

Understorey light profiles in temperate deciduous forests: recovery process following selection cutting

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Summary

1 We investigated recovery following small-scale disturbance, i.e. selection cutting, by determining how understorey light profiles vary over time in temperate deciduous forests in Quebec (Canada).

2 We measured light availability (% PPFD, photosynthetic photon flux density) 0.2, 1, 2 and 5 m above the forest floor, as well as the density of saplings < 5 m in height, in seven *Acer saccharum*–*Betula alleghaniensis*–*Fagus grandifolia* stands that had been subjected to selection cutting 1–13 years before the study, and in adjacent uncut plots.

3 In the most recent cut (1 year old), mean % PPFD was 3.5 to 5 times higher (depending on height) than in the uncut plot. Light availability rapidly decreased over time following selection cutting, especially near the forest floor. By about 13 years after cutting, light availability was similar to levels observed in the uncut plots.

4 Light profiles were used to assess the temporal pattern of recovery of the understorey after selection cutting, and four recovery phases could be identified. Uncut stands were characterized by profiles with low light near the forest floor and with a rather slow increase in light with increasing height, and recent cuts (1–4 years old) were characterized by J-shaped light profiles with relatively high % PPFD at all heights. Intermediate-age cuts (7–8 years old) were characterized by reverse J-shaped profiles that had a high % PPFD (13–46%) at 5 m, and very dark conditions (< 2%) near the forest floor, and were associated with high abundance of saplings. The relative frequency of the various profiles found in older cuts (11–13 years old) was generally similar to that observed in the uncut stands, except that the reverse J-shaped profiles were slightly more frequent.

5 As the microsuccession that follows canopy disturbance is very much influenced by local understorey structure and composition, forestry practices should consider such microscale forest characteristics in their harvest planning to regenerate the desired tree species.

Key-words: *Acer saccharum*, *Betula alleghaniensis*, canopy disturbance, *Fagus grandifolia*, light gradients, regeneration dynamics

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Introduction

Spatio-temporal variations in canopy structure resulting from natural or man-made gaps can have a major impact on understorey light conditions and affect the regeneration of tree species (Nicotra *et al.* 1999). Gap formation generally results in increased light availability (Canham & Marks 1985), but the mid- and long-term effects of a canopy opening will depend on how long the gap persists in the canopy. Gap closure rate and associated changes in understorey light availability

are likely to play an important role in forest dynamics through their influence on the establishment and recruitment of tree species (Runkle & Yetter 1987; Canham 1990). The temporal variation in light availability associated with the processes of gap formation and closure is important for light-demanding species through its influence on their long-term probability of survival and, for shade-tolerant species, because it will determine the relative duration of suppression and release periods until final recruitment into the canopy (Runkle & Yetter 1987; Canham 1990). Although a few studies have estimated the rate and investigated the mechanisms of gap closure (e.g. Hibbs 1982; Runkle & Yetter 1987; Valverde & Silvertown 1997; van der Meer 1997; Beaudet & Messier 2002), the associated patterns of

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temporal variation in understorey light availability have not yet been described for temperate deciduous forests.

The characterization of vertical patterns of light attenuation in the understorey is another aspect of forest light regimes that requires further study. Because light availability at the forest floor is often quite different from that above the understorey vegetation, measures of mean light availability at a single height do not adequately describe the complexity of light conditions found in most forest understoreys (Montgomery & Chazdon 2001). The vertical gradient of light availability in forest understoreys might be an important environmental characteristic influencing regeneration dynamics (Terborgh 1985; Davies *et al.* 1998; Messier *et al.* 1999). It could be, for instance, a determinant of optimal height growth patterns for tree seedlings (King 1990; Sakai 1995; Henry & Aarssen 1997; Claveau *et al.* 2002). Light transmission in forest understoreys is also influenced by the characteristics of the understorey vegetation, such as its abundance and species composition (Messier *et al.* 1998; Aubin *et al.* 2000). Understorey light profiles might be used as an indicator describing variation in understorey structure following various kinds of disturbances. In recent years, there has been a growing interest in the study of understorey light profiles in various forest types (e.g. Lawton 1990; Canham *et al.* 1994; Constabel & Lieffers 1996; Messier *et al.* 1998; Aubin *et al.* 2000; Bartemucci 2001; Montgomery & Chazdon 2001; Shropshire *et al.* 2001). However, information is lacking for temperate deciduous forests.

Finally, although much research has been performed to evaluate the effects of harvesting practices such as selection cutting on tree species regeneration in temperate deciduous forests (e.g. Willis & Johnson 1978; Mader & Nyland 1984; Crow & Metzger 1987; Majcen & Richard 1992; Majcen 1995), no studies have evaluated their effects on understorey light dynamics.

We characterized the light conditions at different heights from 0.2 to 5 m above ground, and assessed the density and species composition of the regeneration of the main tree and shrub species in *Acer saccharum*–*Betula alleghaniensis*–*Fagus grandifolia* stands that had been subjected to selection cutting at different times (1–13 years) before the onset of the study, as well as in adjacent uncut plots. Our objectives were: (i) to determine how understorey light conditions were affected by selection cutting; (ii) to characterize the temporal variation in understorey light conditions following such a disturbance; and (iii) to identify the main types of light attenuation profiles observed in the understorey of these forests.

Methods

STUDY SITES AND SAMPLING DESIGN

Seven *A. saccharum*–*B. alleghaniensis*–*F. grandifolia* stands were sampled in 1996 at two locations in Québec

(Canada): four in Duchesnay (46°50' to 47°00' N; 71°35' to 71°45' W), near Québec city, and three in Sainte-Véronique, near Mont-Laurier (46°33' to 46°37' N; 74°55' to 74°59' W). Climatic conditions at the two locations are similar: mean annual precipitation is 1200 mm, mean annual temperature varies from 3 to 4 °C, and mean daily temperature ranges from –12 to –13 °C in January, and from 18 to 19 °C in July (Environment Canada 1998). The main stand characteristics are presented in Table 1. The most common herbaceous and shrub species were *Lycopodium lucidulum*, *Dryopteris spinulosa*, *Streptopus roseus*, *Trillium erectum*, *Oxalis montana*, *Clintonia borealis* and *Taxus canadensis*. Signs of beech bark disease were present, but at the time of the study the disease appeared to have only a minor effect in this forest.

The study stands (Table 1) are uneven-aged with heights of dominant and codominant trees ranging from 20 to 25 m. All sites have probably been subjected to high grading (partial harvest removing only the most valuable trees without regard for the condition of the residual stand) prior to the 1950s, but precise records of harvesting are not available. More recently (1–13 years prior to this study), the stands were harvested using the single-tree selection silvicultural system (Matthews 1989; Majcen *et al.* 1990), which involves the periodic cutting of individual trees, in an uneven-aged stand, in order to recover the yield and maintain an uneven-aged stand structure, while aiming at creating conditions favourable for tree growth and seedling establishment. A portion (> 2 ha) of each stand was kept as an uncut control. Sampling plots were established in both the logged and uncut portions of the stands (generally 2 ha and 1 ha, respectively, Table 1). Within each plot, 4 m² quadrats were established along a systematic grid with 20-m spacing. Some were therefore under canopy gaps, while others were at the margin of gaps or in undisturbed patches of forest. A total of 40 quadrats (4 × 10 grid) were sampled in the 2-ha plots, and 20 quadrats (4 × 5 grid) in the 1-ha plots.

The different-aged cuts were used as a chronosequence to evaluate temporal variation in the light conditions following logging. It is well known that the use of spatially distinct sites to characterize temporal trends can be complicated by the fact that sites may differ in terms of factors other than the one under study (e.g. soils, slope, aspect, vegetation, and disturbance history) (Pickett 1989; Frazer *et al.* 2000). Analysing the differences observed between cuts of different ages and their paired uncut plots allowed us somewhat to control for among-stand variation (see Beaudet & Messier 2002). We selected stands that were as similar as possible, given the constraint of finding those cut at different times in recent years with an uncut area also available for sampling. Care was taken to intersperse the ages of the cuts between the two sampled locations (Sainte-Véronique 1983, 1985, 1993; Duchesnay 1988, 1989, 1992, 1995).

Table 1 Main characteristics of the study stands

Stand	DU95		SV93		DU92		DU89		DU88		SV85		SV83	
	Cut	Uncut	Cut	Uncut	Cut	Uncut	Cut	Uncut	Cut	Uncut	Cut	Uncut	Cut	Uncut
Location	DU	DU	SV	SV	DU	DU	DU	DU	DU	DU	SV	SV	SV	SV
Cutting history*	Cut (95/96)	Uncut	Cut (93/94)	Uncut	Cut (92/93)	Uncut	Cut (89/90)	Uncut	Cut (88/89)	Uncut	Cut (85/86)	Uncut	Cut (83/84)	Uncut
Drainage class†	3	3	2	2	3	3	2	2	2	2	2	3	2	2
Slope (%)	~0	~0	2–5	2–5	5–10	5–10	9–12	7–10	5–10	5–10	5–10	2–5	5–10	5–10
Aspect	–	–	E-SE	NE	NE	N-NE	S-SE	S	S-SE	S-SE	SE	NE	N	E-SE
Elevation (m)	210	210	400	400	160	180	280	280	280	270	390	400	400	380
B.A. prior to harvest (m ² ha ⁻¹)	21.9	23.8	28.9	29.3	24.5	24.8	27.9	28.2	25.6	26.4	25.5	26.8	26.7	26.5
B.A. after harvest (m ² ha ⁻¹)	17.3	–	19.8	–	18.7	–	19.5	–	17.5	–	18.1	–	19.3	–
Harvesting intensity (% B.A.)	21	–	31	–	24	–	30	–	32	–	30	–	28	–
Species composition (% M.V.)‡														
<i>A. saccharum</i>	46	39	73	60	52	38	63	50	68	56	92	93	82	94
<i>B. alleghaniensis</i>	39	46	6	15	41	37	23	12	20	15	3	2	4	2
<i>F. grandifolia</i>	15	4	20	23	0	4	14	36	12	26	4	5	12	4
Others	0	11	1	2	7	21	0	2	0	3	1	0	2	0
Size of sampling plot (ha)	2	1	2	1	2	1	2	2	2	1	2	1	2	2
Number of 4 m ² quadrats sampled	39§	15§	40	20	40	20	40	40	40	20	40	20	40	40
Mean regeneration density (n ha ⁻¹)¶	46 154	92 167	141 063	91 500	225 188	66 875	93 625	43 063	62 125	51 875	99 188	93 000	62 938	72 500
Regeneration composition (% of total density)														
<i>A. saccharum</i>	50	65	80	57	61	72	83	43	56	78	80	94	67	94
<i>B. alleghaniensis</i>	3	1	2	6	32	4	3	4	15	1	4	0	2	1
<i>F. grandifolia</i>	15	2	5	6	1	1	6	30	16	10	2	1	7	2
<i>V. alnifolium</i>	9	10	8	28	1	4	3	13	7	4	12	2	15	3
Others	23	23	5	3	5	19	5	10	6	6	2	3	9	0
Regeneration stocking (%)**														
<i>A. saccharum</i>	77	93	100	100	100	90	98	80	98	90	95	100	98	98
<i>B. alleghaniensis</i>	10	20	25	25	60	35	28	23	35	10	50	0	28	5
<i>F. grandifolia</i>	69	33	85	70	5	15	78	93	78	70	33	20	55	30
<i>V. alnifolium</i>	26	47	53	85	23	15	23	28	18	15	38	20	38	13

DU = Duchesnay; SV = Sainte-Véronique; B.A. = basal area; M.V. = merchantable volume; NA = not available.

*Cut = selection cut performed at the time indicated in parentheses (fall/winter); Uncut = stands that had not been cut in recent years.

†Drainage class: # 2 indicates a well-drained site, and #3 a moderately well-drained site, in a classification system that comprises classes ranging from 0 to 6.

‡For cuts, the species composition is as observed *after* harvesting.

§In DU95-Cut, one quadrat was excluded because it was in a forest trail, and in DU95-Uncut five quadrats were excluded because they were too close to a forest road.

¶Of all woody species < 5 m in height, with the exception of *Taxus canadensis* and *Rubus idaeus*.

**For a given plot, percentage of the quadrats in which at least one individual (< 5 m in height) of a given species was found.

LIGHT MEASUREMENTS AND VEGETATION SAMPLING

Light measurements and vegetation sampling were performed in July and August 1996. Understorey light conditions were characterized using measurements of the percentage of above-canopy photosynthetic photon flux density (% PPF) made under overcast sky conditions as described in Gendron *et al.* (1998), who showed that the % PPF measured at any time during an overcast day is representative of the mean daily % PPF reaching a location in the understorey under both clear and overcast conditions. One instantaneous light measurement (Q_x) was taken at 0.2, 1, 2 and 5 m above ground at the centre of each quadrat using point quantum sensors (LI-190SA, LICOR, Lincoln, NE, USA). A telescopic pole was used for measurements at 5 m. Due to problems encountered with the batteries of one of our light meters, it was not possible to obtain Q_x (and therefore % PPF) measurements at 5 m height at all sampling points in some of the plots (only 28 out of 40 quadrats were sampled in SV85-Cut, none in SV85-Uncut, and 20 out of 40 in SV93-Cut; see Table 1 for stand nomenclature). Above-canopy PPF (Q_0) was measured using a quantum sensor fixed on a 5-m pole installed in the open, less than 500 m from each of the study stands. This sensor was linked to a datalogger (LI-1000, LICOR) programmed to record 1-min averages of readings taken at 5-s intervals. Percentage PPF was calculated for each sampling point as $(Q_x/Q_0) \times 100$, where Q_x and Q_0 are recorded at the same time (± 1 min). In each 4-m² quadrat, individuals of all tree and shrub species (except the low-spreading shrubs *Taxus canadensis* and *Rubus idaeus*) were tallied by height class (0–0.2 m, > 0.2–1 m, > 1–2 m, and > 2–5 m).

STUDY SPECIES

A total of 14 tree and shrub species was observed in our sites (see Results). Due to the small sample size for many of these species, statistical analyses were performed only on the four most abundant species (*A. saccharum*, *B. alleghaniensis*, *F. grandifolia* and *Viburnum alnifolium*), which all had relative abundance > 5%. *Acer saccharum* and *F. grandifolia* are very shade-tolerant trees (Baker 1949), particularly *F. grandifolia* (Kobe *et al.* 1995; Beaudet *et al.* 1999). Both can survive for many years under a closed canopy as advance regeneration, and are able to sustain multiple episodes of growth suppression (Canham 1985, 1990). *Betula alleghaniensis* is generally classified as a mid-tolerant tree (Baker 1949) and its establishment is favoured by canopy opening coupled with soil disturbance (Erdmann 1990). Finally, *V. alnifolium* is a shade-tolerant shrub (Gill *et al.* 1998).

STATISTICAL ANALYSIS

To assess the effect of selection cutting on light conditions, we compared the mean PPF between the cut

and uncut plot in each pair, at each measurement height, using *t*-tests performed on log-transformed data. To characterize the temporal variation in light conditions following logging, we used our seven cut plots as a chronosequence. As each cut plot was paired with an uncut plot, we performed the analysis on the difference (D) between the plot-level mean PPF (or plot-level range in PPF) of the two plots. The relationships between D and time since harvest were analysed using linear and non-linear (logarithmic, exponential and quadratic models) regression analysis. We selected the model providing both a significant regression and the highest adjusted R^2 value.

We used the K-means clustering algorithm (SYSTAT, version 7.0) to identify the main patterns of light attenuation. This algorithm allowed us to categorize the light profiles into different types by maximizing the variation between relative to that within clusters. Different numbers of profile types (from 3 to 15) were considered. Four types were finally selected that allowed us to distinguish the main differences among the types of profiles, while minimizing redundancy among profile types. As the clustering procedure is sensitive to outliers, we excluded from the analysis the data from one quadrat in a very large canopy gap. PPF measurements taken at different heights were expressed on the same scale and their standardization was therefore unnecessary.

To assess whether different light profiles occurred more or less frequently in recent (1–4 years old) vs. intermediate-age (7–8 years old) vs. older cuts (11–13 years old) and vs. uncut plots, we performed a contingency analysis. We calculated the relative frequency of occurrence of the different types of light profiles in each of the four groups of plots. For each group of plots, a goodness of fit test was used to compare the observed relative frequency of occurrence of the light profiles with an expected distribution in which relative frequency was equal to the total proportion of quadrats in each type of light profile. When an overall significant departure of values from those expected was detected, we used Freeman–Tukey deviates to test for the significance of individual cells in the contingency table. Absolute Freeman–Tukey deviate values were compared with the criterion suggested by Sokal & Rohlf (1981). Because of multiple comparisons within each group of plots, we used a Bonferroni corrected alpha level.

Associations between species (*A. saccharum*, *B. alleghaniensis*, *F. grandifolia* and *V. alnifolium*) and types of light profiles were investigated using a contingency analysis. For each of these species, four different height classes (described earlier) were considered. In the contingency table, each of the 16 lines (four species \times four size classes) presents the relative abundance of individuals in each of the four types of light profile. A goodness of fit test was used to compare the observed distributions with an expected distribution in which species would not show any association with profiles (i.e. their relative frequencies would be equal to the proportion of quadrats in each type of light profile). When a significant

departure from expected values was observed for a given line of the contingency table, we used the Freeman–Tukey deviates to test for the significance of individual cells using Bonferroni corrected alpha levels.

Results

EFFECTS OF SELECTION CUTTING ON UNDERSTOREY LIGHT CONDITIONS

In the uncut plots, the stand-level mean % PPFD at 0.2 m ranged from 1.4 to 4.0% among the plots (Fig. 1), and individual % PPFD values ranged from 0.4 to 9.3%. Light availability increased with increasing height, and the mean % PPFD at 5 m ranged from 5.1 to 10.5%, depending on plot (Fig. 1), while individual % PPFD values ranged from 1.3 to 25.5%. In the selection cuts, light levels were generally higher and more variable than in the uncut plots. At 0.2 m, the mean % PPFD ranged from 1.5 to 11.1% among plots (Fig. 1), and individual % PPFD values ranged from 0.4 to 34.8%. At 5 m above ground, the mean % PPFD ranged from 10.9 to 21.5% among plots (Fig. 1), and individual % PPFD values ranged from 1.3 to 58.3%.

The difference in mean % PPFD between cut and uncut plots varied in magnitude according to time since harvest (Fig. 1). In the more recently cut stands (< 5 years ago), the mean % PPFD in cut plots was significantly higher than in the paired uncut plots at all heights up to 5 m (Fig. 1a,b,c). With increasing time since selection cutting, the light conditions in the plots (cut vs. uncut) became more similar. In some cuts, light levels were even significantly lower than in the uncut portion of the stand, particularly near the forest floor (Fig. 1e). No significant differences were observed between the oldest cut plot and its paired uncut plot (Fig. 1g).

The variation in understorey light availability as a function of time since harvest was also investigated using non-linear regression (Fig. 2). The differences between cut and uncut plots, both in terms of mean % PPFD and range of % PPFD, were greatest in the youngest cut and decreased over time (Fig. 2). For difference in mean % PPFD, we observed a significant temporal trend at all heights, characterized by an initial rapid decrease in the difference between cut and uncut plots (Fig. 2a). The difference in range of % PPFD decreased over time only up to 2 m (Fig. 2b). The initial decrease was more rapid near the forest floor, and was not statistically significant at 5 m (Fig. 2b).

TYPES OF LIGHT ATTENUATION PROFILES

Four main types of light profiles were identified using a K-means classification algorithm (Fig. 3). The most frequent type of profile (referred to as type 1 and found in 69% of all quadrats) was characterized by relatively low light availability at all heights: mean % PPFD ranged from 2.3% at 0.2 m above ground to 7.7% at 5 m (Fig. 3a). The other types of light profile differed both

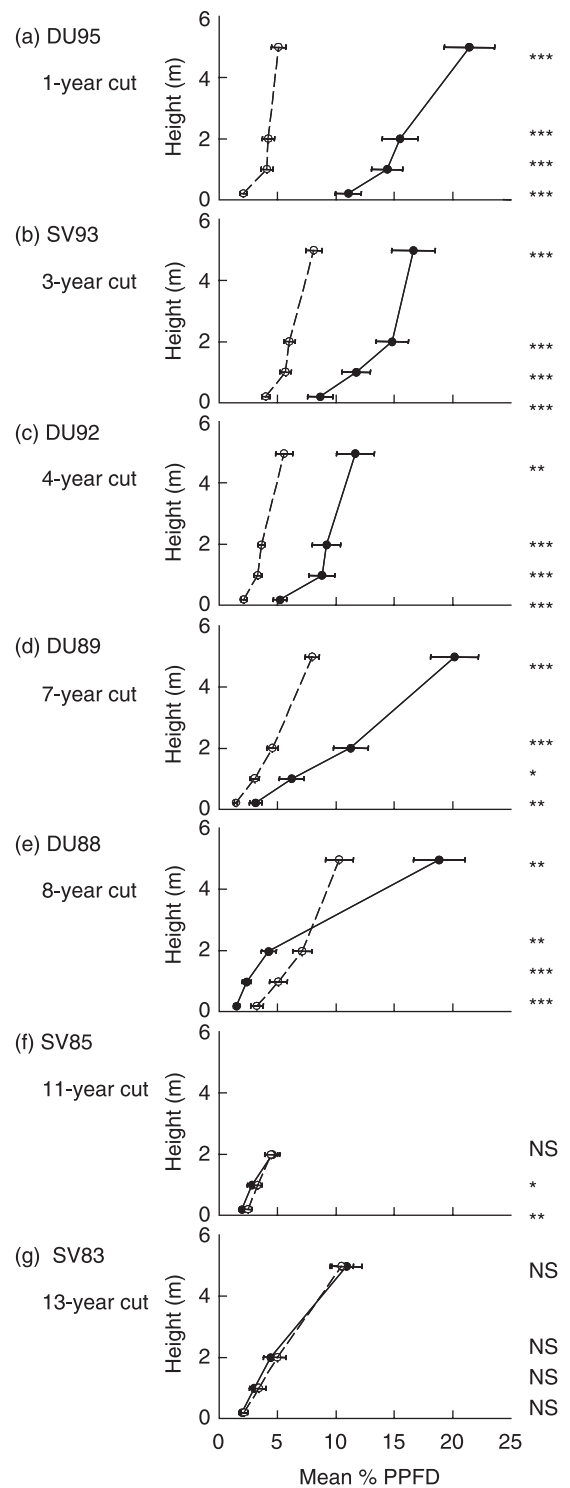


Fig. 1 Vertical profiles of light availability in cut and uncut plots in seven different stands (See Table 1 for stand descriptions). Each dot is a plot-level mean \pm 1 SE (open circle = uncut; closed circle = cut). For each measurement height and each pair of plots, mean % PPFD in the cut and uncut plots were compared with a *t*-test performed on log-transformed data (NS = $P \geq 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

in mean % PPFD values and in shape (Fig. 3). In types 2 and 3 (both J-shaped) PPFD changed more rapidly near the ground (between 0.2 and 1 m) but type 2 had higher mean light availability at all heights (13.6% at

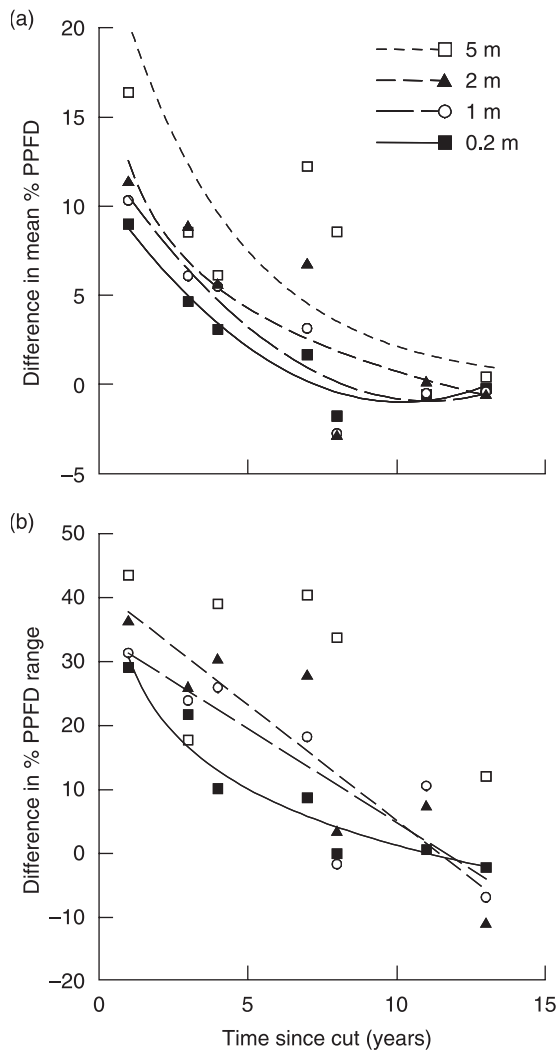


Fig. 2 Difference in (a) mean % PPFD, and (b) range of % PPFD between cut plots and their paired uncut plots, as a function of time since harvest, for % PPFD measured at 0.2, 1, 2 and 5 m above ground. The regression equations for (a) are: at 0.2 m above ground, $y = 10.99 - 2.35x + 0.12x^2$, $P = 0.003$, $R^2_{adj} = 0.920$; at 1 m, $y = 12.94 - 2.50x + 0.11x^2$, $P = 0.013$, $R^2_{adj} = 0.833$; at 2 m, $y = 12.5 - 5.1 \ln x$, $P = 0.014$, $R^2_{adj} = 0.682$; at 5 m, $y = 26.07 * \text{EXP}(-0.249x)$, $P = 0.047$, $R^2_{adj} = 0.586$. For (b) at 0.2 m, $y = 30.7 - 12.8 \ln x$, $P = 0.001$, $R^2_{adj} = 0.911$; at 1 m, $y = 34.2 - 2.9x$, $P = 0.008$, $R^2_{adj} = 0.738$; at 2 m, $y = 41.4 - 3.6x$, $P = 0.005$, $R^2_{adj} = 0.790$; at 5 m, no significant relationship.

0.2 m to 39.6% at 5 m, Fig. 3b, vs. 7.1% at 0.2 m to 17.9% at 5 m for type 3, Fig. 3c). Profile type 4, which was found in 9% of all quadrats, had a reverse J-shape in which PPFD changed rapidly between 2 and 5 m: light availability was high at 5 m (28.5%) but decreased markedly with decreasing height and reached very low levels near the ground (1.5% at 0.2 m) (Fig. 3d).

FREQUENCY OF OCCURRENCE OF THE LIGHT PROFILES IN UNCUT PLOTS AND CUTS OF DIFFERENT AGES

For each of the four groups of plots, the frequency distribution of the types of profiles differed from expectation (G tests $P < 0.001$ for uncut, young and

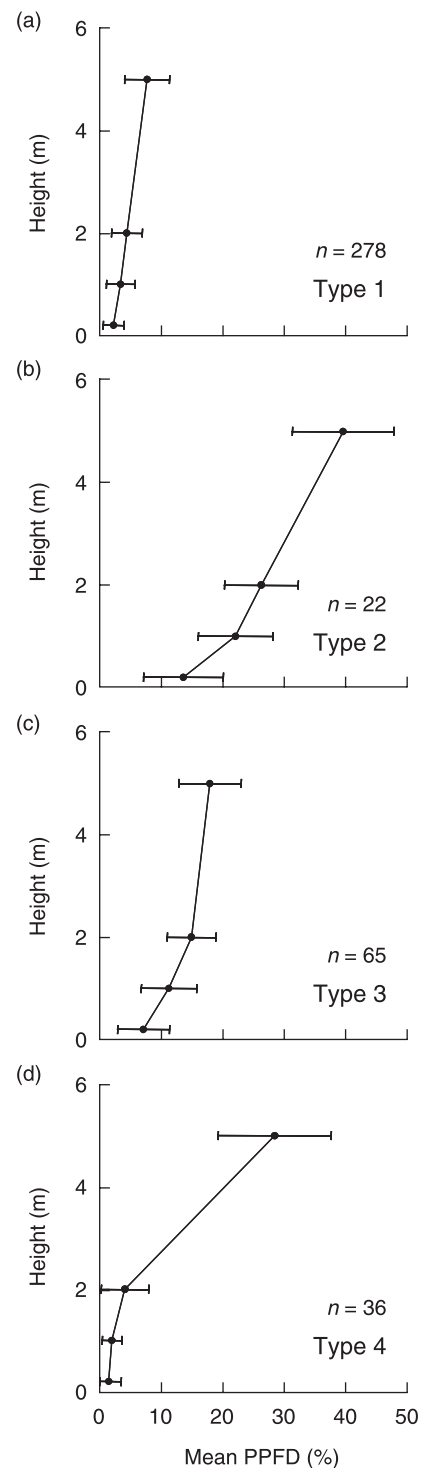


Fig. 3 Mean (± 1 SD) light availability at different heights above ground for the four main types of light attenuation profiles identified using the K-means clustering algorithm (see Methods). The number of quadrats corresponding to each profile type is indicated.

intermediate-aged cuts, and $P < 0.005$ for older cuts). In uncut plots, type 1 was by far the most frequent, being present in 89% of the quadrats, whereas type 2 was never observed (Fig. 4a). In the recent cuts (1–4 years old), we observed an increase, compared with uncut plots, in the relative frequency of both J-shaped

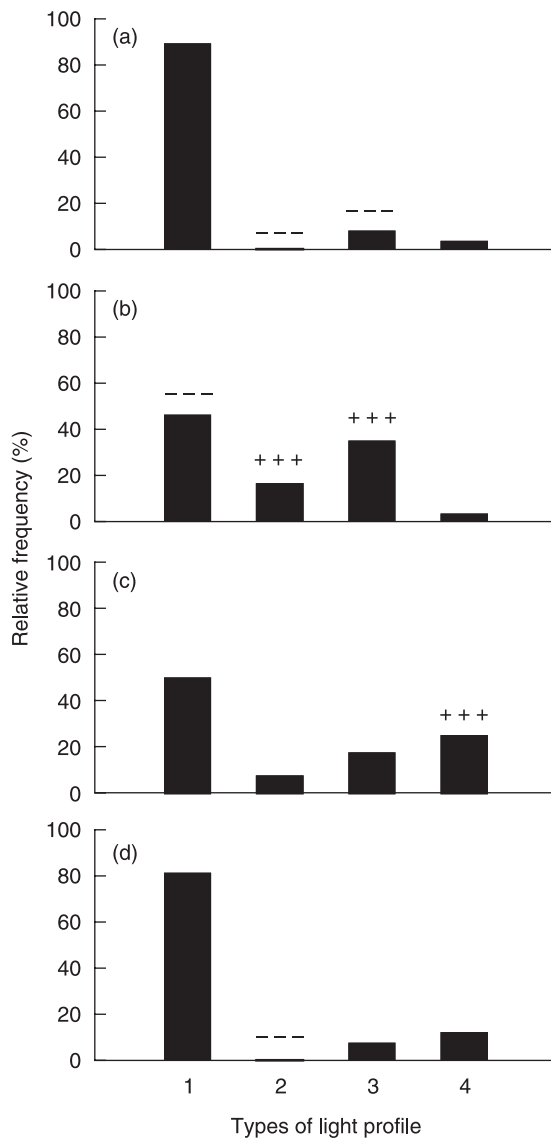


Fig. 4 Relative frequency of occurrence of the four main types of light profiles in (a) uncut plots, and in (b) recent (1–4 year), (c) intermediate-aged (7–8 year), and (d) older (11–13 year) selection cuts. Frequencies that were significantly higher or lower than expectation are identified, respectively, by +++ and ---. Light profiles are shown in Figure 3.

profiles (types 2 and 3, Fig. 4b). Relative frequencies were significantly higher than expected (16% and 35%, respectively). In intermediate-age cuts (7–8 years old), the relative frequency of J-shaped profiles decreased, and the relative frequency of type 4, the reverse J-shaped profile, increased to 25% of the quadrats, which was significantly higher than expected. In older cuts (Fig. 4d), we observed a marked increase in the relative frequency of type 1 compared with intermediate-age cuts and, as in the uncut plots, type 2 was never observed.

RELATIONSHIPS BETWEEN PATTERNS OF LIGHT ATTENUATION AND REGENERATION

A total of 16 494 individuals < 5 m in height of 14 different tree and shrub species were recorded in the

quadrats. Of these 14 species, the four with relative abundance > 5% together accounted for 93.3% of all sampled stems (*A. saccharum*, 70.8%; *B. alleghaniensis*, 9.7%; *V. alnifolium*, 7.2%; and *F. grandifolia*, 5.6%). Three other species had a relative abundance between 1 and 5% (*Acer pensylvanicum*, 2.4%; *Acer rubrum*, 2.0%; and *Acer spicatum*, 1.2%). These, together with the remaining species that had a relative abundance < 1% (in decreasing order of relative abundance: *Sambucus pubens*, *Abies balsamea*, *Prunus pensylvanica*, *Corylus cornuta*, *Ulmus rubra*, *Picea glauca* and *Picea mariana*), were excluded from statistical analyses.

The relative abundance of *B. alleghaniensis* seedlings (up to 1 m in height) was higher than expected in the J-shaped profiles associated with young cuts (types 2 and 3), but lower than expected in the profiles associated with older cuts and uncut plots (types 1 and 4) (Table 2). In the case of type 1, the relative abundance of *B. alleghaniensis* was also lower than expected for the 1–2 m size class (Table 2). The relative abundance of *B. alleghaniensis* saplings was higher than expected in type 3 for 1–2 m individuals and in type 4 for those 2–5 m tall (Table 2). The relative abundance of *A. saccharum* seedlings (< 0.2 m) was higher than expected in type 1, a light profile characteristic of uncut plots and older cuts, but all sizes up to 5 m in height were scarcer than expected in type 2 (Table 2), a profile associated with young cuts (Fig. 4b). We also observed a higher than expected relative abundance of 2–5 m *A. saccharum* saplings in type 4 (Table 2). The relative abundance of *F. grandifolia* in the various light profiles did not differ from expectation for seedlings up to 1 m in height (Table 2), but larger individuals were less abundant than expected in the J-shaped profiles (Table 2). The relative abundance of *V. alnifolium* was similar to expectation, except for individuals in the 2–5 m size class, for which we observed a much higher than expected relative abundance in type 4 (Table 2).

Discussion

TEMPORAL VARIATION IN LIGHT CONDITIONS FOLLOWING SELECTION CUTTING

Studies of the effects of gaps on understorey light conditions have mainly described static differences between gap and closed-canopy microsites (Lieberman *et al.* 1989). The temporal pattern of change in light conditions following canopy disturbance (either natural or human induced) has been much less documented. As expected, we found that light availability was higher in recent selection cuts than in adjacent uncut forests. In the most recent cut (1 year old), the light availability was 3.5–5 times higher, depending on height, than in the uncut portion of the stand. Such an increase in mean light availability is similar in magnitude to that observed by Brisson *et al.* (2001) in an *A. saccharum*–*F. grandifolia* forest the first summer after a severe ice

Table 2 Relative abundance (%) of species (by size class) in four types of light profile. Expected relative abundances (last line) were defined as the proportion of quadrats associated with each type of light profile. Goodness of fit tests (*G* values) were used to compare the distribution of observed and expected relative abundances. Single-cell differences between observed and expected values were tested using Freeman–Tukey deviates. Relative abundances that were significantly higher than expectation are in bold, while those that were lower than expectation are in italics. A Bonferroni corrected alpha level was used to determine the significance of the Freeman–Tukey deviates

Species	Size class	<i>n</i> species ⁻¹	Types of light attenuation profiles				<i>G</i>	<i>P</i>
			1	2	3	4		
<i>B. alleghaniensis</i>	< 0.2 m	719	33.2	25.6	40.6	0.6	729.5	<i>P</i> < 0.001
	0.2–1 m	633	37.0	36.8	25.4	0.8	713.5	<i>P</i> < 0.001
	1–2 m	124	45.2	9.7	35.5	9.7	36.4	<i>P</i> < 0.001
	2–5 m	76	60.5	3.9	11.8	23.7	14.8	<i>P</i> < 0.005
<i>A. saccharum</i>	< 0.2 m	5068	79.8	2.2	14.8	3.3	461.0	<i>P</i> < 0.001
	0.2–1 m	3649	69.4	1.9	21.0	7.7	168.7	<i>P</i> < 0.001
	1–2 m	719	68.4	2.8	13.9	14.9	37.5	<i>P</i> < 0.001
<i>F. grandifolia</i>	2–5 m	301	70.8	0.0	6.3	22.9	102.3	<i>P</i> < 0.001
	< 0.2 m	85	69.4	10.6	15.3	4.7	5.3	NS
	0.2–1 m	347	69.2	8.4	15.3	7.2	6.0	NS
<i>V. alnifolium</i>	1–2 m	134	72.4	0.0	11.9	15.7	22.0	<i>P</i> < 0.001
	2–5 m	256	78.1	0.0	7.8	14.1	50.9	<i>P</i> < 0.001
	< 0.2 m	37	64.9	16.2	8.1	10.8	7.1	<i>P</i> < 0.05
	0.2–1 m	695	71.8	3.7	17.6	6.9	9.3	<i>P</i> < 0.05
	1–2 m	185	67.6	0.5	16.2	15.7	21.3	<i>P</i> < 0.001
	2–5 m	40	55.0	0.0	2.5	42.5	38.9	<i>P</i> < 0.001
Number of quadrats			278	22	65	36		
Expected relative abundance (%)			69.3	5.5	16.2	9.0		

storm affected the canopy (although the gaps created by selection cutting may have a different effect on the variability in the light conditions than the thinning of the canopy resulting from an ice storm). As time since selection cutting elapsed, we observed a relatively rapid decrease in both the mean and the range of light intensities. By about 8 years after cutting, light availability near the forest floor was no longer higher than in uncut areas. This is a shorter time interval than the 10–15 years reported by Emborg (1998) for a temperate deciduous forest dominated by *Fagus sylvatica* and *Fraxinus excelsior*. It is, however, slower than reported by Fraver *et al.* (1998) for a Panamanian tropical forest where gap formation led to a fivefold increase in light availability near the forest floor, but light availability returned to pre-gap levels within 2 years. In our study sites, the mean light conditions 5 m above the forest floor returned to the levels observed in the uncut plots 13 years after harvesting. However, the range of light intensities remained greater than in the uncut forest.

The non-linear decrease in light availability observed over time following selection cutting is in agreement with the trend reported by Beaudet & Messier (2002) for canopy openness in the same study sites. Similarly, Brisson *et al.* (2001) observed that the variation in understorey light availability which occurred in a *A. saccharum*–*F. grandifolia* forest after an ice storm was more pronounced soon after the disturbance, and decreased in magnitude over time. Non-linear temporal trends have also been observed in other forest ecosystems. In a rain forest, van der Meer & Bongers (1996)

found that the rate of gap closure slowed down as gap age increased, while in temperate forests in Britain, Valverde & Silvertown (1997) observed a negative exponential rate of canopy closure.

The decrease in light availability during recovery from selection cutting occurred more rapidly near the forest floor than at 5 m, consistent with turnover time at the floor of a tropical rain forest being four to eight times shorter than at the forest canopy (van der Meer *et al.* 1994). The rapid decrease in light availability observed near the forest floor suggests that, in our forests, the development of the understorey vegetation is an important factor leading to the post-disturbance decrease in understorey light availability. These conclusions concur with observations made by Brisson *et al.* (2001), who found that the rapid decrease in light availability was mainly due to the recruitment after an ice storm of pre-established saplings (although, in their case, the development of lower branches on canopy trees was also an important factor).

The relatively rapid decrease in light availability following cutting has important implications for stand dynamics. For shade-intolerant or mid-tolerant species that cannot rely on pre-established regeneration, successful establishment must occur quickly after the cut for seedlings to be able to benefit from higher light conditions, outgrow competing vegetation and maintain their foliage in high light conditions. A shade-avoidance strategy with a growth pattern that favours rapid height growth, such as observed in *B. alleghaniensis* (Beaudet & Messier 1998), should be advantageous under such

conditions (Grime & Jeffrey 1965; Henry & Aarssen 1997), although other factors, including the dynamics of seedbed availability, will also be important. The temporal variation in light availability associated with gap formation and closure will also affect shade-tolerant species because it determines the relative duration of suppression and release periods prior to final recruitment in the canopy (Runkle & Yetter 1987; Canham 1990). Our characterization of vertical and temporal patterns of light availability will provide basic empirical information that could be used in conjunction with tree-level growth models (e.g. LIGNUM, Perttunen *et al.* 2001) to determine which growth pattern is optimal under a given light regime.

VERTICAL PROFILES OF LIGHT ATTENUATION AND RELATIONSHIPS WITH UNDERSTOREY VEGETATION

Light availability measured at a single height generally does not adequately describe the complexity of light environments found in forest understories (Montgomery & Chazdon 2001). Studies of vertical gradients of light availability have been performed in various forest ecosystems and have shown much variation in gradient steepness (Canham *et al.* 1994; Messier *et al.* 1998; Beaudet *et al.* 1999; Aubin *et al.* 2000). Two studies performed in North American deciduous forests showed much less vertical variation in light levels than observed here (Canham *et al.* 1994; Beaudet *et al.* 1999), but this may be due to the sites of these other studies both having a relatively sparse understory vegetation. However, light gradients as pronounced as or even steeper than those observed at our study sites have been reported for other forest types, such as in boreal mixed wood forests (Aubin *et al.* 2000), and in a tropical forest (Montgomery & Chazdon 2001).

The light measurements performed in this study allowed us to identify four main light profiles. The most frequent type of light profile in both the uncut plots and the older cuts (type 1) was characterized by having low light availability at all heights, and the lowest light level of all profiles at 5 m above ground. The relative abundance of *B. alleghaniensis* was significantly lower than expected for all size classes in quadrats with this type of light profile, and this might be linked to its known mid-shade-tolerance status. *Acer saccharum* seedlings, however, were more abundant than expected under this light profile, relating well to its strategy of maintaining an abundant seedling bank in shaded conditions (Godman *et al.* 1990). Profile 1 was also present in younger and intermediate-age cuts, but at much lower frequency of occurrence than in uncut plots and older cuts. The persistence of microsites with this type of light profile, even in recent selection cuts, is probably made possible by the fact that harvesting is not spatially homogeneous and that patches of forest are left relatively undisturbed.

The recent selection cuts were characterized by having a higher than expected relative frequency of

occurrence of J-shaped light profiles (types 2 and 3). Such light profiles could therefore be considered characteristic of recently disturbed stands. These profile types had the highest light availability of all profiles at 0.2 m, with mean values of 7 and 14% PPFD, respectively. This relatively high light availability near the forest floor is due to decreased light interception by the canopy as a result of recent tree removal, and to the fact that establishment of new regeneration and recruitment of pre-established regeneration have not yet had time to occur. This is in agreement with our observation of a low relative abundance of seedlings and saplings 1–5 m in height in these light profiles. Finally, the most rapid change in light in these profiles occurs near the ground (between 0.2 and 1 m), where most of the leaf area intercepting light was located (i.e. there was higher than expected relative abundance of one or more species in size classes < 0.2 m and/or 0.2–1 m). Within this height range (< 1 m), we observed that the relative abundance of *B. alleghaniensis* was significantly higher than expected.

The last type of light profile (type 4), which was especially frequent in intermediate-age cuts and older cuts, was characterized by its reverse J-shape with a relatively high light availability at 5 m, a very strong light attenuation between 2 and 5 m, and very dark conditions near the forest floor. This type of light profile might be characteristic of large gaps that are closing due to the rapid and strong regrowth of the understory vegetation. The high density of saplings associated with this type of light profile induced strong light attenuation and led to very dark conditions near the ground. Therefore, although the prevailing microsites might have allowed the establishment and recruitment of some *B. alleghaniensis* shortly after the cut, the time window of conditions suitable for the establishment of mid-tolerant species was quite short. Seven to eight years after harvesting, the light conditions were in fact so dark that even seedlings of the shade-tolerant *A. saccharum* were less abundant than expected. These conditions are somewhat similar to those described in many other studies reporting the presence of dense sub-canopies of saplings or shrubs that lead to very dark forest floor light levels and inhibition of the regeneration of less tolerant species (Lorimer *et al.* 1994; Emborg 1998; Yanai *et al.* 1998; Ray *et al.* 1999; Beckage *et al.* 2000).

As described by Ehrenfeld (1980), the recovery process following a disturbance depends on the interaction between patches of destroyed canopy superimposed over patches of understory vegetation that can vary greatly in terms of composition and abundance. When a canopy gap is created above a sparse lower stratum, or when the understory vegetation is completely or partly destroyed by a disturbance, an establishment response can be observed, as long as other conditions, such as the proximity of a seed source and the presence of adequate seedbeds, are met. When a canopy gap is formed above a patch of pre-established tree saplings and/or shrubs, a recruitment response is more likely to

be observed and, in these cases, the disturbance can in fact accelerate succession by allowing the release of shade-tolerant species pre-established in the understorey. In our temperate deciduous sites, where shade-tolerant species such as *A. saccharum*, *F. grandifolia* and *V. alnifolium* are dominant in the understorey, the recruitment response is the most prevalent (Beaudet 2001) and is responsible for the creation of reverse-J shape light profiles. The variety of light profiles observed in our study sites suggests that the regeneration dynamics of these stands is affected by both spatially and temporally heterogeneous patterns of canopy opening superimposed over heterogeneous patterns of pre-established vegetation and understorey disruption. Therefore, to better understand the recovery process following disturbance in this forest type, further studies are required to characterize the mechanism responsible for the spatial pattern of occurrence of pre-established shade-tolerant saplings and shrubs, how these patterns vary among stands and how this type of vegetation is affected by and responds to different types of disturbance.

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References

- Aubin, I., Beaudet, M. & Messier, C. (2000) Light extinction coefficients specific to the understorey vegetation of the southern boreal forest (Québec). *Canadian Journal of Forest Research*, **30** (1), 168–177.
- Baker, F.S. (1949) A revised tolerance table. *Journal of Forestry*, **47**, 179–181.
- Bartemucci, P. (2001) *Overstorey influences on understorey plant communities and light environments in mixedwood boreal forests of Québec*. Msc thesis, Université du Québec à Montréal, Montréal.
- Beaudet, M. (2001) *Caractérisation et modélisation des effets du couvert forestier sur la dynamique de la lumière et de la régénération dans l'érablière*. PhD thesis, Université du Québec à Montréal, Montréal.
- Beaudet, M. & Messier, C. (1998) Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Canadian Journal of Forest Research*, **28**, 1007–1015.
- Beaudet, M. & Messier, C. (2002) Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agricultural and Forest Meteorology*, **110** (3), 217–228.
- Beaudet, M., Messier, C., Paré, D., Brisson, J. & Bergeron, Y. (1999) Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Bois-des-Muir old-growth forest, Quebec. *Écoscience*, **6**, 264–271.

- Beckage, B., Clark, J.S., Clinton, B.D. & Haines, B.L. (2000) A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understoreys. *Canadian Journal of Forest Research*, **30**, 1617–1631.
- Brisson, J., Lareau, C., Beaudet, M., Millet, J., Messier, C. & Bouchard, A. (2001) *Rétablissement de l'érablière suite aux dommages causés par le verglas – Le cas d'une forêt ancienne du sud-ouest du Québec*. Final report, submitted to the Quebec Ministry of Natural Resources. Institut de Recherche en Biologie Végétale, Montreal.
- Canham, C.D. (1985) Suppression and release during canopy recruitment in *Acer saccharum*. *Bulletin of the Torrey Botanical Club*, **112**, 134–145.
- Canham, C.D. (1990) Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club*, **117** (1), 1–7.
- Canham, C.D., Finzi, A.C., Pacala, S.W. & Burbank, D.H. (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, **24**, 337–349.
- Canham, C.D. & Marks, P.L. (1985) The response of woody plants to disturbance: patterns of establishment and growth. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 197–216. Academic Press, New York.
- Claveau, Y., Messier, C., Comeau, P.G. & Coates, K.D. (2002) Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Canadian Journal of Forest Research*, **32**, 458–468.
- Constabel, A.J. & Lieffers, V.J. (1996) Seasonal patterns of light transmission through boreal mixedwood canopies. *Canadian Journal of Forest Research*, **26**, 1008–1014.
- Crow, T.R. & Metzger, F.T. (1987) Regeneration under selection cutting. *Managing Northern Hardwoods* (ed. R.D. Nyland), pp. 81–94. Society of American Foresters, University of New York, College of Environmental Science and Forestry, Syracuse, New York.
- Davies, S.J., Palmiotto, P.A., Ashton, P.S., Lee, H.S. & Lafrankie, J.V. (1998) Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology*, **86** (4), 662–673.
- Ehrenfeld, J.G. (1980) Understorey response of canopy gaps of varying size in a mature oak forest. *Bulletin of the Torrey Botanical Club*, **107**, 29–41.
- Emborg, J. (1998) Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, **106**, 83–95.
- Environment Canada (1998) *Canadian Climate Normals 1961–90*. Web page <http://www.cmc.ec.gc.ca/climate/normals/>, accessed in 2000.
- Erdmann, G.G. (1990) *Betula alleghaniensis* Britton – Yellow Birch. *Silvics of North America*, Volume 2 (eds R.M. Burns & B.H. Honkala), pp. 133–147. United States Department of Agriculture, Washington, DC.
- Fraver, S., Brokaw, N.V.L. & Smith, A.P. (1998) Delimiting the gap phase in the growth cycle of a Panamanian forest. *Journal of Tropical Ecology*, **14** (5), 673–681.
- Frazer, G.W., Trofymow, J.A. & Lertzman, K.P. (2000) Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Canadian Journal of Forest Research*, **30**, 239–256.
- Gendron, F., Messier, C. & Comeau, P.G. (1998) Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agricultural and Forest Meteorology*, **92**, 55–70.

- Gill, D.S., Amthor, J.S. & Bormann, F.H. (1998) Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. *Tree Physiology*, **18**, 281–289.
- Godman, R.M., Yawney, H.W. & Tubbs, C.H. (1990) *Acer saccharum* Marsh. – Sugar Maple. *Silvics of North America*, Volume 2 (eds R.M. Burns & B.H. Honkala), pp. 78–91. United States Department of Agriculture, Washington, DC.
- Grime, J.P. & Jeffrey, D.W. (1965) Seedling establishment in vertical gradients of sunlight. *Journal of Ecology*, **53**, 621–642.
- Henry, H.A.L. & Aarssen, L.W. (1997) On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos*, **80** (3), 575–582.
- Hibbs, D.E. (1982) Gap dynamics in a hemlock-hardwood forest. *Canadian Journal of Forest Research*, **12**, 522–527.
- King, D.A. (1990) The adaptive significance of tree height. *American Naturalist*, **135** (6), 809–828.
- Kobe, R.K., Pacala, S.W., Silander, J.A. Jr & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
- Lawton, R.O. (1990) Canopy gaps and light penetration into a wind-exposed tropical montane rain forest. *Canadian Journal of Forest Research*, **20**, 659–667.
- Lieberman, M., Lieberman, D. & Peralta, R. (1989) Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70** (3), 550–552.
- Lorimer, C.G., Chapman, J.W. & Lambert, W.D. (1994) Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology*, **82**, 227–237.
- Mader, S.F. & Nyland, R.D. (1984) Six-year response of northern hardwoods to the selection system. *Northern Journal of Applied Forestry*, **1**, 87–91.
- Majcen, Z. (1995) *Résultats après 10 ans d'un essai de coupe de jardinage dans une érablière*. Mémoire de Recherche Forestière no. 122. Gouvernement du Québec, Ministère des Ressources Naturelles, Sainte-Foy, Québec.
- Majcen, Z. & Richard, Y. (1992) *Résultats après 5 ans d'un essai de coupe de jardinage dans une érablière*. *Canadian Journal of Forest Research*, **22**, 1623–1629.
- Majcen, Z., Richard, Y., Ménard, M. & Grenier, Y. (1990) *Choix des tiges à marquer pour le jardinage d'érablières inéquennes-guide technique*. Mémoire no. 96. Gouvernement du Québec, Ministère de l'Énergie et des Ressources, Sainte-Foy, Québec.
- Marie-Victorin, Fr. (1964) *Flore Laurentienne*, 2nd edn. Les Presses de l'Université de Montréal, Montréal, Québec.
- Matthews, J.D. (1989) *Silvicultural Systems*. Oxford University Press, Oxford.
- van der Meer, P.J. (1997) Vegetation development in canopy gaps in a tropical rain forest in French Guiana. *Selbyana*, **18** (1), 38–50.
- van der Meer, P.J. & Bongers, F. (1996) Formation and closure of canopy gaps in the rainforest at Nouragues, French-Guiana. *Vegetatio*, **126** (2), 167–179.
- van der Meer, P.J., Bongers, F., Chatrou, L. & Riera, B. (1994) Defining canopy gaps in a tropical rain forest: effects on gap size and turnover time. *Acta Oecologica – International Journal of Ecologica*, **15** (6), 701–714.
- Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C. & Lechowicz, M.J. (1999) Functional ecology of advance regeneration in relation to light in boreal forests. *Canadian Journal of Forest Research*, **29**, 812–823.
- Messier, C., Parent, S. & Bergeron, Y. (1998) Effects of overstorey and understorey vegetation on the understorey light environment in mixed boreal forests. *Journal of Vegetation Science*, **9**, 511–520.
- Montgomery, R.A. & Chazdon, R.L. (2001) Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology*, **82** (10), 2707–2718.
- Nicotra, A.B., Chazdon, R.L. & Iriarte, S.V.B. (1999) Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, **80** (6), 1908–1926.
- Perttunen, J., Nikinmaa, E., Lechowicz, M.J., Sievänen, R. & Messier, C. (2001) Application of the functional-structural tree model LIGNUM to sugar maple saplings (*Acer saccharum* Marsh) growing in forest gaps. *Annals of Botany*, **88**, 471–481.
- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. *Long-Term Studies in Ecology* (ed. G.E. Likens), pp. 110–135. Springer-Verlag, New York.
- Ray, D.G., Nyland, R.D. & Yanai, R.D. (1999) Patterns of early cohort development following shelterwood cutting in three Adirondack northern hardwood stands. *Forest Ecology and Management*, **119** (1–3), 1–11.
- Runkle, J.R. & Yetter, T.C. (1987) Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology*, **68** (2), 417–424.
- Sakai, S. (1995) Evolutionary stable growth of a sapling which waits for future gap formation under closed canopy. *Evolutionary Ecology*, **9**, 444–452.
- Shropshire, C., Wagner, R.G., Bell, F.W. & Swanton, C.J. (2001) Light attenuation by early successional plants of the boreal forest. *Canadian Journal of Forest Research*, **31**, 812–823.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry: the Principles and Practice of Statistics in Biology Research*, 2nd edn. W.H. Freeman, New York.
- Terborgh, J. (1985) The vertical component of plant species diversity in temperate and tropical forests. *American Naturalist*, **126**, 760–776.
- Valverde, T. & Silvertown, J. (1997) Canopy closure rate and forest structure. *Ecology*, **78** (5), 1555–1562.
- Willis, G.L. & Johnson, J.A. (1978) *Regeneration of Yellow Birch Following Selective Cutting of Old-Growth Northern Hardwoods*. Ford Forestry Center, Michigan Technological University, Michigan.
- Yanai, R.D., Twery, M.J. & Stout, S.L. (1998) Woody understorey response to changes in overstorey density: thinning in the Allegheny hardwoods. *Forest Ecology and Management*, **102** (1), 45–60.

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