Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine

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Abstract: Information on the dynamics of sapling growth of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm), two dominant species in the interior of British Columbia, Canada, is incomplete and thus the objective of this study was to understand how light availability and sapling size interact to influence their growth and crown morphology. In an undisturbed forest, 360 saplings were randomly selected in three light classes 0–15, 15–30, and >30% PPFD (photosynthetic photon flux density). A number of morphological and growth parameters were measured, including height and lateral branch growth. Douglas-fir had a more plastic crown morphology than lodgepole pine with its leader to lateral branch growth ratio, live crown depth, and number of branches increasing with increasing light class. Sapling size had little effect on morphological characteristics, but larger saplings of both species had greater absolute height growth and lateral branch growth than did smaller saplings. Both Douglas-fir and lodgepole pine were able to survive up to 50 years and attain a height of 3 m at less than 5% PPFD. These results further suggest that shade tolerance is greater on drier sites, although the mechanisms for such increases in tolerance are unknown. The ecological implications of these findings are discussed in a forestry context.

Résumé : L'information sur la dynamique de croissance des gaules du Douglas taxifolié (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) et du pin tordu (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm), deux espèces dominantes de l'intérieur de la Colombie-Britannique, Canada, est incomplète. L'objectif de la présente étude était, par conséquent, de comprendre comment la disponibilité en lumière et la dimension des gaules interagissent pour influencer leur croissance et la morphologie de leur cime. Dans une forêt non perturbée, on a choisi, au hasard, 360 gaules dans trois classes de lumière : 0–15, 15–30 et >30% de DFPP (densité du flux de photons photosynthétiques). On a mesuré un certain nombre de paramètres morphologiques et de croissance, incluant la hauteur et la croissance des branches latérales. Le Douglas taxifolié présentait une morphologie de cime plus plastique que celle du pin tordu avec un rapport entre la croissance de sa pousse terminale et celle de ses branches latérales, une profondeur de sa cime vivante et un nombre de branches qui augmentaient avec l'augmentation de la classe de lumière. La dimension des gaules avait peu d'effet sur les caractéristiques morphologiques, mais les gaules de plus forte dimension, des deux espèces, avaient une croissance en hauteur absolue et une croissance des branches latérales plus grandes que celles des gaules de plus faible dimension. Le Douglas taxifolié et le pin tordu étaient tous deux capables de survivre jusqu'à 50 ans et d'atteindre une hauteur de 3 m à moins de 5% de DFPP. Les résultats suggèrent, en outre, que la tolérance à l'ombre est plus grande sur les sites plus secs, bien que le mécanisme de cet accroissement de tolérance soit inconnu. Les implications écologiques de ces résultats sont discutés dans le contexte de la foresterie.

[Traduit par la rédaction]

Introduction

Trees with different shade tolerances have different degrees of morphological and physiological plasticity in the face of environmental change (Givnish 1988). This has been supported by several recent studies examining the growth and crown morphology of shade-tolerant and -intolerant conifer species in relation to understory light conditions (O'Connell and Kelty 1994; Carter and Klinka 1992; Parent and Messier 1995; Chen et. al. 1996). Findings indicate that shade-tolerant species exhibit greater changes in crown morphology along a light gradient than do the more shade-intolerant species. This morphological change is often referred to as plasticity. For conifers, morphological plasticity may be considered in terms of number of branches per whorl, crown depth, and the leader height to lateral branch growth ratio. This latter phenomenon, reported for a variety of shade-tolerant conifer species, is the variation from a conical crown form in full light to a more "flat-topped" or "umbrella form" in the forest understory (Oliver and Larson 1990; Kohyama 1980; Parent and Messier 1995; Chen et al. 1996) because of reduced height growth relative to lateral

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Table 1. Stand characteristics of the two study areas.

Overstory characteristics	Site 1	Site 2
Basal area (m^2/ha)	15–20	15–20
Density (stems/ha)	1100–1400	900–1200
Height (m)	12–15	12–15
DBH (cm)	18–28	18–28 (pine), a few fir veterans 60 cm
Age (years)	90	120 (with a few fir veterans 300–350 years old)
Composition	Pure pine (>95%)	Pine, with a few fir veterans

branch extension as well as to the death of the lower branches (O'Connell and Kelty 1994; Parent and Messier 1995). Therefore, crown morphology may have important implications with regard to the tree's ability to conduct efficient photosynthesis in a light-limiting environment and to compete with other species (Daniel et al. 1979; Beaudet and Messier 1998; Messier et al. 1999).

In terms of growth and survival, a decrease in tree growth and an increase in mortality with increasing shade was found to be species dependent (Kitajima 1994; Kobe and Coates 1996). For example, shade-intolerant species often have greater height growth in low light conditions than more shade-tolerant ones (Beaudet and Messier 1998). Messier et al. (1999) describe how certain shade-tolerant species can survive long periods of suppression by sharply reducing their height growth in deep shade. Traditionally, height growth rates have been used as indicators of vigour; however, it has been shown that, for some species on some sites, height growth rate and survival are negatively correlated under shady conditions (Hiura et al. 1996).

Certain authors have also observed that small saplings have a better chance of surviving under a dense canopy than do larger, pole-sized individuals because maintenance costs increase dramatically with size (Waring 1987; Kelly et al. 1998). Tree height and biomass therefore influence optimal leaf area index and the whole-plant or ecological compensation point (sensu Givnish 1988). By having a higher ecological compensation point, the increased mass of a taller understory sapling will indirectly dictate the minimum light level required for survival. The height at which different species reach their ecological compensation point has been hypothesized to vary among boreal tree species according to their shade tolerance (Messier et al. 1999). Shade tolerance under a given light regime is therefore dynamic, changing as a result of tree size (Givnish 1988). Taller saplings, as they approach their ecological compensation point, may therefore be expected to grow less vigorously, with possible subsequent effects on their crown morphology.

A review of optimal patterns of tree architecture suggests that functional constraints vary with the size of the individual and that different morphological patterns would be optimal across an individual's life-span (Farnsworth and Niklas 1995). However, few growth and morphological studies have explored the relationship between sapling size and different light environments for species with different shade tolerances. The objective of this study was thus to understand how light availability and sapling size interact to influence tree growth and crown morphology by studying two tree species: Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm). These trees are major species of the interior montane forests of central British Columbia (Krajina 1969; Meidinger and Pojar 1991). Douglas-fir is considered to be a moderately shade-tolerant species (Herman and Lavender 1990), and lodgepole pine is a shade-intolerant, early seral species (Daniel et al. 1979).

Materials and methods

Study area

Two study sites were located within 8 km of each other in the Dry Cool Interior Douglas-fir biogeoclimatic subzone (Meidinger and Pojar 1991) near Williams Lake, British Columbia. In the understory, both sites had abundant naturally established regeneration (both sites averaged 6000 stems/ha) composed of approximately 60% lodgepole pine and 40% Douglas-fir. The mean annual precipitation averages between 360 and 560 mm, and the mean annual temperature is 4.1°C (Environment Canada 1994). The Orthic Gray Luvisolic soils in this area have developed on deep deposits of medium-textured glacial till (Annas and Coupé 1979).

Ecological information such as elevation, aspect, topography and soil morphological properties, vegetation, ground surface materials, humus form, and soil moisture were recorded. Two ecologically similar sites were then chosen based on similar soil characteristics, topography, and indicator plants: moderately dry and nitrogen-medium sites with fairly sparse understory vegetation (Steen et al. 1990), the most common being pinegrass (*Calamagrostis rubescens* Buckl.). The two sites also have similar overstory tree characteristics and disturbance histories, although site 1 was burned more recently (Table 1). Field work was conducted in the summer of 1994.

Sapling selection

The selected saplings were of a range of sizes, growing in an undisturbed forest with a gradient of light environments ranging from high overstory canopy coverage to medium-sized gaps. The study sites had well established saplings of both species, varying in height from 10–600 cm. As changes in stand density or the competitive environment of an individual may affect its growth and crown morphology we selected only individuals having grown under constant conditions. On each site, over 500 saplings were identified that had been growing under relatively stable light conditions as judged from minimal variation in height growth increments in the previous 5 years. These saplings had been exposed to little or no competition from other vegetation and had no apparent damage. Of these, 180 sample saplings were randomly selected along the four light gradient transects (total saplings for two sites were 360 and 180 for each species).

Light measurements

The overall light environment of each sample tree was determined by readings taken on five different dates with a hand-held

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sensor positioned above the apical bud. The quantum sensor (LI-190SA, LI-COR Inc., Lincoln, Neb.) was placed on an extension pole when terminal buds were above arm's reach. Because of its major role in photosynthesis, light is measured in the 400- to 700-nm wave band and is termed "photosynthetic photon flux density" (PPFD). The ratio of light at the apical bud (Q_o) to the light above the forest canopy (Q_i) was transformed into %PPFD by the following equation:

$$\%\text{PPFD} = (Q_o / Q_i) \times 100$$

The value of (Q_i) was determined by placing a sensor Quantum 190A, connected with a LI-1000 Datalogger (LI-COR Inc.) in an adjacent opening. The datalogger was programmed to measure the PPFD density every 5 s and to record the average value each minute. The calculated %PPFD thus represents the daily proportion of incident light received by the apical bud of each study seedling (Messier and Puttonen 1995; Parent and Messier 1995). The readings were taken on cloudy days, as the diffuse light under these conditions has a uniform penetration from all directions. The weak spatiotemporal variability of diffuse light gives a radiation index specific to each point in the understory. According to Messier and Puttonen (1995) and Parent and Messier (1995), the proportion of radiation received at a given point in the understory is relatively constant throughout the day.

The approach adopted in this study makes the assumption that %PPFD provides an integrative index of the effects of the overstory canopy on an understory tree. Thus, the degree to which the foliage of the overstory canopy shades the understory plants is roughly proportional to other growth factors associated with shade such as light quality (Messier and Puttonen 1995; Messier 1996) and soil and air temperatures. According to Spurr and Barnes (1980), relative illumination gives a measure of the relative density of the forest and of all the environmental factors associated with this density. Its measure does not quantify the independent effect of light alone.

Morphological and growth measurements

The following measurements were taken from all sampled saplings: basal diameter in the study year and height growth increments for the years 1994, 1993, and 1992. Additional measurements were taken on 72 saplings (36 of each species) representing a stratified random subsample of the study saplings:

(1) total length of all lateral branch segments for the years 1992–1994, using only data from the first-order lateral branch segments (adjacent to the trunk) for the statistical analyses to eliminate the confounding influences of apical dominance and self-shading;
(2) removal of basal disc for age measurements;
(3) live crown depth and diameter; and
(4) number of branches per whorl for the years 1992–1994.

The relative height growth (RHG) for each year *i* was calculated according to the following equation:

$$\text{RHG} = (\ln H_{t_2} - \ln H_{t_1})/(t_2 - t_1)$$

where H indicates the seedling height for the growing season of year t.

The leader to lateral branch growth increment ratio was calculated according to the following equation:

$$R_{\text{l/b}} = f_i/[(\text{BL}_i)/n]$$

where f_i is the annual leader height growth length in year i ; BL_i is the total length of all the first-order branches from the node of year i; and n is the number of living nodal branches produced for the year i. The leader to lateral branch growth ratio is used to determine the degree of apical dominance over lateral branch growth. Greater apical dominance is indicated by a higher ratio.

Statistical analyses

For statistical analysis, the light measurements were divided into three classes of %PPFD as follows to represent low, medium, and high light class values: (*i*) 0–15%; (*ii*) 15–30%; and (*iii*) >30%. The minimum and maximum light values recorded were 3 and 74% PPFD, respectively. Naturally occurring sampled saplings were divided into small, medium, and large size classes: (*i*) 30–100 cm; (*ii*) 101–200 cm; and (*iii*) 201–450 cm. These class definitions not only enable us to evaluate the effect of different light and size classes for each species but importantly also the interactions between these variables. They would also be more useful to forest managers than a continuous analysis as they could be quickly evaluated and thus also quickly interpreted in the field.

The data was summarized and analysed using SYSTAT 7 statistical software (Wilkinson et al. 1997). The relationships between the different variables were examined by analysis of variance (ANOVA) and descriptive statistics. ANOVA and Tukey pairwise comparisons were used to determine the principal factors explaining variability. The experimental design was completely randomized.

Results

Crown morphology

Crown morphology differs significantly between the two species for two of the three measurements used (Table 2). For pine's leader to lateral branch ratio (L/B ratio), the differences were not significant because of the high variability and lack of lateral branches in the small and medium size classes. For live crown depth and number of branches the different response of these two species across increasing light classes results in significant species × light interactions. Lodgepole pine saplings have fewer branches per whorl at low light levels than Douglas-fir but pine's number of branches increases dramatically in the highest light class (Figs. 1E and 1F). In terms of live crown depth, both species have similar ratios of live crown to total tree height at low light, but the more tolerant Douglas-fir saplings increase the depth of their live crown to a greater extent than pine in the higher light classes (Figs. 1C and 1D).

Light class affects all three morphological measurements, with values generally increasing with greater % PPFD light classes for Douglas-fir (Figs. 1A, 1C, and 1E). For lodgepole pine, the response differs depending on the index and height class used in the evaluation (Figs. 1B, 1D, and 1F). For this species, measured values of the L/B ratio decrease with increasing light, whereas the number of branches per whorl increases with increasing light. Medium-sized pines (101–200 cm) also have higher values than large individuals (201–450 cm) at moderate light classes (15–30% PPFD) for all three morphological measurements used (L/B ratio, crown depth, and number of branches produced).

Sapling size did not have much influence on crown morphological characteristics as only the number of branches increased with increasing sapling size. There was no effect of size on crown depth for Douglas-fir, but as indicated by a species × height interaction in Table 2, crown depth varied for lodgepole pine according to size and light classes (Fig. 1D).

Table 2. ANOVA of sapling morphological characteristics (L/B ratio, live crown depth, and no. of branches), growth (absolute height growth, relative height growth, and lateral branch growth), allocation (height to diameter ratio), and age as a function of species, light class, and height class.

		L/B ratio		Live crown depth		No. of branches		Absolute height growth		Relative height growth		Lateral branch growth		Height to diameter ratio		Age	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species (S)	1	0.308	0.582	6.565	0.013	69.18	<0.001	4.85	0.028	1.732	0.189	19.373	<0.001	55.65	<0.001	17.078	0.073
Light class (L)	2	6.211	0.004	30.195	<0.001	33.65	<0.001	44.61	<0.001	22.785	<0.001	16.865	<0.001	3.83	0.029	5.917	0.005
Height class (H)	2	1.758	0.185	0.992	0.377	6.93	0.002	88.96	<0.001	108.99	<0.001	42.209	<0.001	9.60	<0.001	3.337	<0.001
S×L	2	2.209	0.106	6.473	0.003	6.67	0.003	0.56	0.572	1.595	0.204	0.189	0.828	0.02	0.983	2.995	0.140
S×H	2	1.235	0.301	4.373	0.017	1.00	0.373	3.82	0.023	8.156	<0.001	8.461	0.001	1.20	0.309	0.108	0.898
L×H	4	0.689	0.604	1.836	0.135	1.11	0.362	10.82	<0.001	1.654	0.160	8.020	<0.001	0.94	0.446	2.037	0.026
S×L×H	4	1.878	0.122	1.421	0.240	1.85	0.132	0.83	0.506	0.330	0.858	0.598	0.666	1.29	0.288	1.208	0.318

Growth

Although it would be expected that larger saplings would not be found in lower light classes, especially for shade-intolerant species such as lodgepole pine, no obvious decline in maximum sapling size was found in the lower light range for either species (Fig. 2). In contrast, individuals of all size classes and all ages were found in all light classes for both species, including pine saplings greater than 4 m in height at below 15% PPFD. Douglas-fir saplings vary in age from 15 to 58 years (mean 33) and lodgepole pine from 7 to 60 years (mean 29), and there are no statistical differences in age between these species (Table 2, $p > 0.05$). However, older seedlings of both species are found in the lowest light classes (Table 2, Fig. 2), and the interaction between species and light is explained by a slight negative relationship between PPFD and sapling age for lodgepole pine ($r^2 = 0.19$). There is a positive relationship between height and age ($r^2 = 0.49$ both species) as more time is required to grow taller seedlings (relationship not shown).

Height to diameter ratios decrease globally for both species with increasing light class and decreasing size class (Table 2, Fig. 3). A comparison of the two species shows that Douglas-fir has a smaller height to diameter ratio than pine.

Growth, as evaluated using any of the three measurements, generally increases with increasing light class (Table 2, Fig. 4). In the highest light class, the larger saplings outgrew medium saplings, which outgrew the smaller saplings in terms of absolute height growth and lateral branch growth. However, at low light levels the growth of the large saplings was greatly reduced, and no differences could be observed between absolute height growth and lateral branch growth for sapling of either species across size classes. In terms of relative height growth, small saplings of both species outgrew large saplings in the lower light classes, although for pine the larger saplings had equal relative growth rates in the highest light class (Table 2, Fig. 4).

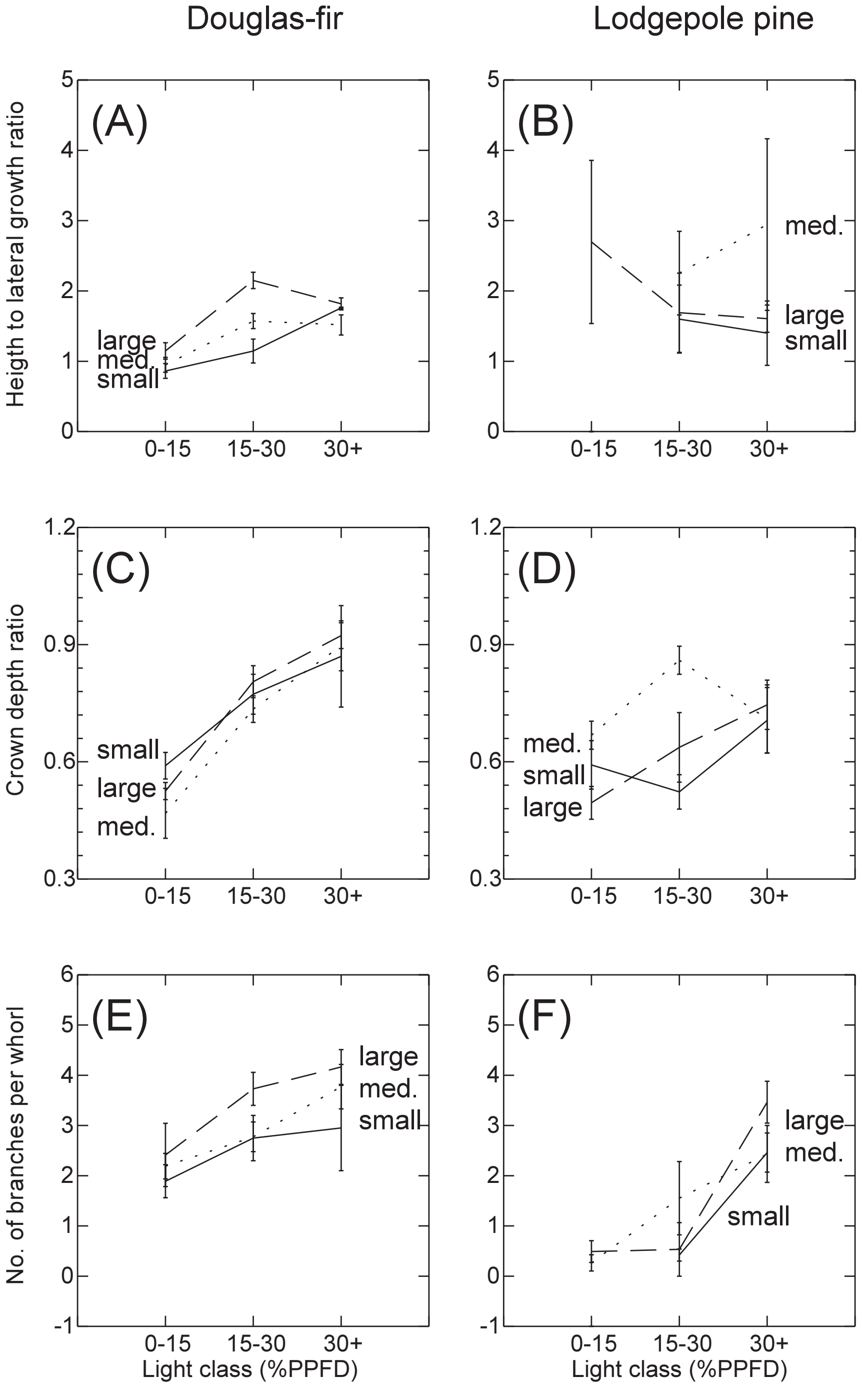
No differences were noted between the two species in terms of relative height growth (Table 2), but fir's lateral branch growth was much greater than pines at low light levels. However, in the high light class, the lateral growth of pine was equal to (and in the case of large pine saplings greater than) that of Douglas-fir, as shown by a positive interaction between species and height (Table 2, Fig. 4). The same general pattern can be observed for absolute height growth in which pine, especially the largest size-class saplings, grew poorly in the low light class but had greatly increased growth in the highest light class.

Discussion

Crown morphology

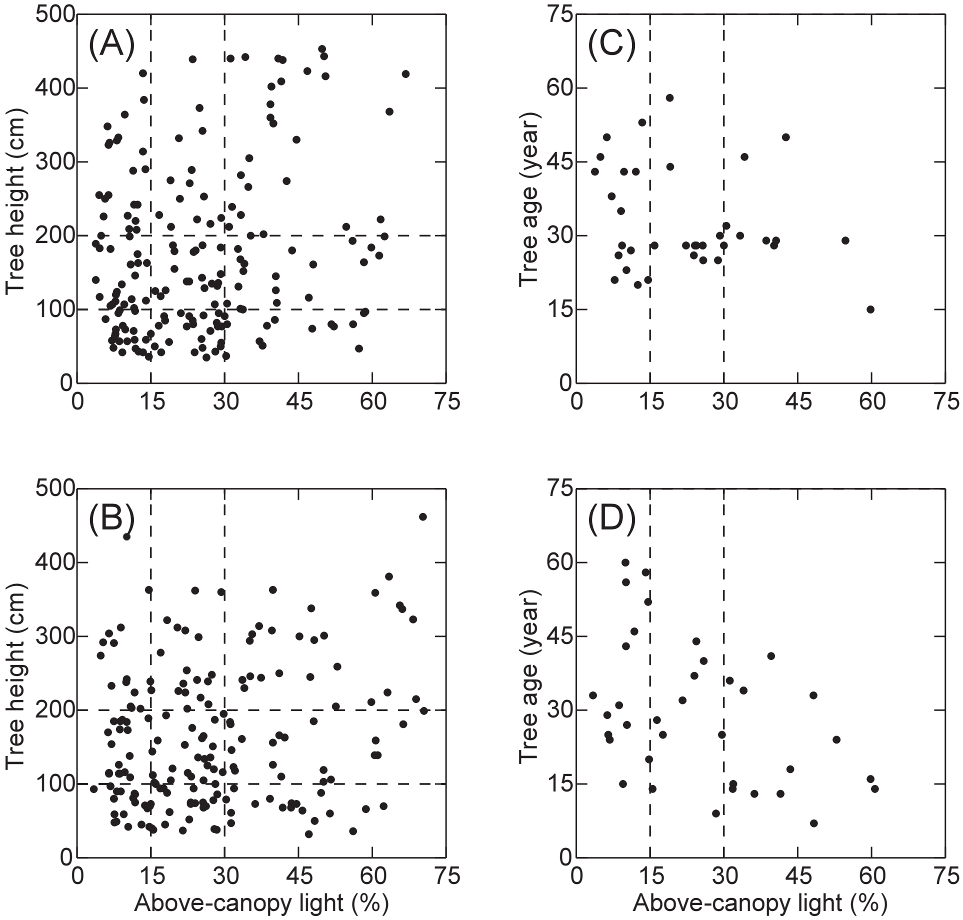
Differences in crown morphology between species have been linked to characteristics associated with shade tolerance. In our study, the more shade-tolerant Douglas-fir is better able to modify its crown morphology than lodgepole pine in the different understory conditions and small gaps investigated (Fig. 1). In an earlier study of small-sized saplings (0.8–1.3 m), Chen et al. (1996) also found Douglas-fir to be more plastic in its growth form across a light gradient, with fir increasing lateral branch growth over terminal

Fig. 1. Crown morphological plasticity of saplings in relation to three height and three light classes. Height classes are as follows: 30–100 cm (bold lines); 100–200 cm (dotted lines); 200–450 cm (broken lines). Light classes are as follows: (1) <15% PPFD; (2) 15–30% PPFD; (3) >30% PPFD. Error bars are ±1SE. (A) Height to lateral growth ratio of Douglas-fir. (B) Height to lateral growth ratio of lodgepole pine. (C) Crown depth ratio of Douglas-fir. (D) Crown depth ratio of lodgepole pine. (E) Number of branches per whorl for Douglas-fir. (F) Number of branches per whorl for lodgepole pine.



leader growth in low light environments, whereas pine did not. Our results confirm this finding and further show that fir decreases its live crown depth and number of branches produced in shady conditions. Douglas-fir therefore responds to low light conditions by maintaining a limited number of healthy branches in the live crown and allocating more resources to lateral growth than apical growth. This “horizontal” growth form increases the possibility of intercepting sunflecks and capturing light that may otherwise go to competing vegetation (Givnish 1988). Alterations in crown morphology, such as horizontal growth forms in low light conditions, have thus been identified as characteristics of shade-tolerant species (Chen et al. 1996; Oliver and Larson 1990).

Fig. 2. Different-sized and different-aged Douglas-fir (A and C, respectively) and lodgepole pine (B and D, respectively) saplings sampled along a light gradient. The sampling population *n* of both species was divided into three height classes and three light classes.



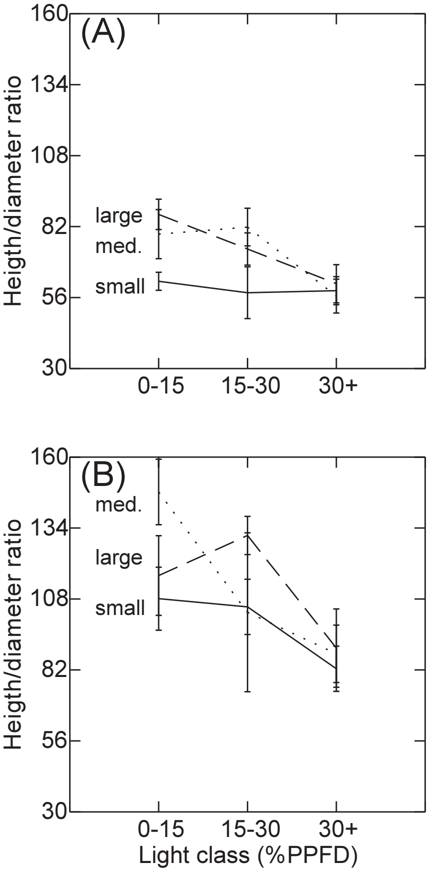
Moderate increases in light (from one 15% PPFD class to another), reduced the mortality of lower branches, presumably because of slightly less self-shading. An experimental study investigating the effect of changes in overstory conditions on shade-tolerant balsam fir (*Abies balsamea* (L.) Mill.) also found that only slight changes in overstory cover were required to increase seedling leader to lateral branch ratios and branch production (Kneeshaw et al. 1998). As light increases, the tree increases allocation to terminal growth instead of to lateral growth; thus, more light is available to the lower branches, and the crown depth increases. For Douglas-fir, crown depth therefore can be used as an index of vigour, reflecting the strong relation between crown depth and increasing light (Fig. 1C).

In comparison, pine invests most of its resources in height growth (Wang et al. 1994; Chen et al. 1996), and for this species, most of the morphological measurements that we used are only poorly correlated with the different light classes. In low light, with a vertically oriented crown, high branch mortality, and branches well separated from each other on the stem, there is low self-shading and the species may retain a few efficient branches well distributed along the stem. In this way, pine may be able to survive in shady conditions with a minimum of photosynthetic tissue (Takahashi 1996). In high light, the number of lower branches increases, but total live crown depth is only slightly greater than in low light. Although it has been suggested that pine is less efficient at low light, since it is unable to alter its needle morphology across a light gradient (Chen et al. 1996), Messier et al. (1999) found that a clear difference in the leaf level photosynthetic compensation point between shade-tolerant and -intolerant boreal forest tree species does not seem to exist. This suggests that pine needles are as efficient as fir needles in shade. The increase in branches per whorl with increased light can be used as an index of tree vigour and performance for lodgepole pine (Fig. 1F).

Sapling growth rates

Although height growth is important for improved light interception (King 1990), it has associated costs as well. Greater plant size, irrespective of the individual's age, leads to greater requirements for resources, and therefore, it has strong implications for the survival of large individuals growing under low light conditions (Messier et al. 1999). It was thus surprising to find "shade-tolerant" Douglas-fir and "shade-intolerant" lodgepole pine up to 3 m in height in as low as 5% full sunlight (Fig. 2). The presence, in the lowest light class, of 30- to 60-year-old pine that are 2–4 m in height and their slow growth (Fig. 4B) suggests that these saplings have been growing in low light for most of their life and thus that both of these species can grow and develop in deep shade in these forests.

Fig. 3. Height to diameter ratio of saplings in relation to three height and three light classes. Height classes are as follows: 30–100 cm (bold lines); 100–200 cm (dotted lines); 200–450 cm (broken lines). Light classes are as follows: (1) <15% PPFD; (2) 15–30% PPFD; (3) >30% PPFD. (A) Douglas-fir. (B) Lodgepole pine.



In contrast, in a study on balsam fir, only small seedlings were found at low light levels (<3%), but seedlings larger than 30 cm were found under higher light conditions (Parent and Messier 1995). Similarly, Kelly et al.[2] found that the maximum height of shade-intolerant, understory trembling aspen (*Populus tremuloides* Michx.) sprouts increased from 1 m at 10% full light to 7 m at 40%. From a whole-plant perspective, sapling light requirements, irrespective of age, should increase with height resulting from increasing maintenance costs (Waring 1987, Givnish 1988), and thus, small saplings should have a greater availability of carbon in the shade than larger individuals. Increasing costs may be in terms of carbon allocation and respiration associated with the structural and maintenance functions of wood (Walters et al. 1993).

Although light conditions may have changed during the life of the older saplings, our sampling of saplings (in which evidence of any change in light conditions in the past 5 years excluded saplings from being evaluated), the presence of old saplings in the lowest light class (Fig. 2) and the lack of changes (gap formation and closure) in the canopy suggest that survival of large saplings is not due to age-related changes but rather to a greater shade tolerance on these relatively dry sites. Krajina (1969) and Carter and Klinka (1992) have suggested that some species might actually be more shade tolerant under drier conditions. Chen et al. (1996) reported, for example, that seedlings of Douglas-fir could be found at lower light levels on drier sites. Three explanations can be suggested to explain this: (*i*) seedlings in drier environments allocate more resources belowground, which increases their survival in shade; (*ii*) the absence of competing understory vegetation on drier sites may reduce the effects that this vegetation might have on stimulating height growth through a reduction in the red to far-red ratio; and (*iii*) it may allow for a greater part of the tree crown to receive maximum light. Beyond the correlation of sapling growth and crown morphology with light our study suggests that future work should also evaluate the potential role of soil moisture in affecting a species growth, crown morphology, and shade tolerance.

Growth differences between different-sized individuals were not the same, although individuals of all sizes were found in all light classes. Irrespective of their age, small- and medium-sized individuals of both pine and fir (no difference between the species $p = 0.189$; Table 2) tended to have greater relative height growth across all light classes than the larger individuals. This slower relative growth rate may be due to the taller saplings being carbon limited and thus at or near their ecological compensation point (sensu Givnish 1988). Similarly, Gerrish (1990) speaks of "carbon starvation" caused by an unfavourable ratio of photosynthetic to nonphotosynthetic tissue as sapling size increases, increasing mortality.

In full light the taller saplings have, however, greater absolute growth rates. This strong increase in growth for tall trees in full light is attributed to their capacity to modify their morphology (including a greater number of branches per whorl, more sharply angled branches, sun leaves, greater apical control, greater crown depth, and needles positioned on all sides of the branches) to maximize carbon production in a environment that is not light limiting.

This high absolute growth rate in high light is especially obvious in the case of lodgepole pine. Takahashi (1996) noted that the smaller crowns and thinner trunks of intolerant tree species enable them to grow faster than tolerant species in high light environments as a smaller biomass increment is required per unit of height growth. Although we didn't measure crown size, lodgepole pine has a greater height to diameter ratio than Douglas-fir and, with the exception of large saplings in high light, smaller lateral branch growth. This again reflects the differences in growth allocation between these two species.

Ecological and silvicultural implications

Although lodgepole pine is considered more shade intolerant than Douglas-fir, both of these species were found in very shady understory conditions. This is a somewhat puzzling result, especially for pine, but it seems to confirm the idea that intolerant tree species tend to be found under lower

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[2] Kelly, C., Messier, C., and Bergeron, Y. Mechanisms of intolerant deciduous tree recruitment between catastrophic disturbance in the southern boreal mixed-wood of Quebec. Submitted for publication.

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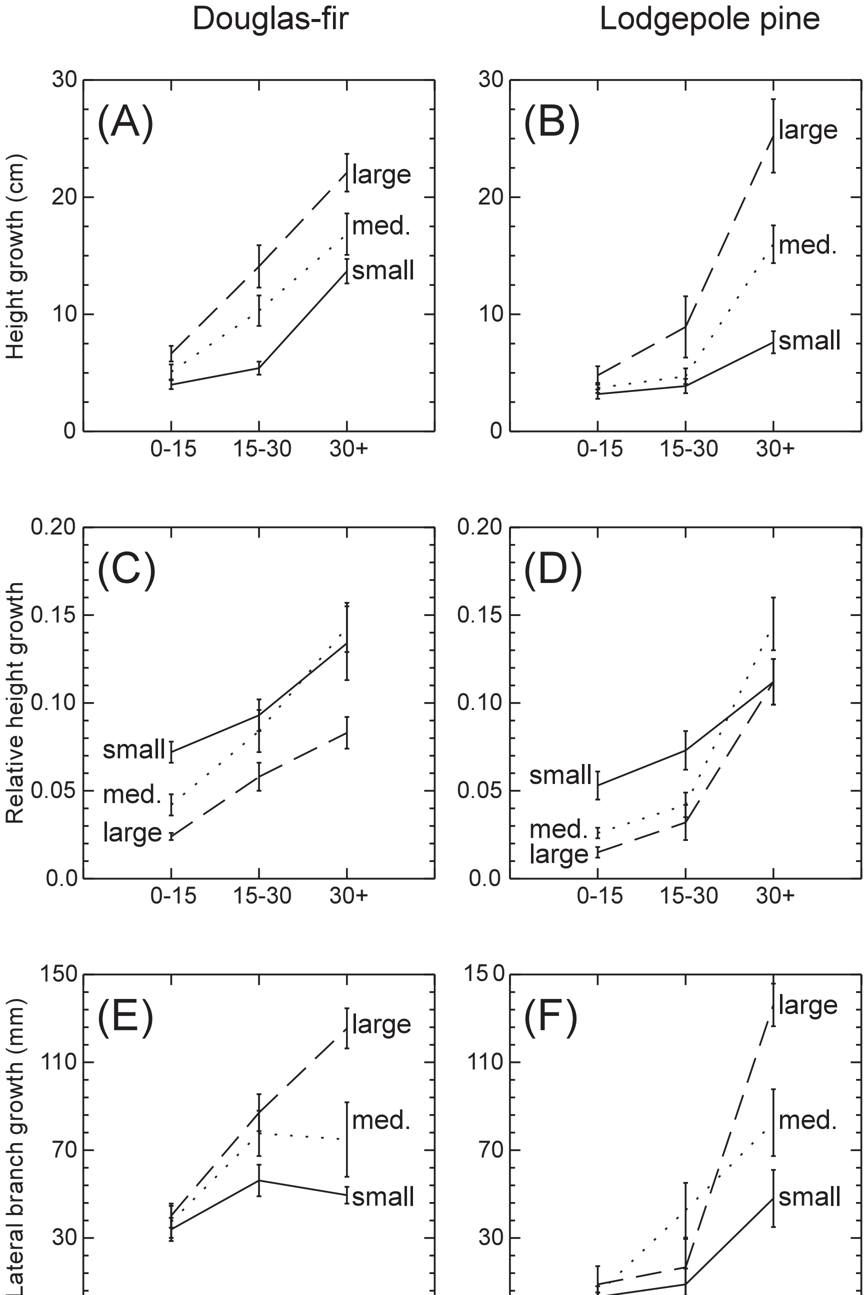
Fig. 4. Growth of saplings in relation to three height and three light classes. Height classes are as follows: 30–100 cm (bold lines); 100–200 cm (dotted lines); 200–450 cm (broken lines). Light classes are as follows: (1) <15% PPFD; (2) 15–30% PPFD; (3) >30% PPFD. Error bars are ±1SE. (A) Absolute height growth (cm) of Douglas-fir. (B) Absolute height growth (cm) of lodgepole pine. (C) Relative height growth of Douglas-fir. (D) Relative height growth of lodgepole pine. (E) Lateral branch growth (mm) of Douglas-fir. (F) Lateral branch growth (mm) of lodgepole pine.



light conditions in drier ecosystems (sensu Krajina 1969). Both species also had the ability to reduce their height growth in low light, which according to recent findings (see Messier et al. 1999) might explain their ability to survive for many years in shade. In terms of crown morphology, pine was not as able to modify its crown morphology as much as fir, as predicted by the literature (O'Connell and Kelty 1994; Chen et al. 1996). The crown morphology displayed by fir in deep shade is believed to be an adaptation to maximize light interception when light availability is low. The presence of pine trees up to 3 m tall and 50 years old in very low light (despite pine saplings not being able to modify their crown morphology as fir saplings do) suggests that generally accepted ideas regarding shade-tolerance morphology might need to be reconsidered, especially in dry environments with almost no competing understory vegetation. In such moisture-limiting environments, there might be an advantage (or trade-off) in terms of carbon gain and reduction in respiratory costs in maintaining a few short lateral branches that are well distributed from top to bottom along the stem. This obviously deserves further research.

These results suggest that both species can grow and develop in very low light environments in these forests and that it might be possible to maintain both tree species under a partial cutting system such as is being developed for this region of British Columbia. There is no indication that different gap sizes are required for each species, but they need to be large enough to allow for the possible increase in light requirements as size increases. In this study, light as low as 5% full sunlight appears to be enough for the survival of both species up to 3 m in height. However, much greater height growth can be achieved in higher light, especially for large pine saplings. Further testing should be pursued to determine how shade tolerance of these different-sized individuals changes with increasing size up to 10 m. Other applications of this research is in making forecasts of tree growth and vigour based on the light environment, and predictions of future forest structure based on the density and survivorship of naturally regenerated saplings.

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