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Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings

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Abstract

This paper characterizes the growth and crown morphology of young balsam fir saplings naturally regenerated under a gradient of understory light environments and intraspecific competition densities for two size classes (50–100 cm and 100–200 cm). Most growth and crown morphological parameters investigated were strongly related to the natural light gradient investigated (3–83% full sunlight), but the relationship tended to plateau at around 25% full sunlight. The relationships were generally better for the larger size class. Intraspecific competition did not significantly affect growth and crown morphology of saplings receiving less than 25% full sunlight, but it affected relative height growth, relative radial growth and the apical dominance ratio for those receiving more than 25% full sunlight ($R^2=0.506$; $p<0.001$; $R^2=0.403$; $p<0.002$; $R^2=0.348$; $p<0.001$, respectively). These results suggest that live crown ratio, apical dominance ratio and the number of internodal branches can provide, alone or in combination, useful indicators of vigour for understory fir. Such a study provides the basic data inputs required for the development of empirically-derived mechanistic models that can predict understory tree growth and survival. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Abies balsamea*; Crown morphology; Understory saplings; Competition; Light; Advanced regeneration

1. Introduction

Several studies have shown how light availability in the understory of a forest affects growth and crown morphology of several tree species (Hellmers, 1964; Logan, 1969; Canham, 1988; Klinka et al., 1992; Lord et al., 1993; Pacala et al., 1994; Wang et al., 1994; Chen et al., 1996; Williams et al., 1999). In saplings of highly shade-tolerant conifer species, it is generally

observed that crown morphology varies from a conical crown form in full sun to a flat-topped form in understory shade. This understory crown form, sometimes referred to as a plate-shaped or umbrella form, is the result of two changes in crown development patterns: reduction in apical control, and reduction in crown length from the death of lower branches (Kohyama, 1980; Parent and Messier, 1995). Species that can modify their crown morphology in response to light conditions have a better chance of surviving understory conditions to achieve an overstory crown position (O'Connell and Kelty, 1994; Messier et al., 1998). In general, more shade-tolerant species exhibit a greater survivorship than less shade-tolerant species

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in light-limiting environments (Oliver and Larson, 1990; Kobe and Coates, 1997).

Balsam fir (*Abies balsamea* (L.) Mill.) is a very shade-tolerant species (Frank, 1990) whose regeneration pathway often consists of germination and establishment beneath cover, persistence as a seedling or sapling in the understory, and response with rapid growth when a canopy disturbance increases the light environment (Ghent, 1958; Fye and Thomas, 1963; Ruel and Huot, 1993; Morin, 1994). Previous studies have investigated balsam fir growth and crown morphology in relationship to light (Logan, 1969; Honer, 1971; Parent and Messier, 1995) or canopy positions (Gilmore and Seymour, 1997). Nevertheless, no studies have quantified the combined effects of light, intraspecific competition and size on growth and crown morphology of naturally established balsam fir saplings. Competitive interactions where the growth of an individual is reduced by the presence of neighbours have been shown to be important (Lavigne, 1988; Frank, 1990; Jobidon, 1994; Umeki, 1995; Takahashi, 1996). Intraspecific competition is thought to be important for balsam fir, since it often regenerates in great quantity. Thus, the main objectives of this paper are (1) to quantify growth and crown morphology as influenced by gradients of light and intraspecific competition for two size classes (50–100 cm and 100–200 cm) and (2) to develop simple crown morphological indicators of vigour for understory firs.

2. Study area

This study was conducted near the 50th parallel, about 100 km north of Lac Saint-Jean (72°35'; 49°48'), Québec. The study area is in the boreal zone,

in the black spruce-moss ecological region (#12b) (Thibault, 1987). This region constitutes one of the main reservoirs of pulpwood in Québec. It is characterised by black spruce populations, yet some balsam fir stands are found on till soils in mountainous regions where they were greatly affected by the last spruce budworm outbreak. The associated vegetation may be compared to the balsam fir-white birch type of the more southern balsam fir-white birch zone (Grandtner, 1966). Mean annual temperature is -0.7°C (ranging from -19°C in January to 15.8°C in July) and mean annual precipitation is 421.7 cm (356.6 cm falling as snow) (Environment Canada, 1992).

Balsam fir stands in this study area have never been logged or protected from spruce budworm defoliation through spraying treatments. General characteristics of the three selected sites are presented in Table 1. The first two sites are separated by a distance of 5 km, and the third site (L24) is located 25 km away from the second site.

3. Methods

3.1. Sample selection

The first step in choosing understory trees was to locate three areas with different light environments (under completely closed canopies, in small gaps and in large gaps) at each site in order to obtain a good representation of the light gradient for our analyses. In each of these areas, tree zones having three levels of intraspecific competition (very little, some and very high levels of interference by other fir) were selected for the same reason as for the light environment. This was done by systematically traversing stands to mark sample areas that met all the pre-determined

Table 1
Ecological characteristics of the three study sites^a

Site	Canopy closure	Mean establishment year	Last spruce budworm outbreak (years)	Age distribution	Total density (stems>5 cm DBH/ha)	Balsam fir density (stems>5 cm DBH/ha)	Balsam fir basal area (% living +dead)
L26	Closed	1934	1944–1953	Unimodal	17150	16400	91
L20	Intermediate	1922	1944–1953	Bimodal	7600	7300	80
L24	Open	1883	1909–1923	Unimodal	2475	2325	76

^a Modified from Morin and Laprise, 1997.

combinations of light and competition. A preliminary analyses of the light and competition gradients was then conducted to ensure that this approach successfully provided us with good and continuous light (3–82% full sunlight) and competition (0–1.12 competition index) gradients. Finally, in each of these pre-selected zones, saplings in each of two height classes (50–100 cm and 101–200 cm), and having healthy apical leaders were randomly selected for a total of 63 trees (2 trees×3 light levels×3 competition levels×2 stands+3 trees×3 light levels×3 competition levels×1 stand).

3.2. Light measurements

The understory light environment was assessed using the method developed by Messier and Puttonen (1995a) and Parent and Messier (1996) at the end of the growing season in mid-August. Instantaneous lectures (Q_o) of photosynthetic photon flux density (PPFD= $\mu\text{mol photon m}^{-2} \text{s}^{-1}$; 400–700 nm) were taken above the apical leader with a quantum sensor Li-190SB (LI-COR Inc. US). Incident PPFD above the canopy (Q_i) was estimated by placing a second quantum sensor in a large adjacent clearing. This sensor was connected to the datalogger of the Li-6200 photosynthetic system which was synchronized and programmed to compute the mean PPFD measured every 5 s over a 1 min period. Percent PPFD was calculated as follows:

$$\% \text{ PPFD} = \left(\frac{Q_o}{Q_i} \right) \times 100$$

Light measurements were measured under a completely overcast day in order to represent mean daily light penetration under the forest canopy (Messier and Puttonen, 1995a).

3.3. Measurements of intraspecific competition

Intraspecific competition was measured using a method similar to that developed for balsam fir by Ruel (1992). The competition index (I) takes into account only competing individuals located in a circular area (1.13 m radius) surrounding the sample tree. This circular area was then divided into four quadrants, and the competition index (I) determined as

follows:

$$I = \frac{1}{H_{\text{fir}}} \times \frac{1}{4} \sum_{j=1}^4 \frac{C_j H_j}{D_j}$$

H_{fir} represents the total height of the sample tree, C_j the percent surface covered by competing fir saplings in quadrant j , H_j the mean height of competing fir saplings in quadrant j , and D_j the mean distance between the competing saplings in quadrant j and the sample tree.

3.4. Measurements of growth and crown morphology

Trees selected were harvested at the base at the end of the growing season (mid-October 1996) and brought back to the laboratory to characterize their age and growth pattern. Then, a series of easily measurable parameters was measured to develop simple crown morphological indicators of vigour for understory firs.

Growth pattern was assessed by measuring, on each individual, total height, apical leader length, radial growth for 1996, stem diameter and number of rings found at the base of the tree were measured. Following this data collection, relative height growth (RHG) was calculated by dividing the length of the apical leader by total height, and relative radial growth (RRG) was calculated by dividing radial growth of current year by stem diameter.

For each tree, a sample of 40 needles was randomly selected in order to determine mean length, width and foliage surface. To accomplish these measurements, needles were scanned and the projected image (as pixels) analysed by computer with a specialized software (MacNEEDLE, Régent Instruments, Québec city, Canada). Needles were then dried and weighed to determine the ratio of needle surface area to dry weight (SLA=specific leaf area ($\text{mm}^{-2} \text{mg}$)).

Crown morphology was assessed by calculating the live crown ratio (LCR=live crown length/stem height) and by counting the number of nodal branches per whorl and internodal branches between each whorl on the last year segment. The degree of apical control was also determined by calculating the apical leader growth to lateral branch extension ratio for the first node. This ratio, expressed as the apical dominance ratio (ADR), was derived from a similar coefficient used by Parent and Messier (1995). Their coefficient

has been modified here so that only the longest branch at a given node is considered in order to avoid errors due to environmental damage, and is calculated as follows:

$$ADL = \frac{L}{BL}$$

The ADR represents the apical dominance ratio, L is the length of the leader and BL is the length of the longest nodal branch at the first node.

3.5. Statistical analysis

Both linear and non-linear regressions were used to explain the relationships between the different ecological parameters and measures of PPFD, height and

competition (Sokal and Rohlf, 1981). Since below a certain light threshold the effect of light on growth is much stronger than that of most other biotic and abiotic factors including competition (Chazdon, 1988), a second analysis was performed on saplings established below and above different light thresholds. 25% PPFD was found to be a significant light level since the effect of competition below this threshold was not significant.

4. Results

4.1. Growth

No significant relationship ($p > 0.10$) was found among total height, competition index and % PPFD

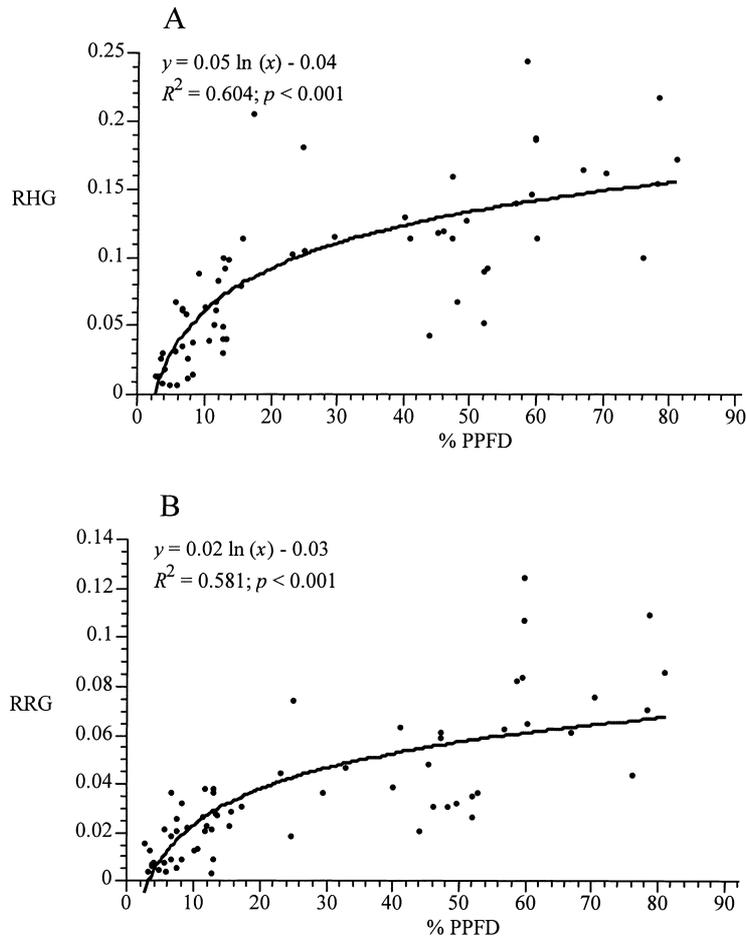


Fig. 1. Relative height growth, RHG, (A) and relative radial growth, RRG, (B) of balsam fir as a function of mean daily percent PPFD.

(data not shown). Results of a multiple regression show that the growth of the apical leader increases with both % PPFD and height ($R^2=0.633$; $p<0.001$), and that radial growth increases with both % PPFD and diameter ($R^2=0.653$; $p<0.001$) (data not shown). When the results were analysed using relative height growth (RHG=apical leader/total height) and relative radial growth (RRG=radial growth of current year/stem diameter), both RHG and RRG were strongly related to % PPFD (Fig. 1).

The first regression analysis of the effect of intraspecific competition on relative growth indicated no significant relationship. The analyses were then divided between firs growing in light-limited

environments below 25% PPFD and in high light environments above 25% PPFD to see if the competition effect differs. The 25% understory light value was chosen a priori based on similar studies done by Klinka et al. (1992) and Parent and Messier (1995) that have shown that for shade tolerant firs most of the changes in growth and crown morphology due to light alone occurred below 25–30% full sunlight. Analyses of the effects of competition on RHG and RRG ratios for saplings established below 25% PPFD showed no significant relationship (Fig. 2). However, for saplings growing above 25% PPFD, both ratios significantly decreased with increasing intraspecific competition ($R^2=0.506$; $p<0.001$ for RHG and $R^2=0.403$; $p<$

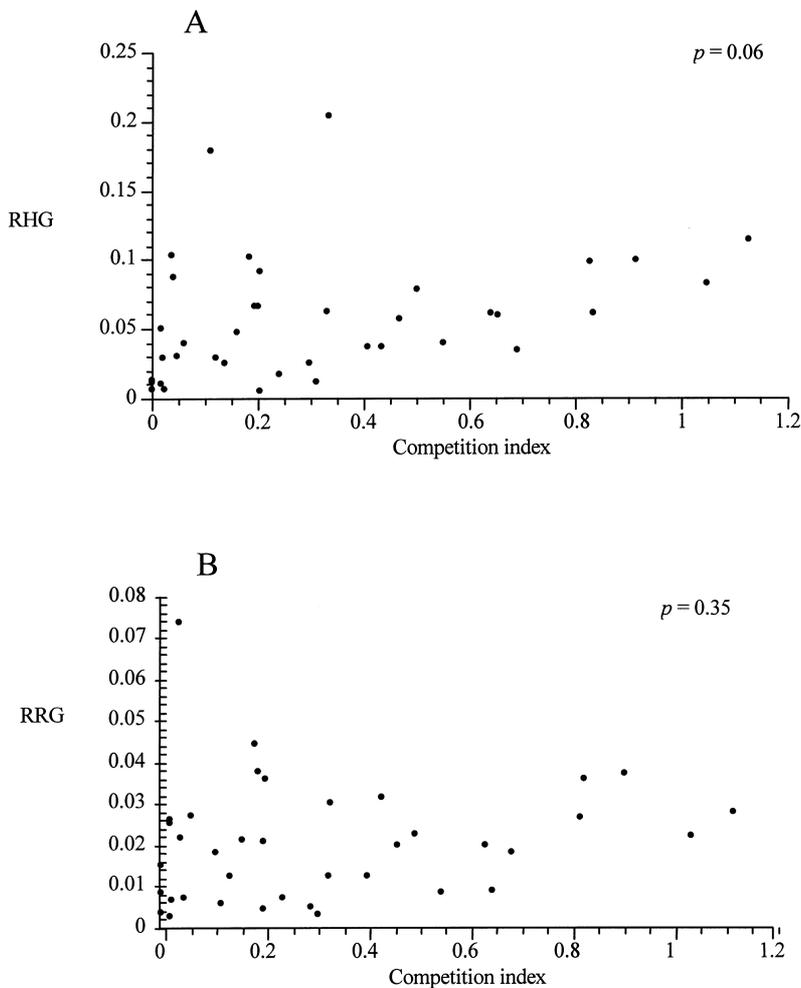


Fig. 2. Relative height growth, RHG, (A) and relative radial growth, RRG, (B) of balsam fir receiving less than 25% PPFD as a function of intraspecific competition.

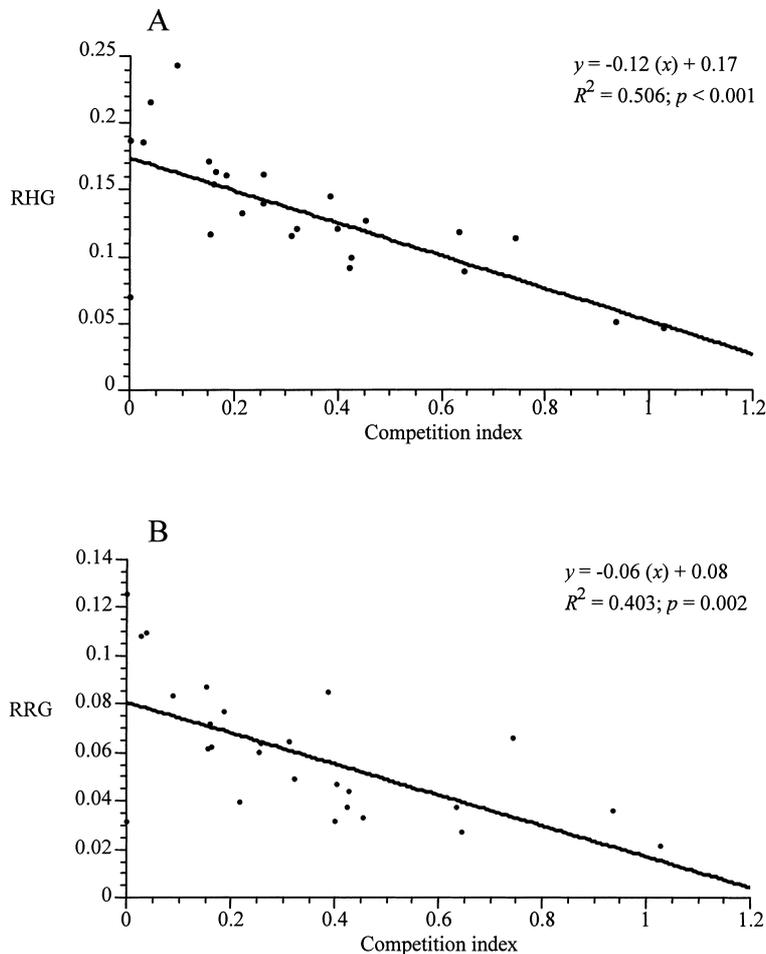


Fig. 3. Relative height growth, RHG, (A) and relative radial growth, RRG, (B) of balsam fir receiving more than 25% PPFD as a function of intraspecific competition.

0.002 for RRG; Fig. 3). Note that the R^2 would have been much higher if it was not for one possible outlier (very low RHG and RRG for a competition index of 0). The value was not removed because it was within the biological range observed in our data set.

4.2. Leaf morphology

No significant relationships were found among length, width and mean foliage surface and percent PPFD (data not shown). Specific leaf area was negatively related to % PPFD ($R^2=0.722; p<0.001$). SLA varied from a low of 13.3 mm²/g at low light to a high of 5.7 mm²/g in high light environments.

4.3. Crown morphology

Percent of live crown ratio (LCR) rapidly increased with understory light availability ($R^2=0.575; p<0.001$; Fig. 4). Above 15% PPFD, measured values of LCR were never below 60%. Neither height nor competition significantly affected this ratio ($p=0.182$ and $p=0.224$, respectively).

The ADR at the first year node increased with light availability. Furthermore, the transfer to apical dominance was influenced by tree height. Apical dominance occurred at 75% PPFD for trees measuring between 50 and 100 cm, and 25% PPFD for trees between 100 and 200 cm in height ($R^2=0.582$;

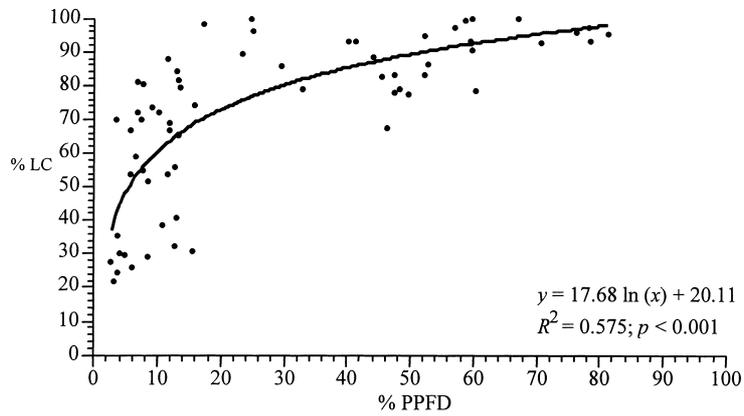


Fig. 4. Relationship between percentage of live crown (LC) ratio of balsam fir and mean daily percent PPFD.

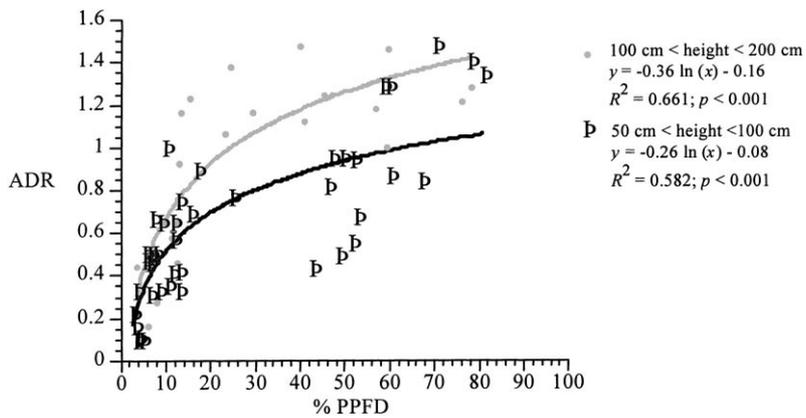


Fig. 5. Relationship between apical dominance ratio (ADR) at the first node for balsam fir measuring 50–100 cm and 100–200 cm and the mean daily percent PPFD (both curves are significantly different at $p < 0.001$).

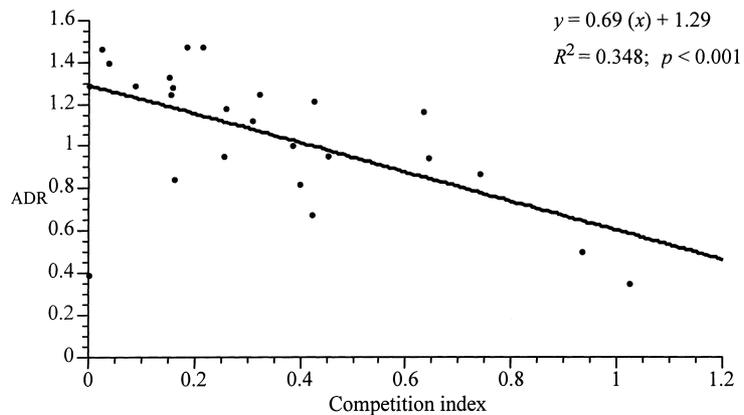


Fig. 6. Relationship between apical dominance ratio (ADR) and intraspecific competition for balsam fir receiving more than 25% PPFD.

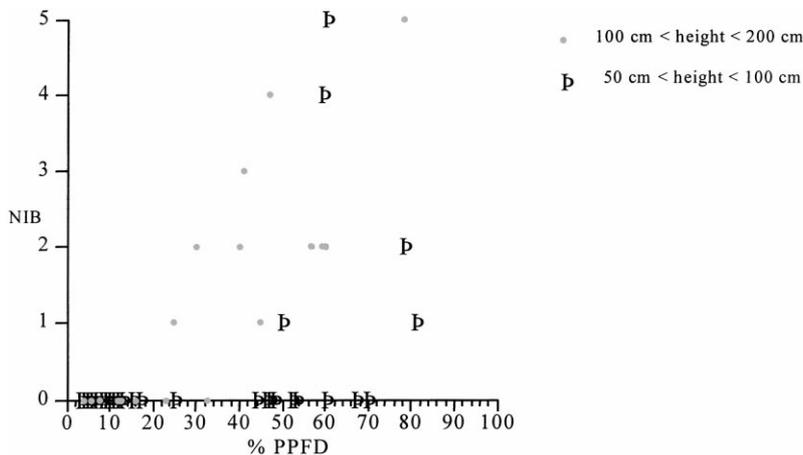


Fig. 7. Number of internodal branches produced on the last internode for balsam fir measuring 50–100 cm and 100–200 cm as a function of mean daily percent PPFD.

$p < 0.001$ and $R^2 = 0.661$; $p < 0.001$; Fig. 5). In a similar manner to RHG and RRG, apical dominance ratios did not vary in relation to competition when all firs were analysed together. However, when intraspecific competition was analysed for saplings growing above 25% PPFD, ADR was found to decrease significantly with increasing competition ($R^2 = 0.348$; $p < 0.001$; Fig. 6). Note again that the R^2 would have been much higher if it was not for one possible outlier (very low ADR for a competition index of 0). The value was not removed for the same reason as mentioned above.

The number of nodal and internodal branches increases with light. Saplings receiving less than 5% PPFD produced one or two nodal branches, while those receiving more than 25% produced two to five nodal branches (data not shown). In all cases, no more than five nodal branches could be found. Saplings receiving less than 25% PPFD did not produce internodal branches (Fig. 7). However, saplings between 50 and 100 cm started to produce internodal branches only when they received more than 45% PPFD, but they often did not produce any even at higher % PPFD (Fig. 7). All saplings between 100 and 200 cm in height always produced at least one internodal branch when growing above 25% PPFD (except in one case at 32.5% PPFD).

5. Discussion

Results of this study confirm the importance of light, sapling size and intraspecific competition on

growth and crown morphology of balsam fir saplings. The effect of intraspecific competition on tree growth was found to be important only for those saplings receiving 25% PPFD or more as measured at the top of the saplings. This confirms earlier findings (Chazdon, 1988) that below a certain light threshold, the effect of light on growth is much stronger than that of most other biotic and abiotic factors, including competition. This would imply that light is the major controlling factor at low light levels (Klinka et al., 1992), but that above 25% PPFD, intraspecific competition become important.

Our results indicate that light availability does not affect needle surface area. This confirms earlier reports for a wide range of plant species (McClendon and McMillen, 1982; Ducrey, 1992; Niinemets and Kull, 1994). On the other hand, SLA increased in low light environments. This well known morphological acclimation usually results in a variation in leaf thickness or needle density (Abrams and Kubiske, 1990; Klinka et al., 1992; Messier and Puttonen, 1995b). For a similar resource allocation, Fitter and Hay (1989) have argued that thinner needles would create a greater overall photosynthetic surface. This would give plants an advantage when light becomes limited (Jordan and Smith, 1993; Chen et al., 1996).

Although percent LCR was affected by light as measured at the top of the saplings, it varied between 20 and 100% below 25% PPFD, and as such it is not a good morphological indicator of vigour. In such low

light conditions, moderate differences in light attenuation within the crown caused by competition could result in substantial changes in the mortality of the lower branches, and thus cause a great variability in the LCR. However, results indicate that LCR is never below 60% when light exceeds 25% PPFD. This has also been verified for white pine (O'Connell and Kelty, 1994) and Douglas fir (Williams et al., 1999).

In low light environments, most nodal branches outgrew the apical leader. This type of relationship which enables the tree to have a relatively higher projected area in shade was also found by Oliver and Larson (1990); Klinka et al. (1992); Parent and Messier (1995). Expanding horizontally at the expense of height growth is believed to increase light interception and thus to maximize carbon gain in the shade (Givnish, 1988). As suggested by Parent and Messier (1995), the ADR could be used as an indicator of the light conditions in which the tree grows. Our results suggest that this relationship changes with sapling size and competition, especially at higher light levels (i.e., >25% PPFD).

Internodal branches are important to increase the total foliage area in high light environment. We found that 25% full sunlight was required to produce at least one internodal branch. This value is much higher than that reported by Parent and Messier (1995) who established it at only 9% PPFD. One possible explanation for such differences could be related to differences in overstory stand composition. Our study site was composed only of conifer trees, whereas, as discussed by Constabel and Lieffers (1996), the presence of deciduous trees on Parent and Messier's (1995) study site presumably allowed more light to be transmitted in the late spring and early fall when the photosynthetic apparatus in conifers is still active. Such a difference could explain why we found a higher light threshold and fewer internodal branches; a maximum of five internodal branches compared to the 23 internodal branches reported by Parent and Messier (1995). As for other crown morphological parameters reported in this paper, the minimum amount of light at which the first nodal branches occurred was different among size classes.

6. Conclusion and silvicultural implications

Most growth and crown morphological parameters investigated in this study were strongly affected by

light availability. The crown morphology of understory fir saplings varied typically from a conical form in full sun to a flat-topped form in understory shade. Other than light, tree height and intraspecific competition for trees growing in more than 25% PPFD also proved to be significant factors affecting several tree growth and morphological parameters. For example, transfer of dominance from lateral branch (when ADR=1) to apical leader occurred at 75% PPFD for saplings measuring between 50 and 100 cm, and occurred at 25% PPFD for those between 100 and 200 cm. Generally, relationships were better for the 100–200 cm saplings size class.

The results of this study provide basic information for the development of empirical relationships between light, sapling size and intraspecific competition and the growth and crown morphological plasticity of understory balsam fir under pure coniferous stands. Such empirically-derived relationships are needed to better evaluate the effects of alternative silvicultural treatments, such as partial cutting, on the growth and development of understory trees. They also provide some easy to measure indices to assess the vigour of understory firs. If we use 25% full sunlight as a threshold for optimal growth of balsam fir, as reported in this study and in Parent and Messier (1995), our results suggest that trees with a percent live crown ratio of less than 60%, an apical dominance ratio of less than 1 and/or a number of internodal branches of less than 1 are likely to be considered light-stressed. Such indices appear to vary with those found by Parent and Messier (1995) because of the very different overstory canopies between these two studies; pure coniferous stands versus mixed deciduous-coniferous stands. In effect, different tree overstories are believed to affect several aspects of light transmission which in turn could affect many growth and morphological traits in plants (Constabel and Lieffers, 1996; Messier, 1998; Messier et al., 1998). These indices appears to work better for understory firs greater than 100 cm in height, however.

Finally, these results will form the basis for the development of an empirically-derived functional-structural tree model (adaptation of LIGNUM for balsam fir: Perttunen et al., 1998; Lo et al., 2000) that will incorporate both 3D structural and physiological parameters. This model will be built to better predict the effects of various stand manipulations on

the growth and survival of understory fir using light and competition for light as the major determinants of growth and survival.

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References

- Abrams, M.D., Kubiske, M.E., 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. *For. Ecol. Manage.* 31, 245–253.
- Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69, 786–795.
- Chazdon, R.L., 1988. Sunflecks and their importance to forest understory plants. *Adv. Ecol. Res.* 18, 1–63.
- Chen, H.Y.H., Klinka, K., Kayahara, G.J., 1996. Effects of light on growth, crown architecture and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. *Can. J. For. Res.* 26, 1149–1157.
- Constabel, A.J., Lieffers, V.J., 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. *Can. J. For. Res.* 26, 1008–1014.
- Ducrey, M., 1992. Variation in leaf morphology and branching pattern of some tropical rain forest species from Guadeloupe (French West Indies) under semi-controlled light conditions. *Ann. Sci. For.* 49, 553–570.
- Environnement Canada., 1992. Sommaire météorologique mensuel, Chibougamau-Chapais Serv. Envir. Atmos., Gouv. du Can., janvier–décembre, 1992.
- Fitter, A.H., Hay, R.K.M., 1989. *Environmental Physiology of Plants*. Academic Press, London.
- Frank, R.M., 1990. *Abies balsamea* (L.) Mill. — Balsam fir. In: Burns, R.M., Honkala, B.H. (Eds.), *Sylvics of North America*, Vol. 1. Conifers. US Dep. Agric. Agric. Handb., 654.
- Fye, R.E., Thomas, J.B., 1963. Regeneration of balsam fir and spruce about fifteen years following release by spruce budworm attack. *For. Chron.* 39, 385–397.
- Gilmore, D.W., Seymour, R.S., 1997. Crown architecture of *Abies balsamea* from four canopy positions. *Tree Physiol.* 17, 71–80.
- Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant. Physiol.* 15, 63–92.
- Grandtner, M.M., 1966. La végétation forestière du Québec méridional. Les Presses de l'Université Laval, Québec, pp. 219–220.
- Ghent, A.W., 1958. Studies of regeneration of forest stands devastated by the budworm. II. Age, height growth and related studies of balsam fir seedlings. *For. Sci.* 3, 184–208.
- Honer, T.G., 1971. Crown shape in open- and forest-grown balsam fir and black spruce. *Can. J. For. Res.* 1, 203–207.
- Hellmers, H., 1964. Distribution of growth in tree seedlings stems as affected by temperature and light. In: Zimmerman, M.M. (Ed.), *The Formation of Wood in Forest Trees*. Academic Press, New York, pp. 533–547.
- Jobidon, R., 1994. Light threshold for optimal black spruce (*Picea mariana*) seedling growth and development under brush competition. *Can. J. For. Res.* 24, 1629–1635.
- Jordan, D.N., Smith, W.K., 1993. Simulated influence of leaf geometry on sunlight interception and photosynthesis in conifer needles. *Tree Physiol.* 13, 29–39.
- Klinka, K., Wang, Q., Kayahara, G.J., Carter, R.E., Blackwell, B.A., 1992. Light-growth response relationships in Pacific silver fir (*Abies amabilis*) and subalpine fir (*Abies lasiocarpa*). *Can. J. Bot.* 70, 1919–1930.
- Kobe, R.K., Coates, K.D., 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. For. Res.* 27, 227–236.
- Kohyama, T., 1980. Growth pattern of *Abies mariesii* saplings under conditions of open-growth and suppression. *Bot. Mag. Tokyo* 93, 13–24.
- Lavigne, M.B., 1988. Growth and net assimilation rates in thinned and unthinned stands of balsam fir. *Can. J. For. Res.* 18, 1205–1210.
- Lo, E., Wang, Z.M., Lechowicz, M.J., Messier, C., Nikinmaa, E., Perttunen, J., Sievanen, R., 2000. Adaptation of the LIGNUM model for simulations of growth and light response in jack pine. *For. Ecol. Manage.*, submitted.
- Logan, K.T., 1969. Growth of tree seedlings as affected by light intensity. IV. Black spruce, white spruce, balsam fir, and eastern white cedar. *Can. For. Serv. Dep. Fish. For. Publ. No 1256*.
- Lord, D., Morissette, S., Allaire, J., 1993. Influence de l'intensité lumineuse, de la température nocturne de l'air et de la concentration en CO₂ sur la croissance de semis d'épinette noire (*Picea mariana*) produits en récipients en serres. *Can. J. For. Res.* 23, 101–110.
- McClendon, J.H., McMillen, G.G., 1982. The control of leaf morphology and the tolerance of shade by woody plants. *Bot. Gaz.* 143, 79–83.
- Messier, C., 1998. Strategies for light capture by understory trees in complex understory light environment. In: *Proceedings of the Second International Workshop on Functional-Structural Tree Models*, October 1998. Clermont-Ferrand, France, 2pp.
- Messier, C., Parent, S., Bergeron, Y., 1998. Characterization of understory light environment in closed mixed boreal forests: effects of overstory and understory vegetation. *J. Veg. Sci.* 9, 511–520.
- Messier, C., Puttonen, P., 1995a. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. *Can. J. For. Res.* 25, 343–354.
- Messier, C., Puttonen, P., 1995b. Growth, allocation, and morphological responses of *Betula pubescens* and *Betula pendula* to shade in developing Scots pine stands. *Can. J. For. Res.* 25, 629–637.

- Morin, H., 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Can. J. For. Res.* 24, 730–741.
- Morin, H., Laprise, D., 1997. Seedling bank dynamics in boreal balsam fir forests, *Can. J. For. Res.*, in press.
- Niinements, Ülo, Kull, K., 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. *For. Ecol. Manage.* 70, 1–10.
- O'Connell, B.M., Kelty, M.J., 1994. Crown architecture of understory and open-grown white pine (*Pinus strobus* L.) saplings. *Tree Physiol.* 14, 89–102.
- Oliver, W.W., Larson, B.C., 1990. *Forest Stand Dynamics*. McGraw-Hill, New York.
- Pacala, S.W., Canham, C.D., Silander Jr., J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* 24, 2172–2183.
- Parent, S., Messier, C., 1995. Effets d'un gradient de lumière sur la croissance en hauteur et la morphologie de la cime du sapin baumier régénéré naturellement. *Can. J. For. Res.* 25, 878–885.
- Parent, S., Messier, C., 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Can. J. For. Res.* 26, 151–154.
- Perttunen, J., Sievanen, R., Nikinmaa, E., 1998. LIGNUM: a model combining the structure and functioning of trees. *Ecol. Modell.* 108, 189–198.
- Ruel, J.-C., 1992. Impact de la compétition exercée par le framboisier (*Rubus idaeus* L.) et les feuillus de lumière sur la croissance du sapin (*Abies balsamea* (L.) Mill.) en régénération. *Can. J. For. Res.* 22, 1408–1416.
- Ruel, J.-C., Huot, M., 1993. Impact de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur la régénération des sapinières après la coupe à blanc. *For. Chron.* 69, 163–172.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry*, 2nd Edition. W.H. Freeman, New York.
- Takahashi, K., 1996. Plastic response of crown architecture to crowding in understory trees of two co-dominating conifers. *Ann. Botany* 77, 159–164.
- Thibault, M., 1987. Les régions écologiques au Québec méridional. Deuxième approximation. Carte. Service de recherche. Min. de l'énergie et des ressources, Québec.
- Umeki, K., 1995. Importance of crown position and morphological plasticity in competitive interaction in population of *Xanthium canadense*. *Ann. Bot.* 75, 259–265.
- Wang, G.G., Qian, H., Klinka, K., 1994. Growth of *Thuja plicata* seedlings along a light gradient. *Can. J. Bot.* 72, 1749–1757.
- Williams, H., Messier, C., Kneeshaw, D., 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas fir and lodgepole pine. *Can. J. For. Res.* 29, 222–231.