{i=1}^N M_{NB_i} + M_{NT} \quad (1)$$

$$M_{SAP} = M_{NSAP} + \sum_{j=1}^N M_{SB_j} + M_T \quad (2)$$

We then regressed M_{NSAP} and M_{SAP} against V_T and V_C to create predictive equations of the form:

$$\ln M_{NSAP} = \gamma \ln V_T + \delta \ln V_C \quad (3)$$

$$\ln M_{SAP} = \alpha + \beta \ln V_T \quad (4)$$

where γ , δ , α , β are species-specific parameters (Kubota and Hara 1996). We also determined the ratio of total needle mass to sapling mass (M_{NSAP}/M_{SAP}) and the ratio of current-year needle mass to total needle mass (M_{N0SAP}/M_{NSAP}), defined as total mass of current-year needles per sapling (M_{N0SAP}) divided by M_{NSAP} . Needle survivorship ratio (%) was measured for each harvested sapling as described by Kimura (1963).

To assess species-specific sapling morphology, additional measurements were carried out at the shade and sun microsites in October 1999. We measured H , L_T , D_T , L_C , W_{Cmax} , W_{Cmin} and H_{p-5} , and calculated A_C , V_C , V_T and R_{HG} . These measurements were made on a total of 74 saplings of the three species. We then calculated M_{SAP} and M_{NSAP} of these saplings from the equations obtained from our biomass data.

To evaluate the effects of microsite differences on needle nitrogen concentration (%) and needle mass per area (M_{N0}/A_{N0} ; g m⁻²), an additional 30 samples of current-year shoots that

were not self-shaded were harvested for each species and each microsite (180 samples in total). Nitrogen concentration was measured with an NC analyzer (Sumitomo Chemical, Tokyo, Japan). Needle area (A_{N0}) was measured with the NIH image system (National Institutes of Health, Bethesda, MD). Abbreviations and definitions for measured and estimated plant parameters are listed in Table 1.

Data analysis

Differences in needle traits between sun and shade saplings were assessed by the Mann-Whitney U test. Differences in needle life span were tested based on the age for 50% survival (Kohyama 1980) and maximum survival age.

To investigate differences in structures and biomass allocation patterns of current-year shoots and lateral branches, we conducted an analysis of covariance (ANCOVA). We also used ANCOVA to evaluate species-specific architectures in relation to light regime. We examined the relationships between shoot, branch or architectural traits by linear regressions of the form $\ln y = a + b \ln x$, and checked the significance of the homogeneity of the slopes. If no significance was found, the interaction term was excluded from the analyses (Sokal and Rohlf 1995). In ANCOVA, if slope (b) differs among groups, a regression with a larger b will show a greater increase in the dependent variable (y) per unit increment in the independent variable (x). If b does not differ but the intercept (a) differs, a regression

with a larger a will have a consistently larger amount of y at any x .

To analyze intraspecific differences in branch age, mean branch age was adjusted to account for variance in branch length by calculating the mean using ANCOVA with branch length as a covariate. From this, mean branch age adjusted for branch length (i.e., mean branch age at a common branch length (CBL)) was compared between sun and shade saplings of each species. All statistical analyses were performed with SPSS software Version 10.0.5 (SPSS, Chicago, IL).

Results

Needle traits

Nitrogen concentrations of current-year needles of all species did not differ between sun and shade needles (Table 2). Needle mass per area was greater in sun needles than in shade needles (Table 2). Needle life span was greater in shade saplings than in sun saplings of the two *Abies* species, but there was no significant difference between sun and shade saplings of *P. jezoensis* (Table 2).

Current-year shoot traits

Stem mass and M_{N0} increased with increasing L_0 , and M_{N0} increased with M_{S0} (Table 3). However, the regression slopes of

Table 1. Abbreviations and definitions for measured and estimated plant parameters.

Abbreviation	Definition	Unit
H	Sapling height	cm
H_{p-5}	Sapling height 5 years ago	cm
D_T	Diameter at ground level	cm
L_C	Vertical crown length	cm
W_{Cmax}	Maximum horizontal crown width	cm
W_{Cmin}	Minimum horizontal crown width	cm
A_C	Horizontally projected crown area	cm ²
V_C	Crown volume	cm ³
V_T	Trunk volume	cm ³
R_{HG}	Relative height growth rate	year ⁻¹
L_0	Length of current-year shoot	cm
M_{S0}	Stem mass of current-year shoot	g
M_{N0}	Total needle mass on each current-year shoot	g
L_B	Length of lateral branch	cm
M_{SB}	Stem mass of lateral branch	g
M_{NB}	Total needle mass on each lateral branch	g
L_T	Length of main trunk	cm
M_T	Mass of main trunk	g
M_{NT}	Total needle mass on main trunk	g
M_{NSAP}	Total needle mass within sapling	g
M_{SAP}	Aboveground sapling mass	g
M_{NSAP}/M_{SAP}	Ratio of total needle mass to sapling mass	
M_{NOSAP}	Total mass of current-year needles within sapling	g
M_{NOSAP}/M_{NSAP}	Ratio of current-year needle mass to total needle mass	
A_{N0}	Needle area per shoot for current-year shoot	m ⁻¹
M_{N0}/A_{N0}	Needle mass per area for current-year needles	g m ⁻¹

Table 2. Comparison of needle traits in understory sun and shade saplings of the three co-dominant subalpine conifers. The values are means \pm SE. Intraspecific differences of the values were subjected to the Mann-Whitney U test. Abbreviation: M_{N0}/A_{N0} = needle mass per area (current-year needles).

Needle trait	Species	Light regime		n	P
		Sun	Shade		
Nitrogen concentration (%)	<i>A. mariesii</i>	1.215 \pm 0.050	1.120 \pm 0.025	60	0.405
	<i>A. veitchii</i>	1.603 \pm 0.050	1.472 \pm 0.070	60	0.257
	<i>P. jezoensis</i>	1.360 \pm 0.130	1.611 \pm 0.072	60	0.096
M_{N0}/A_{N0} (g m ⁻²)	<i>A. mariesii</i>	152.2 \pm 2.268	139.9 \pm 2.559	60	< 0.01
	<i>A. veitchii</i>	136.8 \pm 2.632	125.3 \pm 2.744	60	< 0.05
	<i>P. jezoensis</i>	131.3 \pm 3.545	89.64 \pm 2.451	60	< 0.0001
Age of 50% survival (years)	<i>A. mariesii</i>	5.475 \pm 0.278	7.500 \pm 0.696	8	< 0.05
	<i>A. veitchii</i>	4.050 \pm 0.352	6.700 \pm 0.490	8	< 0.05
	<i>P. jezoensis</i>	4.900 \pm 0.367	5.755 \pm 0.475	8	0.098
Maximum age (years)	<i>A. mariesii</i>	8.750 \pm 0.946	11.50 \pm 0.500	8	< 0.05
	<i>A. veitchii</i>	6.000 \pm 0.408	10.25 \pm 0.946	8	< 0.05
	<i>P. jezoensis</i>	7.250 \pm 0.750	8.500 \pm 0.577	8	0.096

M_{N0} (y) versus M_{S0} (x) were significantly ($P < 0.05$) less than 1.0 in all cases (Table 3), indicating that larger current-year shoots have a lower needle/stem biomass ratio than smaller current-year shoots irrespective of species and light regime. There were no light-related differences in the allometric relationship between M_{S0} (y) and L_0 (x) in current-year shoots of *A. veitchii* and *P. jezoensis*, but M_{S0} of *A. mariesii* increased more rapidly with increases in L_0 in sun shoots than in shade shoots (Table 3). For the regressions of M_{N0} (y) versus L_0 (x)

and M_{N0} (y) versus M_{S0} (x), sun saplings of the two *Abies* species had significantly steeper slopes than shade saplings (Table 3), indicating that, in the *Abies* species, sun saplings produced a larger amount of needle mass per unit shoot length and per unit stem mass than shade saplings. In contrast, *P. jezoensis* showed no difference in the slope of M_{N0} (y) versus M_{S0} (x) between sun and shade saplings, but the intercept of this regression was larger in sun saplings (Table 3), indicating that *P. jezoensis* sun saplings have a higher M_{N0}/M_{S0}

Table 3. Summary of ANCOVA results for differences in allometric relationships of current-year shoots based on the regressions of the two microsites. Significance levels: * = $P < 0.05$; and **** = $P < 0.0001$. Abbreviations: M_{S0} = Stem mass of current-year shoot (g); L_0 = Length of current-year shoot (cm); and M_{N0} = Total needle mass on each current-year shoot (g).

Variable		Species	F value: sun versus shade		Results of regression				
Dependent (y)	Independent (x)		Slope (b)	Intercept (a)	Light regime	r^2	n	Slope (b)	Intercept (a)
M_{S0}	L_0	<i>A. mariesii</i>	8.928 ****	0.406	Sun	0.922 ****	467	2.116	-6.600
					Shade	0.602 ****	193	1.535	-6.123
		<i>A. veitchii</i>	0.185	0.665	Sun	0.835 ****	173	1.964	-6.845
					Shade	0.854 ****	161	2.005	-6.933
		<i>P. jezoensis</i>	2.821	0.505	Sun	0.810 ****	353	1.977	-6.729
					Shade	0.671 ****	183	1.808	-6.504
M_{N0}	L_0	<i>A. mariesii</i>	28.51 ****	20.45 ****	Sun	0.899 ****	467	1.564	-4.367
					Shade	0.749 ****	193	1.285	-4.259
		<i>A. veitchii</i>	4.757 *	91.34 ****	Sun	0.843 ****	173	1.632	-4.824
					Shade	0.842 ****	161	1.467	-4.266
		<i>P. jezoensis</i>	5.500 *	101.04 ****	Sun	0.799 ****	353	1.381	-4.526
					Shade	0.771 ****	183	1.561	-5.101
M_{N0}	M_{S0}	<i>A. mariesii</i>	22.57 ****	41.198 ****	Sun	0.913 ****	467	0.715	0.402
					Shade	0.605 ****	193	0.583	-0.412
		<i>A. veitchii</i>	9.656 ****	87.80 ****	Sun	0.845 ****	173	0.760	0.543
					Shade	0.759 ****	161	0.642	-0.397
		<i>P. jezoensis</i>	3.766	76.04 ****	Sun	0.810 ****	353	0.648	-0.125
					Shade	0.785 ****	183	0.714	-0.144

ratio than shade saplings, irrespective of length and stem mass. Current-year shoots of *A. mariesii* were significantly longer in sun saplings than in shade saplings, whereas L_0 of *P. jezoensis* was greater in shade saplings than in sun saplings (Figure 1). There was no difference in L_0 between sun and shade saplings of *A. veitchii* (Figure 1).

Lateral branch traits

Stem mass and M_{NB} of lateral branches increased with increasing L_B , and M_{NB} increased with M_{SB} in all species and light regimes (Table 4). The slopes of these regressions did not differ between light regimes, but the regressions for M_{NB} (y) of sun saplings versus L_B (x) generally had larger intercepts (Table 4), indicating that sun saplings have a higher ratio of needle mass to branch length than shade saplings. The regression intercepts for M_{NB} (y) versus M_{SB} (x) were not significantly different between sun and shade saplings except in *A. veitchii* (Table 4). Thus, although the amount of tissue per unit branch length differed between sun and shade saplings, the relative proportion of needle and stem mass did not differ between light regimes for *A. mariesii* and *P. jezoensis*; however, for *A. veitchii*, there was a larger proportion of needle mass in branches of shade saplings than in branches of sun saplings.

For the *Abies* species, lateral branches on shade saplings were significantly older than branches of similar length on sun saplings (Table 5), indicating that branches on *Abies* saplings

develop more slowly in the shade. This trend was less clear for saplings of *P. jezoensis*, reflecting the smaller difference in branch age between sun and shade saplings of this species (Table 5). Regression slopes of branch age versus branch length differed significantly among regressions for the different microsites and species (ANCOVA $P < 0.01$). Needle age for 50% survival and maximum needle life span were both positively correlated with the regression slopes (Figure 2), indicating that saplings with slower growing branches have a longer needle life span.

Biomass ratios

Ratios of M_{NSAP}/M_{SAP} did not differ between sun and shade saplings (Figure 3), whereas shade saplings of the two *Abies* species had lower M_{NSAP}/M_{SAP} values than sun saplings (Figure 3). This indicates that needle turnover in the *Abies* species was slower under shade conditions than under sun conditions. Compared with the *Abies* species, the trend of slower needle turnover in shade than in sun was thus less evident in *P. jezoensis* (Figure 3).

Species-specific morphological traits

For all species, sun saplings had greater R_{HG} than shade saplings (Figure 4). In both *Abies* species, L_C of sun saplings was correlated with H , but L_C of shade saplings was not (Figure 5). Shade saplings of the *Abies* species had smaller crown lengths than sun saplings (Figure 5). Thus, shade saplings had flatter crowns compared with sun saplings, and crown lengths of shade saplings were size-independent. In *P. jezoensis*, L_C was positively correlated with H in both sun and shade saplings, although L_C was greater in sun saplings than in shade saplings (Table 6, Figure 5). Horizontal crown area of saplings of all species increased with increasing H irrespective of light regime (Table 6, Figure 5).

In all species, M_{NSAP} and M_{SAP} were correlated with H (Table 6), but these relationships were unaffected by light (Table 6). However, the regression slopes of M_{SAP} (y) versus H (x) differed among species (ANCOVA $P < 0.05$). *Picea jezoensis* had a shallower slope than the *Abies* species (Figure 6), indicating that sapling mass increases less rapidly with height in *P. jezoensis* than in the *Abies* species.

Discussion

Light responses of needle and shoot

Needle and shoot morphologies combine to disperse incoming light over photosynthetic tissue within the shoot (Sprugel et al. 1996), and both are strongly influenced by the light regime (Sprugel et al. 1996, Stenberg et al. 1998). In this study current-year shoots of sun saplings produced a greater needle mass than shade saplings (Table 3). Sprugel et al. (1996) reported that sun shoots pack needles more closely along the shoot thereby intercepting light more completely, although this arrangement imposes greater construction and maintenance costs. In addition, sun shoots have thicker needles (greater needle mass per area; Table 2), so similar nitrogen

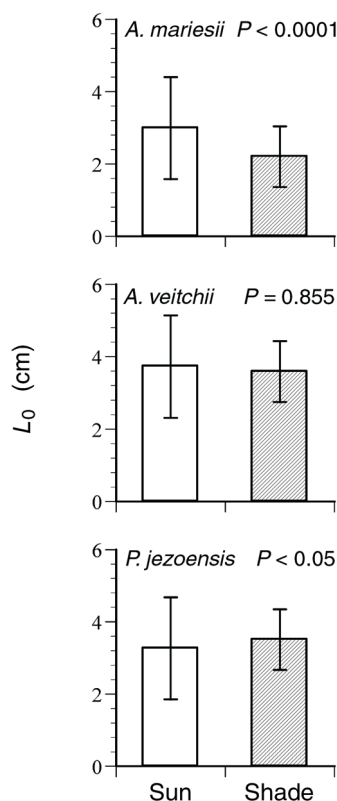


Figure 1. Length of current-year shoot (L_0) in sun and shade saplings. Differences were tested with the Mann-Whitney U test. Bars indicate standard deviations.

Table 4. Summary of results of ANCOVA for differences in allometric relationships of lateral branches based on the regressions of the two microsites. Significance level: * = $P < 0.05$; ** = $P < 0.01$; and **** = $P < 0.0001$. Abbreviations: M_{SB} = stem mass of lateral branches; L_B = length of lateral branch; and M_{NB} = total needle mass on each lateral branch.

Variable		Species	F value: sun versus shade		Results of regression				
Dependent (y)	Independent (x)		Slope (b)	Intercept (a)	Light regime	r ²	n	Slope (b)	Intercept (a)
M_{SB}	L_B	<i>A. mariesii</i>	0.030	23.050 ****	Sun	0.808 ****	71	1.680	−5.311
					Shade	0.900 ****	47	1.704	−5.761
		<i>A. veitchii</i>	0.114	0.337	Sun	0.808 ****	55	1.821	−6.289
					Shade	0.891 ****	68	1.869	−6.459
		<i>P. jezoensis</i>	0.217	6.138 *	Sun	0.877 ****	42	1.961	−6.315
					Shade	0.858 ****	60	2.187	−7.104
M_{NB}	L_B	<i>A. mariesii</i>	0.184	8.705 **	Sun	0.636 ****	71	1.555	−4.428
					Shade	0.701 ****	47	1.467	−4.539
		<i>A. veitchii</i>	0.587	7.946 **	Sun	0.525 ****	55	1.351	−4.352
					Shade	0.749 ****	68	1.503	−4.446
		<i>P. jezoensis</i>	0.836	6.327 *	Sun	0.882 ****	42	1.840	−5.561
					Shade	0.809 ****	60	1.882	−5.968
M_{NB}	M_{SB}	<i>A. mariesii</i>	0.042	0.014	Sun	0.728 ****	71	0.890	0.469
					Shade	0.868 ****	47	0.909	0.473
		<i>A. veitchii</i>	0.010	18.472 ****	Sun	0.790 ****	55	0.818	0.446
					Shade	0.855 ****	68	0.811	0.758
		<i>P. jezoensis</i>	3.128	0.743	Sun	0.918 ****	42	0.954	0.396
					Shade	0.928 ****	60	0.854	0.134

concentrations in sun and shade needles (Table 2) result in a larger amount of nitrogen per unit of intercepted light in sun shoots than in shade shoots (Stenberg et al. 1998), which may contribute to the higher productivity of current-year shoots of sun saplings compared with shade saplings.

In contrast, less needle mass per unit shoot length in shade saplings than in sun saplings (Table 3) suggests less dense packing of needles along the shoot, which increases the ratio of shoot silhouette area to total needle surface area (STAR), resulting in efficient use of limiting light by the avoidance of mutual needle shading (Sprugel et al. 1996, Stenberg 1996, Stenberg et al. 1998). Also, a small needle mass per area of shade needles (Table 2) contributes to increased light capture area with less needle mass (Stenberg et al. 1998). This effective needle arrangement (Stenberg 1996) enables current-year shoots of shade saplings to maintain a positive photosynthesis–respiration balance (Sprugel et al. 1996).

Table 5. Results of the comparison of mean branch age adjusted for branch length (AMBA) between sun and shade saplings. Intraspecific differences in branch age were evaluated by ANCOVA with common branch length (CBL) as a covariate.

Species	AMBA (year)		CBL (cm)	P
	Sun	Shade		
<i>A. mariesii</i>	5.168 ± 0.330	7.490 ± 0.406	19.05	< 0.0001
<i>A. veitchii</i>	3.381 ± 0.288	5.136 ± 0.258	16.45	< 0.001
<i>P. jezoensis</i>	3.732 ± 0.299	4.505 ± 0.248	13.06	0.054

Photosynthetic tissue comprises a greater proportion of total shoot mass in shorter shoots than in longer shoots (Niinemets and Kull 1995, Table 3), because the mechanical requirement for support is less in shorter shoots. Among the study species, current-year shoot length was less in shade saplings than in sun saplings only in *A. mariesii* (Figure 1). This reduces stem biomass investment in the current-year shoots (Table 3), further limiting the quantity of photosynthate required to construct and maintain support tissue. Thus, in shade, *A. mariesii* showed the greatest acclimation as measured by the ability to maintain a positive balance between photosynthesis and respiration.

Needle life span and branch growth

Biomass allocation patterns differed between current-year shoot and lateral branch systems. Within lateral branches, the proportion of foliage biomass was similar in sun and shade saplings (*A. mariesii* and *P. jezoensis*) or larger in shade saplings (*A. veitchii*) (Table 4). Although current-year shoots of shade saplings had smaller needle mass per unit stem mass than sun saplings, lateral branches of shade saplings maintained needles for longer than sun saplings (Table 2). This suggests that, in shade saplings, longer needle life span helps to offset the additional stem construction cost and to compensate for the smaller biomass investment in needles of current-year shoots.

In addition, saplings with slower-growing branches tended to have a longer needle life span (Figure 2), suggesting that plasticity of branch growth rate and plasticity of needle life span are interdependent. Total needle area of a coniferous tree, which directly affects the total carbon fixation, is linked to

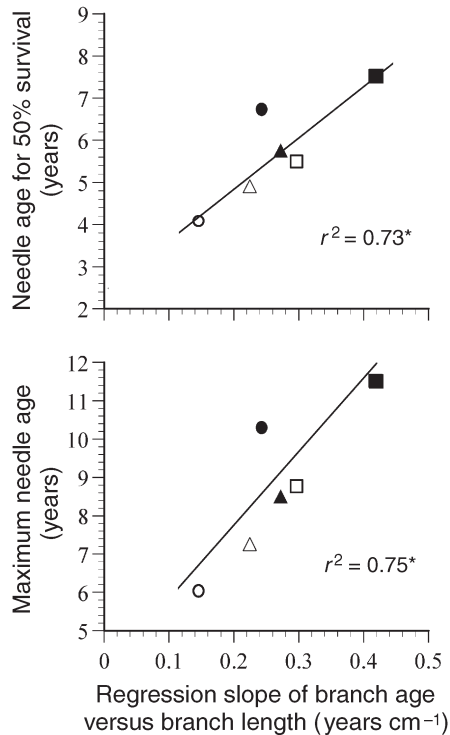


Figure 2. Relationships between regression slope of branch age (y) versus branch length (x) and needle life span. Symbols: squares, *A. mariesii*; circles, *A. veitchii*; triangles, *P. jezoensis*. Open symbols indicate sun saplings of each species, and solid symbols indicate shade saplings. Regression lines and r^2 values are shown. Significance level: * = $P < 0.05$.

needle life span (Kayama et al. 2002). A long needle life span enables shade saplings with slower-growing branches to maintain a high needle surface area despite their limited assimilate supply (Kohyama 1980). Similarly, Niinemets and Lukjanova (2003) showed that decreases in branch irradiance resulted in decreases in extension growth and increases in mean and maximum needle age. However, in this study, plasticity in branch growth and needle life span differed between the genera studied. In the *Abies* species, lateral branches of shade saplings grew more slowly than those of sun saplings (Table 5), but displayed greater variability in needle life span (Table 2) and foliage turnover (Figure 3) with the result that they had a similar (*A. mariesii*) or higher (*A. veitchii*) needle/branch biomass ratio. In contrast, shade did not noticeably inhibit branch growth of *P. jezoensis* (Table 5), which showed less variability in needle life span (Table 2) and turnover (Figure 3) than in the *Abies* species. Consistent with the report that *Abies* has greater plasticity than *Picea* in shoot- and crown-level morphological characteristics (Messier et al. 1999), *Abies* displayed greater plasticity in branch development within crowns.

Effects of within-crown characteristics on crown morphology

For all species, shading restricted height growth (Figure 4); however, there were differences in L_C between the *Abies* species and *Picea*. The absence of an increase in L_C with increas-

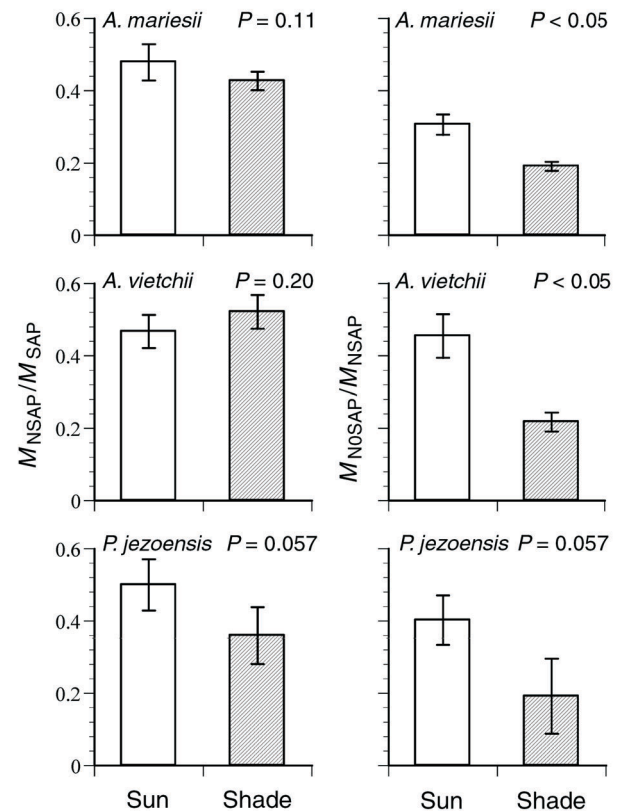


Figure 3. Ratio of total needle mass to sapling mass (M_{NSAP}/M_{SAP}) and ratio of current-year needle mass to total needle mass (M_{NO_SAP}/M_{NSAP}) in sun and shade saplings. Differences were tested by Mann-Whitney U test. Bars indicate standard deviations.

ing height in shade saplings of the *Abies* species (Figure 5) contributes to their flattened crown structure (Kohyama 1980, Messier et al. 1999), which is a major component underlying the greater shade-tolerance of *Abies* species (e.g., Kohyama 1980, Klinka et al. 1992, King 1997, Messier et al. 1999, Claveau et al. 2002). On the other hand, shade saplings of *P. jezoensis* showed increased L_C with H (Figure 5), although their height growth rate was reduced in response to shading (Figure 4). This suggests that *P. jezoensis* saplings have low light-related plasticity with respect to crown development, and thus have relatively conical crowns irrespective of light regime. The conical crown form underlies the lower shade-tolerance of *P. jezoensis* (Mori and Takeda 2003).

Kohyama (1980) observed that *A. mariesii* shade saplings expand lateral branches more slowly and abort lower older branches more gradually than vigorous open-grown saplings. Shade saplings of *Abies* species show much lower vertical trunk extension rates than branch extension rates, resulting in flattened crowns (Kohyama 1980, King 1997). Accordingly, the long needle life span of the two *Abies* species contributes to the development of their flattened crowns through the correlative response of the slower-growing lateral branches. Thus, the greater plasticity of crown morphology of *Abies* (e.g., Messier et al. 1999, Williams et al. 1999, Claveau et al. 2002, Mori and

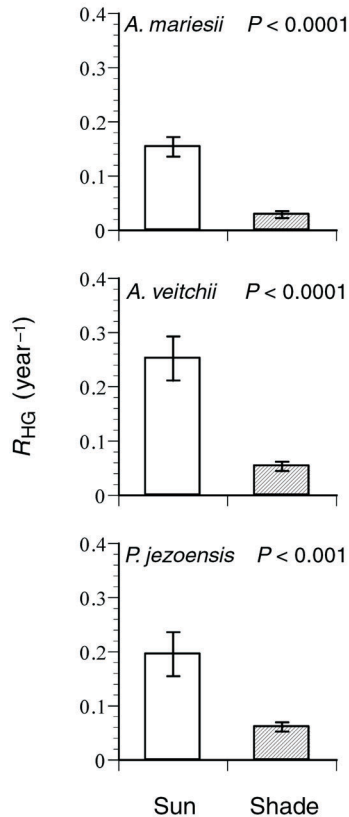


Figure 4. Relative height growth rate (R_{HG}) in sun and shade saplings. Differences were tested with the Mann-Whitney U test. Bars indicate standard deviations.

Takeda 2003) reflects greater variability in branch development in this genus.

Flattened crowns incur substantial mechanical costs to support the laterally expanded branches (Hunter 1997, Poorter and Werger 1999), especially in snowy forests (King 1997). Shade saplings of the *Abies* species that we studied satisfy this mechanical requirement by reducing their annual investment in foliage and allocating more to support tissues. The low annual investment in foliage is compensated for by a longer needle life span and slower foliage turnover (King 1997).

Kaji (1982) and Mori and Takeda (2003) suggested that adaptation to snow loading is greater in *A. mariesii* than in *A. veitchii*. Shoots of *A. mariesii* shade saplings were better able to maintain a positive photosynthesis–respiration balance than shoots of *A. veitchii* shade saplings. Moreover, the shorter current-year shoots of *A. mariesii* imply smaller annual biomass requirements for new shoot production. In shade, these traits may facilitate annual investment in support tissues of older shoots. Combined with the longer needle life span in shade, lateral branches of sun and shade saplings of *A. mariesii* have similar needle/stem biomass ratios. In contrast, because shoot length in *A. veitchii* does not respond much to light (Figure 1) although this species makes a substantial biomass investment in current-year shoots, it appears that *A. veitchii*

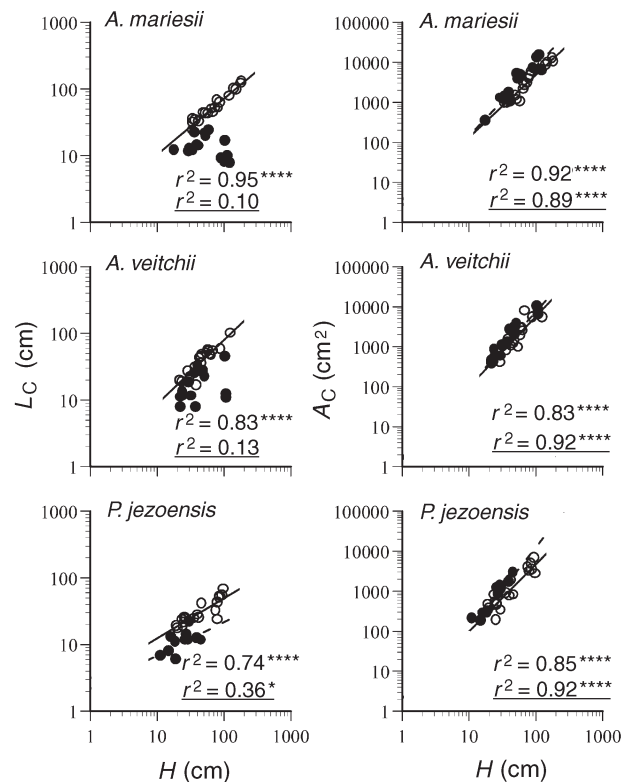


Figure 5. Allometric relationships of vertical crown length (L_C) and horizontal crown area (A_C) with height (H). Symbols: open circles, sun saplings; and solid circles, shade saplings. Dotted regression lines and r^2 values with underlines represent those of shade saplings. Significance level: * = $P < 0.05$; and **** = $P < 0.0001$. Difference within species was tested by ANCOVA and the results are shown in Table 6.

shade saplings cannot increase their annual investment in support tissue of older shoots as much as can shade saplings of *A. mariesii*. Accordingly, in shade, *A. veitchii* allocates less to branch stem and accumulates foliage by extending needle life span, thus developing branches with a high foliage ratio. Stem biomass can be regarded as an indicator of mechanical support costs (Niinemets and Kull 1995). *Abies mariesii* increases its investment in stem biomass in response to shading and so is able to support laterally expanded branches and crowns under shade conditions. As a result, *A. mariesii* exhibits greater tolerance to shading (Kohyama 1984, Mori and Takeda 2003) and snow loading (Kaji 1982, Mori and Takeda 2003) than *A. veitchii*.

Conical crowns require a smaller biomass increment per unit height increase (Takahashi 1996, Hunter 1997, Williams et al. 1999). Compared with the *Abies* species, *P. jezoensis* maintained a smaller sapling mass per unit height increase (Figure 6). As a result, *P. jezoensis* saplings show rapid height growth in well-lit conditions such as gaps. In addition, multi-layered conical crowns can reduce allocation to support investment (Hunter 1997). Thus *P. jezoensis* shade saplings do not

Table 6. Summary of results of ANCOVA of differences in allometric relationships of saplings based on the regressions of the two microsites. Significance levels: * $P < 0.05$; ** $P < 0.01$; and **** $P < 0.0001$. Abbreviations: L_C = vertical crown length; A_C = horizontally projected crown area; M_{NSAP} = total needle mass within sapling; M_{SAP} = aboveground sapling mass; H = sapling height.

Variable		Species	F value: sun versus shade		Results of regression				
Dependent (y)	Independent (x)		Slope (b)	Intercept (a)	Light regime	r^2	n	Slope (b)	Intercept (a)
L_C	H	<i>A. mariesii</i>	44.443 ****	83.440 ****	Sun	0.954 ****	19	0.839	0.356
					Shade	0.102	15		
		<i>A. veitchii</i>	5.382 *	30.154 ****	Sun	0.828 ****	19	0.960	-0.098
					Shade	0.130	15		
		<i>P. jezoensis</i>	0.231	37.173 ****	Sun	0.741 ****	19	0.601	1.091
					Shade	0.358*	11	0.500	0.772
		<i>A. mariesii</i>	0.838	19.921 ****	Sun	0.916 ****	19	1.561	1.208
					Shade	0.891 ****	15	1.742	0.968
A_C	H	<i>A. veitchii</i>	0.140	5.771 *	Sun	0.825 ****	19	1.758	0.461
					Shade	0.919 ****	15	1.852	0.400
		<i>P. jezoensis</i>	1.862	8.801 **	Sun	0.846 ****	19	1.075	0.652
					Shade	0.918 ****	11	2.118	-0.311
M_{NSAP}	H	<i>A. mariesii</i>	4.222	0.000	Sun	0.875 ****	19	2.434	-6.022
					Shade	0.976 ****	15	3.006	-8.380
		<i>A. veitchii</i>	0.010	0.152	Sun	0.856 ****	19	2.352	-5.849
					Shade	0.951 ****	15	2.324	-5.690
		<i>P. jezoensis</i>	0.278	0.631	Sun	0.917 ****	19	2.069	-4.826
					Shade	0.767 ****	11	2.269	-5.644
M_{SAP}	H	<i>A. mariesii</i>	2.874	0.004	Sun	0.884 ****	19	2.515	-5.548
					Shade	0.972 ****	15	2.983	-7.473
		<i>A. veitchii</i>	0.016	0.058	Sun	0.865 ****	19	2.497	-5.627
					Shade	0.959 ****	15	2.533	-5.732
		<i>P. jezoensis</i>	0.321	0.065	Sun	0.924 ****	19	1.453	-1.741
					Shade	0.752 ****	11	1.605	-2.209

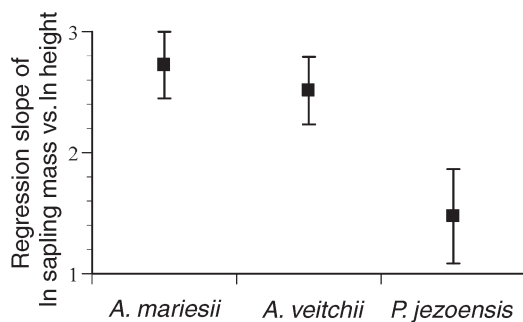


Figure 6. Regression slope of ln sapling mass (y) versus ln height (x) (g cm^{-1}). Bars indicate 95% confidence intervals.

need to compensate for increased mechanical support costs by extending needle life span as much as do shade saplings of the *Abies* species. *Picea jezoensis* therefore shows a lower plasticity in crown morphology and a lower variability in needle life span and branch growth rate compared with the *Abies* species. We suggest that the lower shade tolerance of *P. jezoensis* compared with the two *Abies* species (Mori and Takeda 2003, 2004) is associated with these features. In conclusion, we infer that species-specific crown morphology and plasticity in

crown morphological traits, which strongly affect the shade tolerance of conifer saplings, have close linkages to within-crown characteristics.

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