Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs

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Abstract

The objective of this study was to determine how canopy openness (CO) and light transmission are affected by selection cutting, and how they vary over time following harvesting in northern hardwood stands. We sampled five sugar maple—yellow birch—beech (*Acer saccharum—Betula alleghaniensis—Fagus grandifolia*) stands in Québec (Canada). The stands had been logged, using the selection system, at different times (2–14 years) before the study, and were used as a chronosequence. We also sampled portions of each stand which had been kept as uncut controls. Ten 1 ha plots were sampled (five cuts and five paired controls). We took 20 hemispherical photographs per plot, at 5 m above-ground, which was above most understory vegetation. The CO, light transmission (gap light index (GLI) *sensu* Canham (1988)), sunflecks characteristics, and angular distribution of openings from the zenith were calculated for each photograph. Selection cutting increased CO, especially within 60° of the zenith. The greater CO in the cuts allowed a greater light transmission (GLI), longer sunflecks, and a longer cumulative daily sunflecks duration (CDSD). The differences observed between the cuts and the control plots in terms of CO, GLI, and CDSD were greatest in the more recent cuts, and decreased as a function of time since logging. The relationships were best described by negative logarithmic (CO) and negative exponential (GLI, CDSD) models. In the youngest cut (2 years old), the CO, GLI, and CDSD were on average 2.3–2.5 times higher than in the control, while in the oldest cut (14 years old), the same variables were 1.6–1.7 times higher than in the control. The results of this study emphasize the importance of taking into account the temporal variation in canopy openness and light transmission after canopy disturbances such as selection cutting because that variation will likely have an important influence on regeneration dynamics. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

In forest understories, photosynthetically active radiation (PAR) affects the growth and survival of tree regeneration (Canham and Marks, 1985; Kozlowski et al., 1991; Lieffers et al., 1999). Forest understory light regimes are determined in large part by seasonal and diurnal variations in the sun position, weather, topographic position, and forest canopy structure (Canham, 1988; Rich et al., 1993). In terms of canopy structure, the canopy height and depth, and the spatial organization of overstory stems, branches, and foliage affect the pattern of light transmission (GLI) through the canopy (Baldocchi and Collineau, 1994). In temperate deciduous forests, natural and man-made

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small scale disturbances produce canopy openings that are an important source of heterogeneity in forest understory light regimes, and play a critical role in determining patterns of tree regeneration (Canham and Marks, 1985; Canham et al., 1990; Beaudet and Messier, 1998; Messier and Nikinmaa, 2000).

Hemispherical photographs are now widely used to characterize forest canopy structure (e.g. Chazdon and Field, 1987; Rich et al., 1993; Whitmore et al., 1993; Gendron et al., 1998; Trichon et al., 1998). For a given microsite, an hemispherical photograph can provide a detailed description of the size and distribution of openings in the canopy, and a quantitative measure of total canopy openness (CO) (Whitmore et al., 1993; Valverde and Silvertown, 1997; Walter and Torquebiau, 1997). The hemispherical distribution of canopy openings can be combined to information about the above-canopy spatio-temporal pattern of PAR to obtain an indirect measure of the potential seasonal light regime at the microsite (Chazdon and Field, 1987). Significant positive correlations between direct sensor measurements and indirect photographic estimates of PAR transmission have been reported in numerous published studies (e.g. Chazdon and Field, 1987; Becker et al., 1989; Comeau et al., 1998; Gendron et al., 1998).

The objective of this study was to determine how CO and GLI are affected by selection cutting, and how they vary over time following harvesting in northern hardwood stands. Selection cutting, a partial harvesting method, is increasingly being used in northern hardwood stands in Québec (Majcen, 1994). The effects of selection cutting on CO and GLI are potentially important determinants of post-harvest patterns of tree regeneration. However, most of the studies performed so far to assess the effects of selection cutting have focussed on direct measurements of tree regeneration, but have not characterized the effects of selection cutting on stand-level CO and GLI (e.g. Mader and Nyland, 1984; Crow and Metzger, 1987; Majcen, 1995).

2. Methods

2.1. Study sites and sampling design

Five sugar maple—yellow birch—beech (*Acer saccharum—Betula alleghaniensis—Fagus grandifolia*) stands were sampled in two locations in Québec (Canada) (Table 1). Three stands were at the Duchesnay Forest Station (46°50′ to 47°00′N, and 71°35′ to 71°45′W), near Québec city, and two stands were at the Mousseau Forest (46°33′ to 46°37′N, and 74°55′ to 74°59′W) in Sainte-Véronique, near Mont-Laurier. Climatic conditions at both locations are similar: mean annual precipitation is around 1200 mm, mean annual temperature is 3–4 °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 study stands (Table 1) are uneven-aged with dominant and co-dominant tree heights ranging from 20 to 25 m. They have probably all been subjected to some high-grading prior to the 1950s, but precise records of harvesting are not available. More recently, the stands have been subjected to selection cuts performed at different times (2–14 years) prior to this study (Majcen and Richard, 1991; Majcen, 1995). At the time of harvesting, a portion of each stand was kept as an uncut control. For this study, a 1 ha plot was established in the cut and in the control area of each stand. Within each plot, we took hemispherical photographs at 20 microsites located along a 4 × 5 grid with a 20 m spacing between microsites, for a total of 200 microsites (5 stands × 2 plots/stand × 20 microsites/plot).

We used the five different-aged cuts as a chronosequence to evaluate the temporal variation of CO and light conditions following logging. The use of spatially distinct forest sites to study temporal trends can be complicated by the fact that stands may differ in a number of factors, including soil, slope, aspect, vegetation, and disturbance history (Pickett, 1987; Frazer et al., 2000). We selected stands that were as similar as possible, given the constraint of finding stands that had been cut at different times in the recent years and that also had a contiguous control area available for sampling. Although our chronosequence comprises stands from two different locations, care was taken to intersperse the ages of the cuts between the two locations (Duchesnay: 1989, 1992, 1995; Sainte-Véronique: 1983, 1993). It should also be noted that the temporal effect was not inferred from a direct comparison of selection cuts, but rather from a comparison of the differences observed between cuts and their paired controls. This approach

Table 1
Main characteristics of the study sites[a]

Stand plot	DU95-cut	DU95-ctrl	SV93-cut	SV93-ctrl	DU92-cut	DU92-ctrl	DU89-cut	DU89-ctrl	SV83-cut	SV83-ctrl
Location	DU	DU	SV	SV	DU	DU	DU	DU	SV	SV
Cutting history[b]	Cut (1995/1996)	Uncut	Cut (1993/1994)	Uncut	Cut (1992/1993)	Uncut	Cut (1989/1990)	Uncut	Cut (1983/1984)	Uncut
Slope (%)	~0	~0	2–5	2–5	5–10	5–10	9–12	7–10	5–10	5–10
Aspect	–	–	E–SE	NE	NE	N–NE	S–SE	S	SW	E–SE
Elevation (m)	210	210	400	400	160	180	280	280	390	380
B.A. prior to cut (m^2/ha)	21.9	23.8	28.9	29.3	24.5	24.8	N.A.	28.2	27.4	26.5
B.A. after cut (m^2/ha)	17.3	–	19.8	–	18.7	–	19.5	–	17.0	–
Cutting intensity (% B.A.)	21	–	31	–	24	–	30	–	38	–
Species composition (% M.V.)[c]										
Sugar maple	46	39	73	60	52	38	63	50	85	94
Yellow birch	39	46	6	15	41	37	23	12	6	2
Beech	15	4	20	23	0	4	14	36	7	4
Others	0	11	1	2	7	21	0	2	2	0
Nb of microsites	19[d]	15[d]	20	20	20	20	20	20	20	20

[a] DU, Duchesnay; SV, Sainte-Véronique; B.A., basal area; M.V., merchantable volume; N.A., not available.

[b] Cut indicates a selection cut performed at the time indicated in parentheses (fall/winter).

[c] For cuts, the species composition is as observed after the cut.

[d] In DU95-cut, one microsite was excluded because it was in a forest trail, and in DU95-ctrl, five microsites were excluded because they were too close to a forest road.

allowed an adjustment of our selection cut data for among-stands variations by substracting from them the value observed in paired control plots.

2.2. Hemispherical photographs

Photographs were taken 5 m above-ground at each microsite using a Canon camera equipped with a Canon 7.5 mm *f*/5.6 hemispherical lens, and black and white film (Kodak TMax 400 ASA). Photographs were taken at a height of 5 m to be able to characterize the forest canopy without the interfering presence of the abundant shrub and tree understory vegetation. The camera was mounted on a monopod equipped with a levelling device and was oriented so that the top of the photographs was aligned with geographic north. To minimize glare from direct sunlight, photographs were taken under overcast conditions. Two to three different exposure times were used at each microsite, bracketing the exposure time indicated by a built-in light meter. After processing, the photograph showing the best contrast between sky an canopy foliage was selected for each microsite.

Photographs were digitized and then analysed with the Gap Light Analyser software (GLA, version 2.0) (Frazer et al., 1997; Frazer et al., 1999). A threshold level was selected for each photograph to distinguish between visible sky and foliage. All photographs were analysed by the same person to minimize variation in threshold selection. For each photograph, we computed the following descriptors of canopy structure and light regime.

The angular distribution of canopy openings in the hemisphere was determined by dividing the hemispherical image into concentric rings corresponding to $5°$ intervals of zenith angle. The fraction of sky pixels over total pixels was calculated for each ring and will be referred to as the gap fraction by zenith angle (G_z). CO is the percentage of visible sky across the whole hemisphere, and was computed as the summation of the weighted G_z over the whole hemisphere:

$$\text{CO} = \sum_{z} (G_z W_z) \times 100 \tag{1}$$

where z represents the different intervals of zenith angle, G_z is the gap fraction of interval z, and W_z the weighting factor for interval z. The weighting factor is used to correct for area differences between

a circle and a sphere using a cosine transformation (Frazer et al., 1997). It is calculated for each zenith interval (z) as described by Rich (1989):

$$W_z = \cos q_i - \cos q_j \tag{2}$$

where q_i and q_j are the two angles (in $°$) from zenith defining the interval z (where $q_i < q_j$).The gap light index (GLI) (Canham, 1988) was calculated as a measure of total seasonal PAR transmission:

$$\text{GLI} = (p_{\text{diff}} T_{\text{diff}}) + (p_{\text{beam}} T_{\text{beam}}) \tag{3}$$

where T_{diff} and T_{beam} are the percentages of diffuse and direct radiation transmitted to a microsite through canopy openings, respectively, and p_{diff} and p_{beam} are the proportions of incident radiation received at the top of the canopy as, respectively, diffuse and direct beam radiation (where $p_{\text{diff}} + p_{\text{beam}} = 1$, and p_{diff} and p_{beam} were both set to 0.5). The uniform overcast sky flux distribution model (UOC), a clear sky transmission value of 0.65, and a growing season starting on 1 May and ending on 15 September were used in the calculations.

The GLA software also records the number and duration of sunfleck events based on a user-defined interval of change in solar position throughout the growing season (set to 1 min in this study). This allowed the calculation of the mean number of sunflecks per day, the mean individual sunfleck duration (ISD), and the mean cumulative daily sunflecks duration (CDSD). The duration of a sunfleck evaluated from an hemispherical photograph corresponds to the period of time during which direct beam radiation reaches a microsite through a canopy opening. However, the evaluation of sunflecks duration from hemispherical photographs does not take into account the effects of clouds and foliage motion by wind, which would likely produce sunflecks of shorter duration (Canham et al., 1990).

2.3. Statistical analysis

For each variable (CO, GLI, number of sunflecks per day, ISD, and CDSD), we used *t*-tests to determine if the values observed in each cut were different from those observed in its paired control. Data had to be transformed ($\log[x + 1]$) to meet the normality assumption. To evaluate how CO, GLI, and sunflecks characteristics varied over time following

selection cutting, we calculated, for each pair of cut and control plots, the difference between the median value of the cut and of the control ($D_{cut-ctrl} = median_{cut} - median_{ctrl}$). We then investigated how that difference ($D_{cut-ctrl}$) varied as a function of time since logging, using linear and nonlinear regression (logarithmic, exponential, and quadratic models were tested). If more than one model was significant for a given relationship, we selected the one yielding the highest R^2 value. The distribution of gap fraction as a function of zenith angle was assessed graphically. Statistical analyses were performed with Systat (7.0).

3. Results and discussion

3.1. Canopy openness and light transmission

CO and GLI were higher (Fig. 1, Table 2) and more variable (Fig. 1, Table 3) in selection cuts than

in controls. Microsite-level CO ranged from 3.6 to 24.9% in the cuts and from 2.0 to 11.2% in the controls (Fig. 1A), while plot-level mean CO varied from 7.9 to 12.1% among the cuts, and from 4.5 to 6.2% among the controls (Table 2). Microsite-level GLI ranged from 3.1 to 37.2% in the cuts and from 3.0 to 16.5% in the controls (Fig. 1B), while plot-level mean GLI varied from 10.8 to 17.0% among the cuts, and from 6.5 to 9.2% among the controls (Table 2). In the youngest cut (2 years old), CO and GLI were 2.3 and 2.5 times higher than in the paired control plot, respectively while in the oldest cut (14 years old), the same variables were 1.8 and 1.7 times higher than in the control (Table 2). For both CO and GLI, the coefficients of variation (CV) and ranges of values observed in cut plots were larger than in control plots (Table 3).

Very few published studies have characterized the CO of northern hardwood stands using hemispherical photographs. A mean CO of 11.7% was reported by Sampson et al. (1998) for stands that were
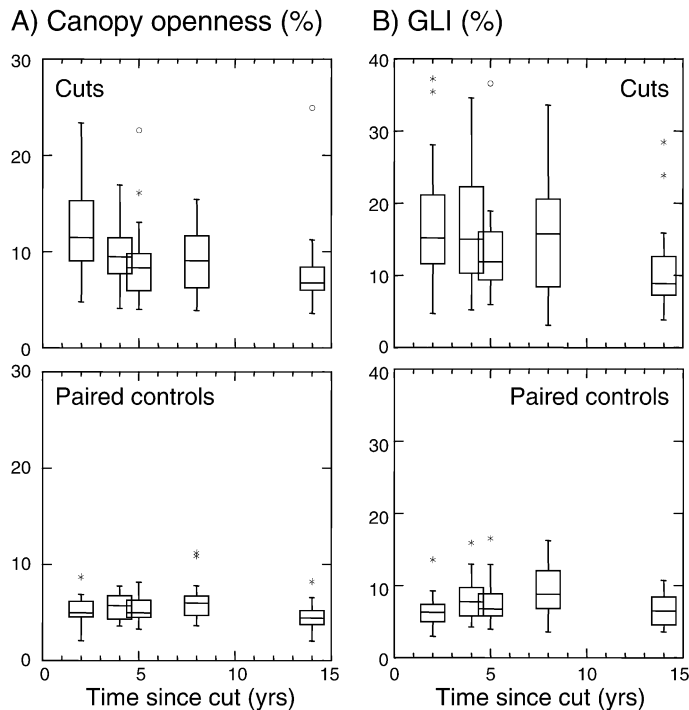

Fig. 1. Box-plots summarizing the distribution of (A) canopy openness, and (B) light transmission (GLI) for five selection cuts and their paired control plots. The horizontal line in each box is the median, the box endpoints represent the 25th and 75th percentiles (interquartile range), the whiskers indicate the smallest and largest values within 1.5 box lengths, and the asterisks and circles are outliers falling outside and far outside the interquartile range.

Table 2

Canopy openness, light transmission (GLI), and sunflecks characteristics in selection cuts performed 2–14 years before this study, and in their paired control plots (mean ± 1 S.E.M.)[a]

Variable	Stand	Time since logging (years)	Cut	Control	P
Canopy openness (%)					
	DU95	2	12.1 ± 1.1	5.2 ± 0.4	<0.001
	SV93	4	9.7 ± 0.7	5.6 ± 0.3	<0.001
	DU92	5	8.9 ± 1.0	5.4 ± 0.3	<0.001
	DU89	8	9.2 ± 0.8	6.2 ± 0.5	0.003
	SV83	14	7.9 ± 1.0	4.5 ± 0.3	<0.001
Light transmission (GLI, %)					
	DU95	2	17.0 ± 2.1	6.7 ± 0.7	<0.001
	SV93	4	16.7 ± 1.9	8.1 ± 0.7	<0.001
	DU92	5	14.4 ± 1.9	7.8 ± 0.7	<0.001
	DU89	8	15.5 ± 1.9	9.2 ± 0.8	0.022
	SV83	14	10.8 ± 1.4	6.5 ± 0.5	0.002
Number of sunflecks per day					
	DU95	2	14.3 ± 1.4	9.8 ± 0.7	0.017
	SV93	4	12.0 ± 0.9	10.0 ± 0.8	0.102
	DU92	5	13.0 ± 0.8	11.7 ± 0.7	0.322
	DU89	8	10.8 ± 0.8	14.6 ± 1.8	0.092
	SV83	14	13.1 ± 0.9	10.7 ± 0.6	0.042
Individual sunfleck duration (min)					
	DU95	2	7.9 ± 1.7	4.3 ± 0.4	0.010
	SV93	4	10.1 ± 1.4	4.7 ± 0.3	0.001
	DU92	5	7.2 ± 0.9	4.2 ± 0.3	0.001
	DU89	8	9.1 ± 1.3	4.7 ± 0.5	0.001
	SV83	14	5.8 ± 0.8	3.9 ± 0.2	0.010
Cumulative sunfleck duration (min/day)					
	DU95	2	106.4 ± 15.8	42.8 ± 5.1	0.002
	SV93	4	112.9 ± 13.4	48.6 ± 5.8	<0.001
	DU92	5	91.7 ± 13.2	49.8 ± 4.8	0.001
	DU89	8	99.8 ± 13.8	61.4 ± 6.5	0.088
	SV83	14	71.9 ± 7.2	42.9 ± 3.9	0.001

[a] The *t*-tests were performed on log-transformed data ($P < 0.05$ are considered significant).

suffering from sugar maple decline. Such a value is similar to our result in a recent selection cut (Table 2). In other forest ecosystems, Trichon et al. (1998) reported microsite-level CO values ranging from 1.4 to 5.1% for building and mature phases forests, and from 7.6 to 28.8% in gap phase forests in a tropical rainforest in Sumatra. Frazer et al. (2000) reported stand-level mean CO ranging from 2.2 to 14.1% for immature, mature, and old-growth Douglas-fir—western hemlock—western redcedar forests on Vancouver Island (BC, Canada).

Canham et al. (1990) reported GLI values ranging from 0.3 to 3.8% for a northern hardwood site

dominated by a uniform canopy of sugar maple and beech. Those values are lower than the GLI values we obtained in our control plots. Differences could be due to the fact that our hemispherical photos were taken at 5 m above-ground (i.e. above the main understory vegetation) compared to 1.5 m in the case of Canham et al. (1990), and our sampling protocol was not specifically aimed at closed canopy microsites in the control plots.

The difference of CO and GLI between cut and control plots decreased as a function of time since logging, and the rate of change was more rapid in the first few years following logging (Fig. 2). A significant

Table 3
Coefficient of variation (CV) and range of canopy openness and light transmission (GLI) values observed in selection cuts performed 2–14 years before this study, and in their paired control plots

Variable	Stand	Time since logging (years)	CV		Range	
			Cut	Control	Cut	Control
Canopy openness (%)						
	DU95	2	0.405	0.317	19	7
	SV93	4	0.330	0.233	13	4
	DU92	5	0.494	0.268	19	5
	DU89	8	0.389	0.327	12	8
	SV83	14	0.566	0.295	21	6
Light transmission (GLI, %)						
	DU95	2	0.542	0.390	32	11
	SV93	4	0.501	0.371	29	12
	DU92	5	0.582	0.411	31	13
	DU89	8	0.561	0.407	30	13
	SV83	14	0.563	0.330	25	7

negative logarithmic relationship was found between the difference of median CO between cuts and their paired controls, and time since logging (Fig. 2). The difference of median GLI between cuts and controls also decreased as a function of time since logging, but the relationship was best described by a negative
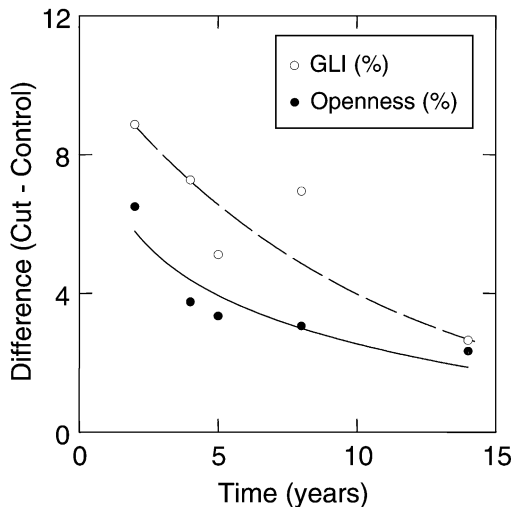

Fig. 2. Differences of median CO and GLI between paired cuts and controls as a function of the number of years since the cut was performed. For canopy openness: $[CO_{cut}-CO_{ctrl}] = 7.2-2.0 \ln time$; $P = 0.025$; $R^2 = 0.805$. For light transmission: $[GLI_{cut}-GLI_{ctrl}] = 10.8 \times \exp(-0.099 \times time)$; $P = 0.037$; $R^2 = 0.747$.

exponential model (Fig. 2). The nonlinear decrease of CO and GLI over time is in agreement with trends reported for other forest ecosystems. van der Meer and Bongers (1996), for instance, took hemispherical photographs in the centers of gaps in a rain forest during three successive years and found that the rate of gap closure slowed down as gap age increased. In temperate forests from Britain, Valverde and Silvertown (1997) observed a negative exponential rate of canopy closure. Since our study of the temporal variation in CO is based on a chronosequence, and hence on plot-level median CO, it does not allow a precise identification of the gap-level processes that might affect the temporal pattern of variation in plot-level CO. It might be hypothesized that since gap closure is in part due to the crown expansion of trees bordering gaps, the decreasing rate of canopy closure over time could be due to the slower growth rate of lateral branches after some length is achieved (Hibbs, 1982). Expansion of individual gaps caused by death of peripheral trees (Foster and Reiners, 1986) is another gap-level process that may influence the temporal variation in mean stand-level CO. van der Meer and Bongers (1996), for instance, monitored over 3 years the canopy openness of individual gaps and found that in 54% of the gaps, the CO increased over time.

The study of gap-generated heterogeneity in light conditions has mainly focused on the description of static differences between gap and closed-canopy microsites (Lieberman et al., 1989). The temporal

pattern of change in CO and light conditions following canopy disturbance has been much less documented (but see Rich et al., 1993; van der Meer and Bongers, 1996; Valverde and Silvertown, 1997 for photographs taken <1.5 m above-ground). The relatively rapid decrease in CO and light transmission observed in this study following selection cutting has important implications for the acclimation response of pre-established regeneration. While leaf-level acclimation to changes in light conditions can occur in a matter of days to weeks (Pearcy and Sims, 1994), acclimation at the whole-plant level through changes in patterns of biomass allocation and architecture may require several years to adjust (Küppers, 1994). The dynamic nature of the canopy openings and light conditions, is therefore, important to consider in studies evaluating the significance of plant-level traits because any given trait may not be optimal at one particular point in time, but may be optimal over the long-term, depending on the disturbance pattern (Messier and Nikinmaa, 2000). The relatively rapid closure of the canopy and decrease in light transmission observed in this study is also an important factor that will determine whether light availability will be sufficient for tree sapling survival in the long-term. The combining effects of rapidly increasing sapling size and light requirements (Givnish, 1988), and decreasing understory light availability, especially in smaller gaps, might be detrimental for trees if they quickly reached what Messier et al. (1999) have called their "maximum sustainable height". This situation can then set up a "decline cascade" driven by a maladaptive canopy architecture that increases the risk of mortality during the subsequent suppression period.

3.2. Sunfleck characteristics

The mean number of sunflecks per day in the cuts was either not significantly different from that observed in the controls (SV93, DU92, and DU89), or higher than in the controls (DU95, SV83) (Table 2). Among all plots, the mean number on sunflecks per day ranged from 9.8 to 14.6 (Table 2). Those numbers are comparable to the value of 11.6 sunflecks per day reported by Messier et al. (1998) for white birch stands. The lack of difference in the number of sunflecks per day between cuts and controls in three out of five stands means that the number of distinct

canopy openings along the solar track was on average the same in those cuts and in their controls. Logging produces new openings in previously closed portions of the canopy and hence, might be expected to increase the number of sunflecks, but can also decrease the number of openings by replacing numerous small gaps with a few larger ones.

The mean ISD was significantly higher in the cuts compared to the controls (Table 2). It ranged from 2.8 to 35.5 min in selection cuts, and from 2.0 to 10.5 min in controls (Fig. 3B). However, time since logging had no effect ($P > 0.25$) on the difference in ISD between cuts and controls. Our ISD values in the control plots were in agreement with those obtained by Canham et al. (1990) who reported mean sunfleck durations (from hemispherical photographs) ranging from 6 to 12 min beneath intact canopies of various temperate and tropical forest types, and a mean duration of 6.7 min for the northern hardwoods. Our results are also similar to the mean sunfleck duration of 4.6 min reported by Messier et al. (1998) based on quantum sensor measurements taken under a white birch canopy.

The CDSD was significantly higher in cuts than in controls for all stands except DU89 (Table 2). CDSD ranged from 13 to 288 min/day in cuts, and from 15 to 139 min/day in controls (Fig. 3C). Our CDSD values were in the same range as those obtained by Chazdon et al. (1988) (11–289 min/day) in a tall evergreen tropical forest in Mexico. The CDSD in the cuts, compared to the controls, decreased over time following selection cutting. The linear, logarithmic and exponential models were all significant, but the exponential model yielded the highest R^2 value ([CDSD$_{cut}$−CDSD$_{ctrl}$] = 55.4 × exp[−0.052 × time], where time is the number of years since logging, $P = 0.032$, $R^2 = 0.771$, graph not shown).

The importance of sunflecks for daily carbon gain is well documented (Pearcy, 1990; Chazdon and Pearcy, 1991). An important proportion of the total carbon gain of tree seedlings is generally associated with sunfleck events. Weber et al. (1985), for instance, estimated that 20–30% of the total carbon gain of sugar maple seedlings occurred during sunflecks. The CDSD, which is often positively correlated with the total light transmission, has been shown to be related to growth rates of tree species (Pearcy, 1983). Longer sunflecks should favor less
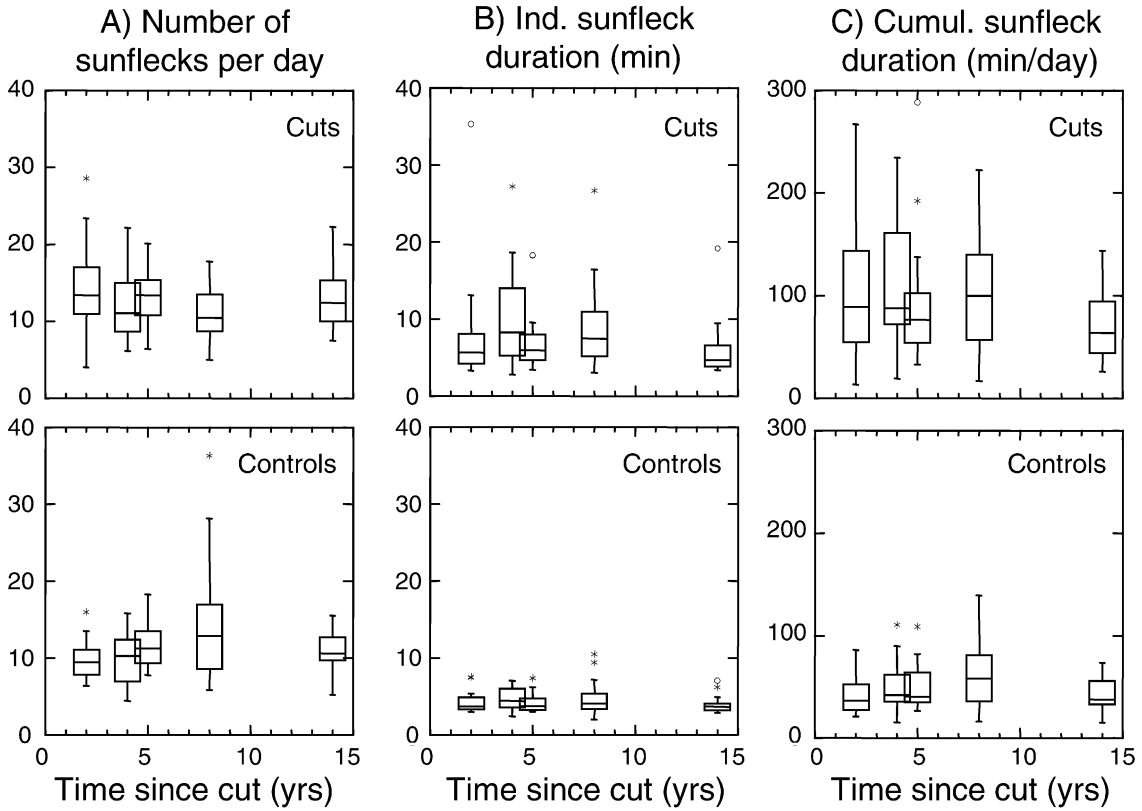
Fig. 3. Box-plots summarizing the distribution of (A) the number of sunflecks per day, (B) the mean individual sunfleck duration (ISD), and (C) the mean cumulative daily sunfleck duration (CDSD) for five selection cuts and their paired control plots.

shade tolerant species with higher photosynthetic capacity because those species tend to (1) respond more slowly to sunflecks (Paliwal et al., 1994), and (2) utilize the increased light intensity more efficiently. A low light-saturation point, such as found in sugar maple (Beaudet et al., 2000), may prevent the optimal utilization of the increased photon flux density associated with long and high intensity sunflecks (Pearcy, 1990), but should favour this species under a light regime of short, low intensity and frequent sunflecks.

3.3. Gap fraction as a function of zenith angle

In general, higher gap fractions were observed in the cuts compared to the control plots (Fig. 4). Gap fractions were higher near the zenith and at intermediate angles, than near the horizon (Fig. 4). In fact,
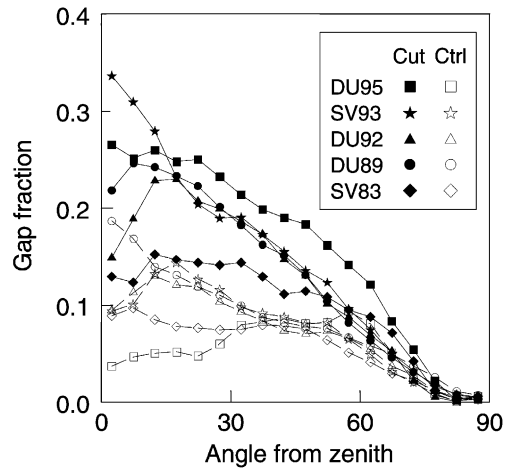

Fig. 4. Mean gap fraction by 5° interval of angle from zenith for five selection cuts and their paired control plots. Plot names are as defined in Table 1.

depending on stand, 56–79% of the total gap fraction originated from within 45° of the zenith, and 82–93% originated from within 60° of the zenith (Fig. 4). Greater gap fractions near the zenith, and smaller gap fractions near the horizon, are presumably due to, respectively, the shorter and longer path length through the canopy (Chazdon and Field, 1987). In some stands, the maximum gap fraction was not at the zenith, but rather at approximately 15° (e.g. DU92-cut, DU89-cut, SV83-cut, Fig. 4). Trichon et al. (1998) suggested that such a pattern can be characteristic of forests on slope. The stands with maximum gap fraction at approximately 15° from zenith were in fact cut sites located on slopes ranging from 5 to 12°, while the other two cut sites were on rather flat ground (0–5°). However, this trend did not hold for control sites. At our latitudes, gap fraction at intermediate angles is important for transmission of beam radiation (Canham et al., 1994). Canham et al. (1999) presented the angular distribution of gap fraction for stands dominated by different species from British Columbia. Near the zenith, the gap fraction ranged from approximately 15% in paper birch stands to 70% in lodgepole pine stands. In our northern hardwood stands, gap fraction directly overhead ranged from 4% (DU95-ctrl, Fig. 4) to 34% (SV93-cut, Fig. 4), and was generally lower than observed in the forests studied by Canham et al. (1999). A higher gap fraction near the zenith, such as observed by Canham et al. (1999), could be characteristic of stands dominated by coniferous species, due to the conical crown shape of those species.

4. Summary and conclusion

This study presented a quantitative description of the central tendency (mean and median) and variability (CV and range) in the CO and light transmission in northern hardwood stands. To our knowledge, it is one of the first studies to use hemispherical photographs to assess the effects of time since partial cutting (selection system) on the canopy structure and light conditions in that forest type. We observed that the difference in CO, GLI, and CDSD between cut and control plots decreased as a function of time since logging, and that the rate of change was more rapid in the first few years following harvesting. The

estimation of the temporal trend reported in this study based on a chronosequence analysis should be complemented by studies of temporal variation based on successive measurements of CO and light regime. A companion study will report how the understory vegetation less than 5 m in height responded to selection cutting and how it affected the transmission of light to the forest floor (Beaudet and Messier, in press).

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