

The effect of light availability and basal area on cone production in *Abies balsamea* and *Picea glauca*

David F. Greene, Christian Messier, Hugo Asselin, and Marie-Josée Fortin

Abstract: Mean annual seed production is assumed to be proportional to basal area for canopy trees, but it is not known if subcanopy trees produce fewer seeds than expected (given their size) because of low light availability. Ovulate cone production was examined for balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) in 1998 and for balsam fir in 2000 in western Quebec using subcanopy stems, near or far from forest edges, or (at one site) planted white spruce trees in fully open conditions. A very simple light model for transmission through mature trembling aspen (*Populus tremuloides* Michx.) crowns and through boles near forest edges was developed to account for the effect of light receipt on cone production. The enhanced light near forest edges (e.g., recent clearcuts) leads to about a doubling of cone production for subcanopy stems. The minimum subcanopy height for cone production far from an edge is about 10 m for balsam fir and 14 m for white spruce, with these minima decreasing near edges. By contrast, the minimum height for white spruce in a plantation (full light) is about 3 m. Accounting for light receipt leads to an increase in the explained variance.

Key words: balsam fir, cone production, light model, regressions, subcanopy stems, white spruce.

Résumé : La production annuelle moyenne de graines est proportionnelle à la surface terrière pour les arbres composant la canopée. Cependant, il reste à démontrer que des individus croissant sous couvert produisent moins de graines que prévu (en fonction de leur taille) en raison de la faible disponibilité de lumière. La production de cônes a été examinée pour le sapin baumier (*Abies balsamea* (L.) Mill.) et l'épinette blanche (*Picea glauca* (Moench) Voss) en 1998 et pour le sapin baumier en 2000 dans l'ouest du Québec. Les arbres étudiés poussaient sous couvert, près ou loin de la bordure forestière, ou (pour un site) faisaient partie d'une plantation. Un modèle très simple de transmission de la lumière à travers la canopée de peuplier faux-tremble (*Populus tremuloides* Michx.) et à travers les troncs en bordure de la forêt a été développé afin de quantifier l'effet de la disponibilité de lumière sur la production de cônes. L'augmentation de disponibilité de lumière près d'une bordure (par exemple une coupe forestière récente) entraîne un doublement de la production de cônes chez les arbres croissant sous couvert. La hauteur minimale pour la production de cônes chez des arbres croissant sous couvert et loin de la bordure forestière est d'environ 10 m pour le sapin baumier et 14 m pour l'épinette blanche, ces valeurs diminuant près de la bordure. En comparaison, la hauteur minimale pour la production de cônes pour les épinettes blanches d'une plantation (lumière = 100%) est d'environ 3 m. Une augmentation de la variance expliquée est obtenue en tenant compte de la disponibilité de lumière.

Mots clés : sapin baumier, production de cônes, modèle de transmission de la lumière, régressions, arbres sous couvert, épinette blanche.

Introduction

Following fire in mixedwood stands in the boreal forest, white spruce (*Picea glauca* (Moench) Voss.) and balsam fir (*Abies balsamea* (L.) Mill.) often colonize the burn in the first few years (Bergeron 2000), especially within 100 m of the burn edge or residual stand edge (MacArthur 1964; Galipeau et al. 1997; Stewart et al. 1998; Greene and Johnson 2000; Asselin et al. 2001). However, they invariably grow more slowly, initially, than the asexually reproduced trembling aspen (*Populus tremuloides* Michx.) (Bergeron 2000) and, thus, are relegated to the understory for many decades. There is now increased interest in mixedwood management with the subcanopy spruce and fir regarded as a second crop following a careful harvesting system where parts or all of the overstory of trembling aspen is removed (e.g., Lieffers et al. 1996). Consideration of natural regeneration options such as

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understory scarification (Lees 1963) or recruitment on skidpaths (Greene et al. 2000) prompts the question: to what degree can subcanopy white spruce and balsam fir act as seed sources either before or after careful logging?

To our knowledge, the only study of seed or ovulate cone production in relation to canopy position (i.e., relative tree height) was by Fowells and Schubert (1956) for three California conifers. Recording crop size in relation to canopy position and vigour classes, they found that the suppressed class accounted for only 0.2% of the total cone production of *Pinus ponderosa* Dougl. ex. P. Laws. & C. Laws. and *Pinus lambertiana* Dougl. and 3.2% for the more tolerant *Abies grandis* (Dougl.) Lindl. However, their data do not permit relating cone production directly to subcanopy height, light availability, or basal area, because it is not known if the subcanopy basal area represented equally low proportions of the total basal area for the three species. While the literature does not permit the dissociation of canopy position from tree size, nonetheless the bulk of the anecdotal reports are unanimous that light plays a role. It appears that small trees with ample light (e.g., plantations) can produce more seeds than equal-sized shaded trees (cf. the largely anecdotal literature of Burns and Honkala (1990)) and that edge trees produce disproportionately more seeds than interior trees (cf. the anecdotal reports mentioned in the reviews of Owens and Blake (1985) and Puritch (1972)).

Greene and Johnson (1994) argued that the mean annual seed production of trees was inversely proportional to seed size (small-seeded species produce more seeds) and directly proportional to tree size (basal area). However, their data on the role of basal area was limited almost solely to studies of canopy trees of intolerant species by Downs and McQuilken (1944; *Quercus* species), Carvall and Korstian (1955; *Liriodendron tulipifera* L.), and Fowells and Schubert (1956; *Pinus* species). Further, these data sets were comprised of different stands lumped together. Since then, Greene and Johnson (1999) have shown that, for *Picea mariana* (Mill.) BSP and *Pinus banksiana* Lamb., the magnitude of their aerial seedbanks was indeed directly proportional to basal area, but again, they purposefully limited the sampling to only canopy trees.

Given that the original equation of Greene and Johnson (1994), adapted by Greene et al. (1999) for a seed production year and rephrased below for cone production (Q_c), was primarily for stems receiving a large amount of light (i.e., dominants and codominants), one might, speculatively, modify the equation by simply multiplying by L (the proportion of full light):

$$[1] \quad Q_c = (k/R)m^{-0.58}BL$$

where Q_c is the mean annual cone production of a tree with basal area, B (m^2), and seed size, m (in grams), and R is the number of filled seeds per cone. Of course, $0 \leq L \leq 1$. If $L = 1$ (the terminal leader is at the top of the canopy) in eq. 1, then this is simply the original argument of Greene et al. (1999), where it is assumed that $k = 3067$ (an empirical value from regression) in a mean year. Note that the exponent for B was 0.92 in the Greene et al. (1999) paper. However, an exponent of 1 is used here for simplicity. Note also that eq. 1 makes the intuitive leap that sexual production is linearly proportional to available light as measured at the terminal leader.

The main objective of this study is to examine the effects of both light and basal area on cone production in balsam fir and white spruce. A young plantation and short edge trees were sampled, as well as canopy and subcanopy stems deep in forest interiors. Given that light is exceedingly cumbersome to measure for taller stems (indeed, below, measurements were made at only one stand), a secondary objective is to assess distance from forest edge and canopy position as proxy measures of light availability.

Materials and methods

Ovulate cone production by balsam fir and white spruce was examined at four aspen-dominated natural stands and a white spruce plantation in western Quebec. All cone counts were made between August 1 and September 15, 1998, or in the first week of August 2000. In all cases, measurements on white spruce and balsam fir consisted of cone number, conifer basal area and height, and the height of the aspen canopy. For trees less than 3 m in height, basal area was measured 0.1 m above the root collar; for taller trees, it was measured at breast height. For small trees, the total cone number (all sides) was tallied, while for larger trees we estimated cone number on the forest edge side only via binoculars and then multiplied by 1.5 (Franklin 1968). Tree height was measured with a tape for smaller trees and with a clinometer for taller trees.

Study sites

All sites were aspen dominated (except the white spruce plantation), and all were on flat or gentle slopes. At all sites, transects were placed so as to avoid very large canopy gaps. Transects were at right angles to the edge and were always at south- or west-facing edges. The first three sites were near Lac Duparquet, Quebec, ca. 555 km northwest of Montréal. At Dup1-98 a transect about 150 m long and 50 m wide was extended through an aspen-dominated forest (averaging about 25 m tall) that abutted a 4-year-old clearing. (All subsequent transects at other sites were only 50 m long as this first exercise made clear that there was no edge effect beyond about 50 m.) The nearby aspen stumps in the clearing indicated a stand age of about 90 years. Both white spruce and balsam fir were present at this stand, although few stems of either species were found within the first 10 m of the south-facing edge.

The second and third sites, Dup2-00 and Dup3-00, were sampled in 2000 and were aspen forests about 85 years old and averaging 22 and 23 m in height, respectively. The forests adjoined 2-year-old clearcuts. Four transects (50 m long and 30 m wide) were extended into the aspen forest at a west-facing edge at both sites. There were very few subcanopy white spruce, and so at these two sites, measurements were only made on balsam fir. (Indeed, although white spruce, like balsam fir, had good seed production in 2000, we could not find a site that contained adequate amounts of subcanopy individuals near a recent clearcut.)

The fourth site (McW-98) was along Highway 11 near McWatters, 65 km southeast of the Duparquet sites, in an aspen forest with a sparse component of spruce, and with the canopy height about 26 m. Three parallel transects (30 m wide) were extended from the south-facing forest edge 50 m

into the forest. Coring a few aspens indicated the stand was about 85 years old.

The final site (Lyt-98) was near Lytton, Que., about 200 km southeast of McWatters, where an 11-year-old white spruce plantation was sampled in 1998. There was no serious shrub or hardwood competition. Stems that were at least 40 m from the adjacent aspen-dominated forest were sampled using a single 10 m wide transect.

In all sites except the plantation, the white spruce and balsam fir were primarily subcanopy and, more rarely, codominant stems in otherwise pure aspen stands. All the Duparquet sites were located on proglacial lacustrine clay, while the McWatters and Lytton sites were on fluvio-glacial sands.

Direct estimates of light availability at 3 and 6 m height as a function of distance from the edge were made at Dup2-00. Sampling was done every 10 m starting at the edge for a distance of 50 m along a series of perpendicular transects for a total of 146 measurements. The percentage of full sunlight was measured using a pair of hand-held LAI-2000 sensors. Open-sky readings were taken in a nearby opening with one LAI-2000 linked to a LI-1000 datalogger (LI-COR, Inc., Lincoln, Neb.). The datalogger took measurements every 5 s and stored 1-min averages. The light measurements were taken under clear or variable sky conditions using a 180° view restrictor that was placed over each sensor to block direct sunlight. Two LAI-2000 readings were taken in opposite directions and at different times during the day for each sampled point. Paired values taken at exactly the same time with sensors oriented in the same direction from understory and open conditions were used to convert all understory readings to percentage of full sunlight (see Gendron et al. (1998) for more information on this method).

Also at Dup2-00, percentage of full sunlight right above the terminal leader of 27 subcanopy balsam fir ranging in height from 3 to 16 m was estimated using the same light method as described above. An experienced climber was hired to climb adjacent dominant aspen trees to obtain light measurements above all 27 subcanopy balsam fir. To our knowledge, this is the first time that such a technique is used, allowing light measurements at heights considerably higher than the top of the shrub layer.

Modelling the light environment

Equation 1 requires L , the proportion of full light, to be defined for each white spruce and balsam fir. The dominant aspen canopy can be viewed as a 5 m thick layer for canopy trees on the order of 25 m in height (D'Astous 2000). Thus, the aspen canopy layer extends from the top of the aspen dominants, z_c , down to $z_c - 5$ m. Even though decreased lower branch abscission near edges could result in slightly thicker canopies compared with those of the forest interiors, edges were created only recently (4 years maximum) in the present study. We thus reasonably assume that the aspen canopy depth is constant all over the stands.

For simplicity, the available light can be divided into two components: the light arriving vertically from above (L_v) and the light arriving perpendicularly from an edge (L_e). According to D'Astous (2000) the light availability at the top of the shrub layer (roughly around 4 m) is approximately 15% of that available at the top of the aspen canopy ($L = 0.15$) when sampling is done far from any edge. This holds for both clay and sandy

sites in western Quebec. Granting that $L = 1$ at the top of the canopy (z_c), then a very simple one-parameter estimate for L_v is a negative exponential decline in light with height:

$$[2] \quad L_v = 0.1 e^{2.3 z_t / z_c}$$

where z_t is the height of a conifer tree. The coefficients 0.1 and 2.3 are required to obtain $L_v = 1$ at the canopy top (assumed 25 m) and $L_v = 0.15$ at 4 m. Clearly, a one-parameter distribution is too simple: a more likely function would allow for a steep decline in light receipt within the aspen crown layer, with a more gentle subsequent decline to the top of the shrub layer. Nonetheless, further elaboration of the relationship seems pointless given that no measure was taken of the tremendous small-scale variation in light receipt at equivalent heights because of small gaps, recent branch loss, etc.

The increased light accruing to subcanopy stems near edges (L_e) must be taken into account. The value for L_e is obtained by multiplying p_e , the fraction of the sky where light reaches a subcanopy terminal leader unimpeded by the aspen canopy, by g , an attenuation factor. Letting x be the distance from the forest edge into the forest, p_e is, using radians, for $x > 0$:

$$[3] \quad p_e = \frac{\tan^{-1}\{(z_c - 5) - z_t\} / x}{\pi}$$

where z_c is reduced by 5 m (the expected aspen canopy thickness). At the simplest level of analysis let us ignore the effect of branches and leaves, and model the attenuation of light from the edge as being due solely to interception by boles. This attenuation factor, g , due to boles is then a simple negative exponential term:

$$[4] \quad g = e^{-x/b}$$

with the assumption that boles are randomly distributed (a reasonable assumption for a scale exceeding, say, 10 m), and thus, the constant probability of interception (p_{int}) per unit distance is given by the product of tree diameter and the square root of the tree density (N_D ; trees/m²). However, we will rephrase the argument using the more familiar forestry measure, basal area density (B_D , summed basal area/m²):

$$[5] \quad p_{int} = \left(\frac{4B_D N_D}{\pi} \right)^{0.5}$$

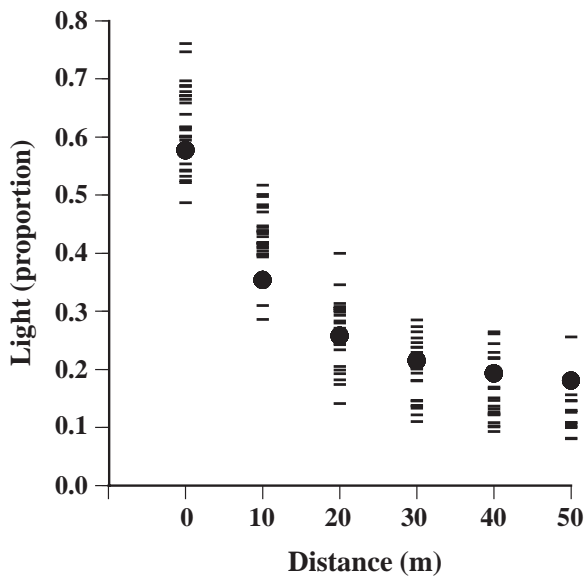
and

$$[6] \quad \frac{1}{b} = \ln(1 - p_{int})$$

We note that this simple equation makes no allowance for the taper of the boles with height. For the nonplantation stands, the product $B_D N_D$ averaged around 0.000 23, and thus, $b = 58$ m. That is, 63% of the edge light fraction (p_e) has been intercepted by boles at that distance. (This distance of 58 m ought to be fairly typical for rotation-age aspen. For example, 100-year-old aspen on productive sites are expected to have about 650 aspen trees/ha and 30 m²/ha (Greene and Johnson 1999), and thus, $b = 63$ m.)

The final equation for L , the fraction of available light at the terminal leader, becomes for a tree:

Fig. 1. Observed (3 and 6 m; bars, presented in continuity without distinction) and predicted (4.5 m; the mean of our two measurement heights; solid circles) light as a function of distance from clearing edge at Dup2-00.



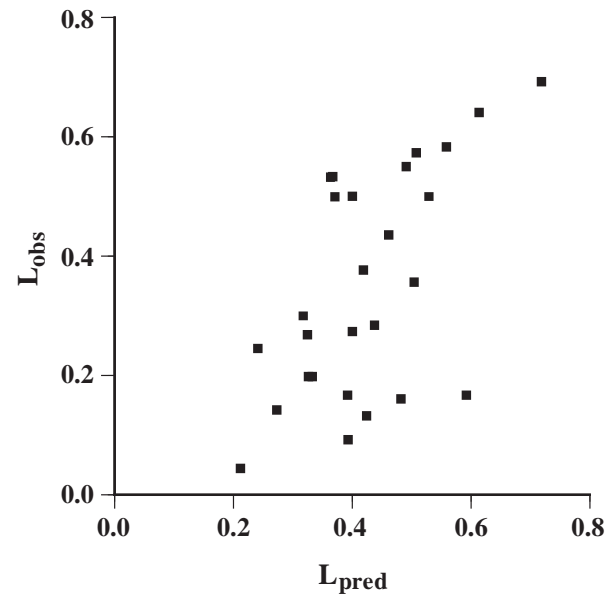
$$[7] \quad L = p_e g + ((1 - p_e)L_v)$$

While the light modelling provided here is admittedly a simplification (and further, it makes the untenable assumption that only the light interception at the terminal leader will affect cone production), it does provide us with two expectations. First, note that both g and p_e decline rapidly with distance into the forest; thus, the edge light contribution ($L_e = p_e g$) is expected to decline abruptly within the first 20 m, and the total light receipt (L) will arrive asymptotically at the value dictated by L_v alone (eq. 2) by about 50 m. Thus, we expect a strong decline in cone production within a very short distance from a clearing. Second, the exponential decline in light with tree height should likewise produce a strong effect on cone production after the role of basal area has been removed. Thus, we might expect that the scalar Q_c/B (cone production divided by basal area) will be proportional to height. That is, given the allometry of height with basal area, we might expect that cone production is proportional to basal area raised to a power of around 1.5 for a very shade-tolerant species (Niklas 1993). Such a value would be far higher than that predicted by Greene et al. (1999), where they relied primarily on species (*Pinus* and *Quercus*) that had no marked shade tolerance and where, therefore, the observations were almost entirely of canopy trees.

Statistical analyses

Cone crops from both study years (1998 and 2000), as obtained by power-law regressions of cone production on basal area, were compared using t tests (Sokal and Rohlf 1995). Cone production near an edge and deep in the forest interiors was also compared using t tests. Partial correlations were used to assess the relative importance of basal area and light availability in the explanation of cone production (Sokal and Rohlf 1995).

Fig. 2. Observed (L_{obs}) versus predicted light (L_{pred}) as a function of height and distance from edge at Dup2-00. The linear regression result was $L_{obs} = -0.05 + 0.94L_{pred}$ ($r^2 = 0.35$, $p < 0.05$).



Results

The light environment

Results of the light measurements at Dup2-00 (3 and 6 m height) are shown in Fig. 1. While the model (eq. 7) tended to overpredict somewhat in the interval $x > 30$ m from the edge (indeed light is already at the expected value of 0.15 by $x = 50$ m), nonetheless the predicted rapid decline in light receipt with distance from edge is apparent.

Figure 2 shows predicted (eq. 7) and observed light at the terminal leaders for 27 subcanopy balsam fir varying in height from 3 to 16 m and in distance from 0 to 50 m. The correlation was significant ($r^2 = 0.35$, $p < 0.05$); the intercept was not significantly different from zero nor was the slope significantly different from one. In short, the model for light receipt is a rough guide to the light environment for, at least, this circumscribed range of tree heights (3 to 16 m).

Balsam fir

Basal area was a significant predictor of cone production (plus one) (Table 1), explaining from 34 to 42% of the variance using power-law regressions. Interestingly, the 1998 intercept and slope (Table 1) were not significantly different from those obtained in 2000 (t tests, $p < 0.05$), indicating no dramatic differences in the size of these two mast crops.

The exponents on basal area in the power law regressions ranged from 1.47 to 1.88 (Table 1), with all three significantly larger than the value of around unity proposed by Greene and Johnson (1994) (eq. 1) but not significantly different from the value of 1.5 expected when considering that height is allometrically well related to basal area (Niklas 1993). Not surprisingly, therefore, semi-log regressions of the scalar $(Q_c + 1)/B$ (cone production divided by basal area) on tree height all yielded significant results (Table 1) with between 9 and 15% of the variance explained. (An example from Dup2-00 is shown in Fig. 3a.) The observed slopes are

Table 1. Regressions for white spruce and balsam fir.

	Regression ^a	<i>N</i>	<i>r</i> ²	<i>a</i> (95% limits)	<i>b</i> or <i>b</i> ₁ (95% limits)	<i>b</i> ₂ (95% limits)
Fir sites						
Dup1-98	$Q_c = aB^b$	94	0.413*	3463.00 (812, 14 765)	1.47 (1.16, 1.79)	—
	$Q_c/B = ae^{b(z_t/z_c)}$		0.153*	88.00 (41, 189)	2.66 (1.36, 3.96)	—
	$Q_c/Bf(z_t/z_c) = ae^{-bx}$		0.041	0.63	0.42	—
	$Q_c = aB^{b_1} L^{b_2}$		0.510*	466.00 (52, 4188)	0.66 (-0.09, 1.41)	1.74 (0.28, 3.20)
Dup2-00	$Q_c = aB^b$	99	0.341*	4359.00 (699, 27 447)	1.48 (1.07, 1.90)	—
	$Q_c/B = ae^{b(z_t/z_c)}$		0.087*	148.00 (62, 354)	2.78 (0.96, 4.60)	—
	$Q_c/Bf(z_t/z_c) = ae^{-bx}$		0.006	1.22	-0.0083	—
	$Q_c = aB^{b_1} L^{b_2}$		0.358*	3463.00 (561, 21 590)	1.17 (0.66, 1.68)	1.24 (0.02, 2.46)
Dup3-00	$Q_c = aB^b$	199	0.421*	24 588.00 (6974, 86 682)	1.88 (1.57, 2.00)	—
	$Q_c/B = ae^{b(z_t/z_c)}$		0.102*	151.00 (77, 292)	2.94 (1.71, 4.16)	—
	$Q_c/Bf(z_t/z_c) = ae^{-bx}$		0.101*	1.73 (1.3, 2.3)	-0.043 (-0.061, -0.025)	—
	$Q_c = aB^{b_1} L^{b_2}$		0.448*	26 903.00 (7863, 92 041)	1.64 (1.30, 1.97)	1.32 (0.56, 2.09)
Spruce sites						
Dup1-98	$Q_c = aB^b$	122	0.513*	74.00 (36, 148)	0.81 (0.66, 0.95)	—
	$Q_c/B = ae^{b(z_t/z_c)}$		0.014	228.00	-0.43	—
	$Q_c/Bf(z_t/z_c) = ae^{-bx}$		0.001	0.80	0.001	—
	$Q_c = aB^{b_1} L^{b_2}$		0.552*	32.00 (14, 73)	0.14 (-0.25, 0.53)	1.67 (0.75, 2.6)
McW-98	$Q_c = aB^b$	42	0.650*	804.00 (268, 2368)	1.02 (0.78, 1.26)	—
	$Q_c/B = ae^{b(z_t/z_c)}$		0.028	496.00	0.72	—
	$Q_c/Bf(z_t/z_c) = ae^{-bx}$		0.068	1.86	-0.024	—
	$Q_c = aB^{b_1} L^{b_2}$		0.722*	483.00 (173, 1338)	0.52 (0.15, 0.88)	2.07 (0.86, 3.27)
Lyt-98 (plantation)	$Q_c = aB^b$	52	0.220	138.00 (13, 1480)	0.66 (0.31, 1.01)	—

Note: For the effect of canopy position, we use an exponential regression (as in eq. 2). Likewise, for the effect of distance from the clearing edge, we use an exponential regression (as in eq. 4). For the plantation, we do not of course evaluate the role of canopy position or edge distance. For the regression $Q_c = aB^{b_1} L^{b_2}$, the adjusted r^2 was used to account for the removal of one degree of freedom (due to the addition of one independent variable). *N*, number of stems in the sample.

^a Q_c , cone production (always done as $Q_c + 1$); *B*, tree basal area (m²); z_t , tree height; z_c , aspen canopy height; *L* expected light receipt at the terminal leader (from eq. 6); *x*, distance from forest edge (m).

*Significant correlation ($p < 0.05$).

all higher than the expected value of 2.3 (eq. 2), but not significantly so. Using *BL* as a predictor of Q_c resulted in an increase in the r^2 , relative to merely using *B*, for all three sites (Table 1). This is further illustrated by the observed minimum height for the production of at least one cone. In very deep shade (as in Fig. 1, for distances greater than 35 m), the values ranged from 9.5 m (Dup1-98) to 10.5 m (Dup3-00). By contrast, for $x \leq 35$ m, the minimum height for cone production was 6.5–8.6 m.

The effect of distance from edge on cone production is much weaker than that of height. Semi-log regressions of the scalar $(Q_c + 1)/Bf(z_t/z_c)$ (where $f(z_t/z_c)$ is the result of the regression of $(Q_c + 1)/B$ on z_t in Table 1) were significant only for Dup3-00 ($r^2 = 0.101$; Table 1; the example of Dup2-00 is given in Fig. 4). Nonetheless, as can be seen in Figs. 1 and 4, we expect the dramatic differences in light receipt to occur in the first 10 m from an edge. There is a discernable effect of distance from edge on cone production at Dup2-00 and Dup3-00 (we cannot perform this analysis with Dup1-98 as there was only one stem within the first 10 m) as we examine the summed scalar $\Sigma Q_c/\Sigma B$ (Table 2). In both cases there are more cones per basal area near the edge than farther away (*t* test, $p < 0.05$).

Table 1 also shows results for a regression of the form $Q_c = aB^{b_1} L^{b_2}$. The exponent on light was significant in all three cases and was not significantly different from one. By contrast, the exponent on basal area was significant only for two sites (not Dup1-98) and was significantly greater than

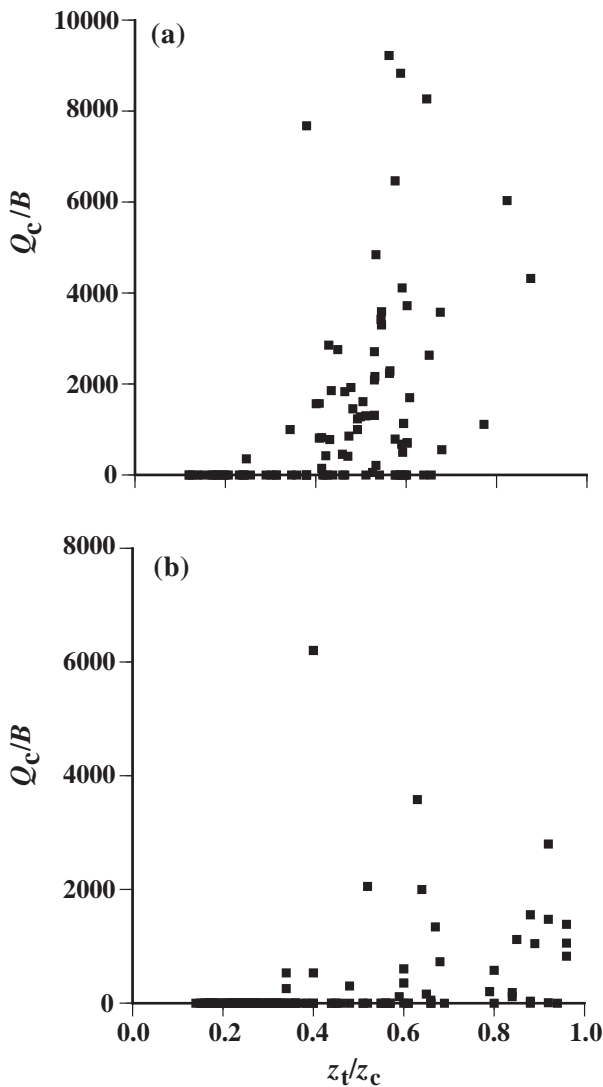
one at Dup3-00. Partial correlation analysis showed that light was a less important predictor of cone production than basal area at two of three sites.

White spruce

Results for white spruce are presented in Tables 1 and 2. Power-law regressions of $(Q_c + 1)$ (cones per tree plus one) on *B* (basal area) were significant at all three sites. The exponents were much lower than for balsam fir, ranging from 0.66 to 1.02 (none of these are significantly different from 1.0). Semi-log regressions of the scalar $(Q_c + 1)/B$ on tree height yielded insignificant r^2 values (the largest was $r^2 = 0.028$ at McW-98). As with balsam fir, the product *BL* was a better predictor of cone production than *B* alone (Table 1). Minimum cone production required a height of 14 m (Dup1-98) at $x > 35$ m (deep shade) but only 8 m at $x \leq 35$ m (McW-98). By contrast, at the plantation (Lyt-98), the minimum observed size for one cone was only 3.1 m. For the regression $Q_c = aB^{b_1} L^{b_2}$, the exponent on light was not significantly different from one at either McW-98 or Dup1-98. Light had a slightly higher partial correlation than basal area at both Dup1-98 and McW-98.

There were no significant correlations for semi-log regressions of $(Q_c + 1)/Bf(z_t/z_c)$ on distance from edge (Table 1; the grouped data for Dup1-98 and McW-98 are presented in Fig. 3b). As with balsam fir, comparison of summed cones per basal area (Table 2) for distances less than or greater than 10 m from an edge showed higher values for the nearer trees

Fig. 3. (a) The scalar cone production/basal area as a function of relative height (height/aspen canopy height) of (a) balsam fir at Dup2-00 and (b) white spruce (grouped data from Dup1-98 and McW-98). Note that Q_c is used here rather than $Q_c + 1$.



at McW-98 ($p < 0.05$; t test; note that we could not do this for Dup1-98 as there were only three trees within the first 10 m).

Discussion

The simple light model presented here constitutes the first attempt to estimate the light accruing to subcanopy stems up to 16 m tall and from the edge to 50 m inside a stand, and it proved to be a reasonable predictor of the measured light. For short stems (3–6 m), there should be little added light from the edge by about 30 m. This conclusion agrees tolerably well with the empirical results of Matlack and Litvaitis (1999) who showed that the effect of light from the edge disappeared by around 15–30 m. The attenuation ought to depend on stem height. According to eq. 7, the attenuation with distance will be more rapid for the taller subcanopy stems.

Greene et al. (1999) argued from a relatively small data set that cone or seed production was proportional to basal area raised to a power somewhat less than 1.00 (they ob-

Fig. 4. The scalar cone production/basal area f (relative height) as a function of distance to edge for balsam fir at Dup2-00. f (relative height) is taken from Table 1. Note that Q_c is used here rather than $Q_c + 1$.

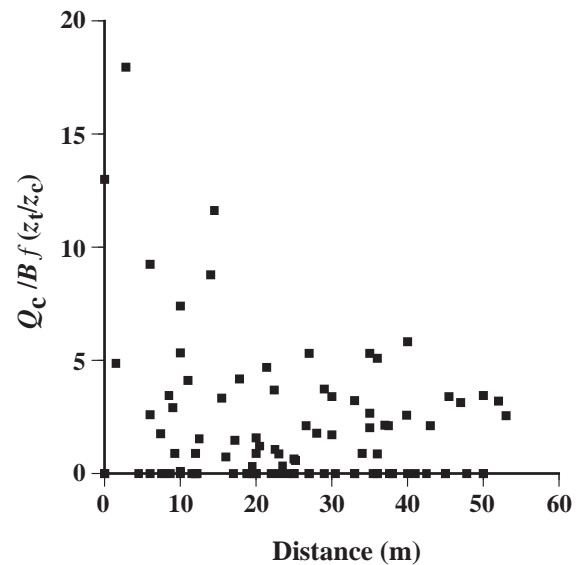


Table 2. The effect of proximity to an edge for white spruce and balsam fir.

Site	$x \leq 10$ m	$x > 10$ m
Dup1-98 (fir)	—	905
Dup2-00 (fir)	2789	1447
Dup3-00 (fir)	1944	1182
Dup1-98 (spruce)	—	356
McW-98 (spruce)	2428	1703
Lyt-98 (spruce plantation)	1246	—

Note: Values are calculated using $\Sigma Q_c / \Sigma B$, where Q_c is cone production and B is basal area (m^2). x , distance from an edge. We have arbitrarily included the plantation site in the column for $x \leq 10$ m. For Dup1-98 there was only one fir and three spruces within the first 10 m from the edge.

tained 0.92). The work presented here corroborates the conclusion that tree size is crucial. Nonetheless, basal area explains only about half the variation in cone production. Indeed, Greene and Johnson (1999) resorted to using basal area class means to obtain significant regressions for the aerial seed banks of two conifer species in Saskatchewan. Initially, we had hoped that light would account for much of the unexplained variation in the relationship between basal area and cone production. However, as we saw, the explanatory power of basal area is increased only between 5 and 23% by including our proxy data for light receipt. Nonetheless, partial correlations for basal area and light were about equal (light availability was slightly more important in three cases and basal area in two).

Interpretation of the results presented here needs to take into account that, all else being equal, and given the large amount of unexplained variance, then it follows that whichever predictor variable has the biggest gradient for observations will have the highest r^2 value. Now, for both balsam fir and white spruce there is about a 100-fold difference in the

basal areas examined. By contrast, given this range of basal areas (and thus heights), the largest range of vertical light receipt values we might see, far from any edge, would be about sevenfold ($0.15 \leq L \leq 1.0$). Finally, the expected range of light at an edge would be (as in Fig. 1) around fourfold (0.60/0.15). Thus, the hierarchy in r^2 values is probably mostly an artefact of the gradient of possible observed values.

Likewise, the r^2 values for balsam fir tended to be higher than those for white spruce when we performed the semi-log regressions using relative height (z_i/z_c) and distance from edge as predictors. However, balsam fir is more shade tolerant than white spruce (Messier et al. 1999) and will be found under a larger gradient of light values than white spruce. Also, it can produce cones at a smaller minimum basal area than white spruce, so that again we have a larger gradient in basal area values. In consequence, we might expect higher r^2 values for balsam fir than for white spruce. Nonetheless, it is noteworthy that the minimum height for cone production was less for balsam fir than white spruce (about 10 vs. 14 m, respectively, for $x > 35$ m). The difference in cone production at low light between white spruce and balsam fir may be related to their markedly different crown adaptation to low light. In very shaded conditions, balsam fir tend to abscise their lower branches and reduce their height growth much more than white spruce (Messier et al. 1999). This characteristic of balsam fir may permit it to maintain enough carbon at low light to produce small numbers of cones.

The degree to which the remaining unexplained variation (typical of canopy trees, e.g., Sork et al. (1993), as well as subcanopy trees) is due to genetic differences within a stand is not understood. The variation cannot be primarily due to asynchrony in masting, as this is a weather-cued regional phenomenon (e.g., Alexander et al. 1982; Sork et al. 1993; Koenig and Knops 1998), although this will bear some share of it. Furthermore, intra- and inter-specific competition probably had different effects from tree to tree. There is a negative relationship between radial growth increment and cone production in some species (Eis et al. 1965; Mart'yanov and Batalov 1990; El-Kassaby and Barclay 1992), and this is also expected to vary between individuals. There is also a possibility that there were light differences our proxy measures could not include or that a measure at the terminal leader does not describe satisfactorily the overall light conditions reaching the crown of an understory tree. Crown form (the ratio of crown height to crown width) was not taken into account here, nor were the roles of sunflecks (see the good review by Chazdon (1988)) and seasonal light variability (Gendron et al. 2001). Subcanopy conifers can benefit from the higher light availability prevailing in late spring and early fall (while aspens do not bear leaves) to fix substantial amounts of carbon (Constabel and Lieffers 1996). This probably lowers the part of the variability in cone production explained by the light-availability gradient. While the goal of the present study was to determine the effect of both mid-growing season light availability and basal area on cone production in *Abies balsamea* and *Picea glauca*, further studies are needed that would quantify other variables to include them in the regression and increase the explained variation.

Cone production, from bud differentiation to ripening (Owens and Blake 1985), is a 2-year process in both species, and it appears that no long period of acclimation is required

for trees suddenly exposed to enhanced light. Dup2-00 and Dup3-00 were adjacent to 2-year-old clearings and Dup1-98 to a 4-year-old clearing. Corroboration of these results is provided by a 6-year record of seed production (via seed traps) of paired shelterwood (25% removal) and control stands in eastern Quebec (Raymond 1998). Within 2 years, spruce reproductive output increased by 70% (relative to controls) in response to the greater light availability while fir showed a more modest 25% increase.

The speculative leap that Q_c was proportional to the product BL is supported by the results presented here. For all five sites (we ignore the plantation), the exponent on light was not significantly different from one. However, contrary to Greene et al. (1999), we have no evidence that basal area has a typical exponent on the order of one when the role of light is factored out. Including the plantation, then for our six sites the exponent on basal area was significantly greater than one (one site), less than one (one site), the same as one (two sites), or not significant at all (two sites).

We see two implications here. First, the contention of Greene et al. (1999) that basal area per area, easily obtained from inventories, can be used as a predictor of mean annual seed production was based on the thinnest empirical underpinning. The data presented here for these two species bolster that assertion. For intolerant species, differential light receipt is not an issue, but clearly for very tolerant and mildly tolerant species, prediction of seed supply based on basal area can overestimate if the great majority of stems are subcanopy trees. A related problem involves stand dynamics simulators, such as those of Ribbens et al. (1994), Clark et al. (1999), or LePage et al. (2000), where it is assumed that reproductive potential is proportional to basal area raised to the power one. Clearly this will lead to simulation results where tolerant, slow-growing, shaded species, initially composed of subcanopy trees, can increase their abundances faster than would really be the case. That is, the rate at which shade-tolerant species come to dominate a stand will be exaggerated.

A second application is the issue of advance regeneration adding to the seed supply near the edges of recent cuts. In the last 15 years, aspen has become commercially valuable, and there are many sites such as Dup2-00 or Dup1-98 where the conifers are present almost entirely as advance regeneration by the time the overtopping aspen have reached rotation age. Seed dispersal into clearcuts is greatly constrained by low horizontal wind speeds deep within the forest, and thus, most of the seeds arriving in the clearing are from trees near the edge (Greene and Johnson 1996). Thus, Table 2 offers a rough guide to the expected enhancement due to increased light: one can expect somewhat less than a doubling of the seed supply and, thus, a corresponding increase in the seedling density. While even 10 m² of basal area per hectare of subcanopy conifers cannot be expected to achieve full stocking, nonetheless this enhancement adds to the arguments for any cutting regime that increases the ratio of edge to harvested area, especially options such as parallel strip-cuts with quite narrow residual strips of seed sources.

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