Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach

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ABSTRACT

In the context of partial harvesting, adequately managing post-harvest light conditions are essential to obtain a desired composition of tree species regeneration. The objective of this study was to determine how varying the intensity and spatial pattern of harvest would affect understory light conditions in boreal mixedwood stands of northwestern Quebec using the spatially explicit SORTIE-ND light model. The model was evaluated based on comparisons of observed and predicted light levels in both mapped and un-mapped plots. In mapped plots, reasonably accurate predictions of the overall variation in light levels were obtained, but predictions tended to lack spatial precision. In un-mapped plots, SORTIE-ND accurately predicted stand-level mean GLI (Gap Light Index) under a range of harvest intensities. The model was then used to simulate nine silvicultural treatments based on combinations of three intensities of overstory removal (30%, 45% and 60% of basal area) and three harvest patterns (uniform, narrow strips, large gaps). Simulations showed that increasing overstory removal had less impact on light conditions with uniform harvests, and a more marked effect with more aggregated harvest patterns. Whatever the harvest intensity, uniform cuts almost never created high light conditions (GLI > 50%). Gap cuts, on the other hand, resulted in up to 40% of microsites receiving GLI > 50%. Our results suggest that either a 30% strip or gap cut or a 45–60% uniform partial harvest could be used to accelerate the transition from an aspen dominated composition to a mixedwood stand because both types of cut generate the greatest proportion of moderately low light levels (e.g., 15–40% GLI). These light levels tend to favour an accelerated growth response among shade-tolerant conifers, while preventing excessive recruitment of shade-intolerant species. A better understanding of how spatial patterns of harvest interact with tree removal intensity to affect understory light conditions can provide opportunities for designing silvicultural prescriptions that are tailored to species' traits and better suited to meet a variety of management objectives.

1. Introduction

There is increasing interest in developing natural disturbance-based forest management practices to preserve the diversity and complexity of forest ecosystems (Gauthier et al., 2009; Puettmann et al., 2009). Bergeron and Harvey (1997) suggested that diversifying silvicultural practices to incorporate both even-aged and uneven-aged regimes could form the basis of a natural disturbance-based forest management framework in boreal mixedwoods. The use of uneven-aged silviculture, or more generally, partial harvesting practices, is intended to generate effects similar to those of secondary natural disturbances that cause partial and heterogeneous removal of the overstory (e.g., insect outbreaks) (Harvey et al., 2002; Franklin et al., 2007). The implementation of such a forest management approach also requires forest managers to be able to control – through silvicultural interventions – the transition rates between forest types of different successional stages (Lieffers et al., 1996; Harvey et al., 2002). For instance, this might

mean favouring the transition from an early-successional, aspen-dominated stand to a mid-successional mixedwood stand using some form of thinning of the aspen overstory to favour the recruitment and growth of shade-tolerant conifers (Prévost and Pothier, 2003; Brais et al., 2004). Successful implementation of such a natural dynamics-based management approach that relies heavily on partial harvesting requires a sound understanding of the multiple interacting factors that affect stand developmental patterns.

Adequately managing post-harvest light conditions is essential to obtaining the desired species composition of tree species regeneration, and is therefore an important component of successful partial harvesting interventions (Lieffers et al., 1999). At the individual tree level, light is a major determinant of growth and survival. At the community level – due to inter-specific differences in response to light – variations in light conditions can affect important processes such as regeneration establishment, competition dynamics and species succession (Lieffers et al., 1999). Maintaining a pattern of variability in light conditions similar to that found in natural forests is also expected to play an important role in preserving understory species diversity (Bartemucci et al., 2006).

Understory light conditions can be controlled, at least in part, by adjusting harvesting intensity, and the size, shape, location and orientation of openings (Carlson and Groot, 1997; Coates and Burton, 1997). Field-based comparisons of silvicultural treatments can provide useful information to determine which silvicultural system will produce the optimal distribution of light levels for a given set of management objectives (Prévost and Pothier, 2003; Brais et al., 2004; Man et al., 2008). However, field experiments are necessarily limited in the number of treatments that can be implemented, and they can be affected by many factors that cannot be controlled (e.g., occurrence of a forest tent caterpillar outbreak following experimental partial cutting treatments in Man et al., 2008).

A complementary approach is to use model simulations to evaluate and compare the effects of various silvicultural treatments on post-harvest light regimes (Coates et al., 2003; Sprugel et al., 2009). Numerous light models have been developed over the years (reviewed in Lieffers et al., 1999). Among these models, spatially explicit, individual-tree models are particularly appropriate in a context where exploring the impact of partial harvesting is of interest, especially in structurally complex and species-diverse forests (Brunner, 1998; Canham et al., 1999; Stadt and Lieffers, 2000). However, the usefulness of forest light models is often limited by the large data requirements of the models. For instance, existing light models often require the measurement of the crown dimensions and precise location of individual trees to obtain predictions of understory light levels. In comparison, the amount of input data required by the SORTIE-ND light model is remarkably small (Canham et al., 1999). Nevertheless, the model can accurately predict microsite-level light conditions in gaps and under various levels of overstory retention, and track how mean stand-level light availability varies as a function of species composition and stand basal area (BA) (Canham et al., 1994, 1999; Beaudet et al., 2002; Coates et al., 2003).

The objective of this study was to determine how varying the intensity and spatial pattern of harvest would affect understory light conditions in partially harvested boreal mixedwood stands. To do so, we parameterized and evaluated the SORTIE-ND light model for boreal mixedwood forests in northwestern Quebec (Canada). We then used the model to obtain spatially explicit predictions of light regimes following various combinations of harvest intensities and patterns (from uniform to more aggregated). We then compared the predicted light distributions in terms of their implications for the successful regeneration and management of mixedwood forests.

2. Methods

2.1. Study area and species

The study was performed in northwestern Quebec (Canada), in the Lake Duparquet Research and Teaching Forest (LDRTF) (approx. 48°30′N; 79°22′W), a ~8000 ha forest located ~45 km northwest of Rouyn-Noranda, in the Western Balsam fir-White birch Bioclimatic Subdomain (Robitaille and Saucier, 1998). Climate is cold continental with a mean (1961–1990) annual temperature of 0.8 °C and a mean annual precipitation of 857 mm, of which 25% falls as snow (Environment Canada, 1993). Mesic clay soils (Grey Luvisols) originating from glaciolacustrine deposits left by the postglacial lakes Barlow and Ojibway predominate in the region (Vincent and Hardy, 1977).

The SORTIE-ND light model was parameterized from field data for six tree species that range in shade tolerance from the very intolerant aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Ait.), to intolerant paper birch (*Betula papyrifera* Marsh.), mid-tolerant white spruce (*Picea glauca* [Moench] Voss), and tolerant to very tolerant white cedar (*Thuja occidentalis* L.) and balsam fir (*Abies balsamea* [L.] Mill.) (Burns and Honkala, 1990).

Successional relationships among these species on rich, mesic sites in the region have been described as typically involving successive rotations dominated by hardwoods, mixedwoods, and shade-tolerant conifers (Bergeron, 2000). Following stand-replacing disturbance (fire), shade-intolerant species such as jack pine, aspen and white birch form mixed or pure stands (Harvey et al., 2009). These stands of pioneer species develop into mixed compositions as more shade-tolerant species (fir, spruces and cedar) establish and grow into the canopy layer. As stands age, small-scale canopy disturbances such as gaps resulting from windthrow, stem senescence in the pioneer cohort or insect outbreaks, influence the structure and composition of stands that have been spared by fire (Haeussler et al., 2007; Harvey et al., 2009). Mature forests in the area are mainly dominated by balsam fir, with white spruce, black spruce (*Picea mariana* [Mill.] B.S.P.), white birch, and white cedar.

2.2. Parameterization of the SORTIE-ND light model for boreal mixedwood species

SORTIE-ND (version 6.09; Canham and Murphy, 2008) is a spatially explicit, individual-tree forest dynamics model in which light conditions can be predicted for any location in a plot based on the species, DBH (diameter at breast height [here defined as 1.35 m above-ground]) and location of trees, species-specific crown openness and allometric relations used to determine tree height and crown dimensions, and local sky brightness distribution (Canham et al., 1999). SORTIE-ND predicts light levels in terms of Gap Light Index (GLI), which specifies the percentage of direct and diffuse light transmission through canopy openings over a growing season (Canham, 1988). The SORTIE-ND light model has been parameterized and tested in a variety of forest types, including northern hardwood forests in northeastern America (Canham et al., 1994; Beaudet et al., 2002), northern temperate forests in western Canada (Canham et al., 1999), and hybrid poplar plantations (Paquette et al., 2008).

2.2.1. Tree height and crown allometry

In SORTIE-ND, individual tree crowns are represented as cylinders. Tree height (m) is described as a function of DBH (cm):

$$\text{Height} = 1.35 + (H_1 - 1.35)(1 - e^{-B \cdot \text{DBH}}) \qquad (1)$$

Eq. (1) produces a curve with an exponential approach to an asymptotic maximum height (H_1), while the exponential decay parameter B controls the steepness of the curve (Canham et al.,

Table 1
Parameter values (H_1, B) and their 95% confidence intervals for the tree height vs. DBH relationship (Eq. (1)). Also presented are the sample size, range of and mean DBH and height observed among sampled trees, R^2 values (mean corrected), and predicted height for a 5 cm DBH and a 30 cm DBH individual of each species. Species are listed in order of increasing shade tolerance based on Harvey et al. (2002).

Species	n	DBH (cm) min–max (mean)	Height (m) min–max (mean)	Parameter H_1	95% C.I. (min–max)	Parameter B	95% C.I. (min–max)	R^2	Height (m) of a 5 cm DBH tree	Height (m) of a 30 cm DBH tree
Aspen	330	2.2–78.0 (18.6)	2.8–35.3 (18.6)	27.2	26.2–28.3	0.070	0.064–0.076	0.766	9.0	24.0
Jack pine	79	9.7–44.5 (25.9)	14.5–27.5 (21.8)	23.9	22.7–25.0	0.102	0.079–0.124	0.347	10.4	22.8
Paper birch	142	2.0–53.4 (15.9)	3.9–29.2 (14.2)	20.5	19.0–21.9	0.088	0.073–0.104	0.682	8.2	19.1
White spruce	104	1.5–53.8 (22.4)	1.5–28.3 (16.4)	34.6	29.3–39.8	0.030	0.023–0.038	0.867	6.0	21.1
White cedar	227	1.0–53.0 (14.5)	1.4–19.7 (8.7)	18.8	17.6–19.9	0.046	0.040–0.051	0.926	4.9	14.4
Balsam fir	279	1.0–36.5 (9.2)	1.4–23.8 (8.9)	21.0[a]	–	0.064	0.061–0.067	0.872	6.7	18.1

[a] Fixed value based on Pothier and Savard (1998) and Grondin et al. (2000).

Table 2
Parameter values (C_1, a) and their 95% confidence intervals for the crown radius vs. DBH relationship (Eq. (2)). Also presented are the sample size, range of and mean DBH and crown radius observed among sampled trees, R^2 values (mean corrected), and predicted crown radius for a 5 cm DBH and a 30 cm DBH individual of each species. Note that tests of the model and simulations were performed using a C_1 value multiplied by 0.5, for all species, as described in Canham et al. (1999). Species are listed in order of increasing shade tolerance based on Harvey et al. (2002).

Species	n	DBH (cm) min–max (mean)	Crown radius (m) min–max (mean)	Parameter C_1	95% C.I. (min–max)	Parameter a	95% C.I. (min–max)	R^2	Crown radius (m) of a 5 cm DBH tree	Crown radius (m) of a 30 cm DBH tree
Aspen	342	2.0–78.0 (19.5)	0.2–4.9 (1.7)	0.180	1.150–0.210	0.766	0.715–0.816	0.722	0.62	2.44
Jack pine	85	9.7–44.5 (25.9)	0.1–3.2 (1.3)	0.014	0.000–0.028	1.369	1.083–1.656	0.522	0.13	1.47
Paper birch	190	2.0–53.4 (16.5)	0.3–4.7 (1.7)	0.452	0.354–0.551	0.498	0.425–0.570	0.500	1.01	2.46
White spruce	165	1.5–53.8 (23.2)	0.5–3.4 (1.6)	0.524	0.361–0.688	0.361	0.265–0.457	0.282	0.94	1.79
White cedar	247	1.6–53.0 (15.6)	0.2–3.2 (1.3)	0.399	0.349–0.449	0.468	0.427–0.510	0.711	0.85	1.96
Balsam fir	243	1.0–36.5 (11.2)	0.2–3.1 (1.2)	0.532	0.452–0.611	0.366	0.308–0.424	0.410	0.96	1.85

1999). Crown radius (m) is predicted from DBH (cm):

$$\text{Crown radius} = C_1 \cdot \text{DBH}^a \tag{2}$$

Crown depth (m), defined as the distance between the top and the bottom of the crown cylinder, is predicted from tree height (m):

$$\text{Crown depth} = C_2 \cdot \text{Height}^b \tag{3}$$

Trees were selected in closed forests, adjacent to recent gaps and in other locations where crowns could be easily seen (e.g., along edges of recent openings or roads) but not adjacent to old openings where crowns may have expanded significantly over time due to reduced competition. Tree height and height of crown base were determined using a clinometer, while crown radius was measured in the four cardinal directions and averaged for each tree. We supplemented our initial sample with a large dataset on tree height and crown allometry collected in plots described in Bergeron (2000). Least squares regression was used to determine the value of parameters in Eqs. (1)–(3). Non-overlapping 95% confidence intervals were considered to be an indication of a significant difference in parameters among species. For balsam fir, H_1 (Eq. (1)) could not be estimated from field data due to an insufficient number of large trees in our sample (Table 1), its value was therefore fixed at 21 m based on Pothier and Savard (1998) using a site index of 18 (Grondin et al., 2000).

2.2.2. Crown openness

Species-specific mean crown openness, defined as the fraction of sky that can be seen on average through the crown of an individual tree of a given species, was evaluated as described in Canham et al. (1999). One fisheye photo was taken per sampled tree using a tripod-mounted digital Nikon Coolpix 950 equipped with a FC-E8 fisheye lens, and positioned so that the tree crown could clearly be distinguished against the sky, with no overlap with neighbor tree crowns. As much as possible, fisheye photos were taken under uniform sky conditions. They were all analysed by the same person with the Gap Light Analyser (GLA v.2) (Frazer et al., 2000) using the procedure described in Astrup and Larson (2006) which involved digitizing the crown outline, thresholding the image, and calculating the ratio of white pixels to all pixels within the crown outline (a fraction ranging from 0 to 1 that corresponds to crown openness). After verifying that conditions for normality and homoscedasticity were met, crown openness was compared among species with a one-way analysis of variance (ANOVA) and a post hoc Tukey multiple comparisons test.

2.2.3. Local sky brightness distribution

For all simulations (Sections 2.3 and 2.4), we used a plot latitude of 48°30′N, a beam fraction of global radiation of 0.5, and a clear sky transmission coefficient of 0.65. The first and last days of the
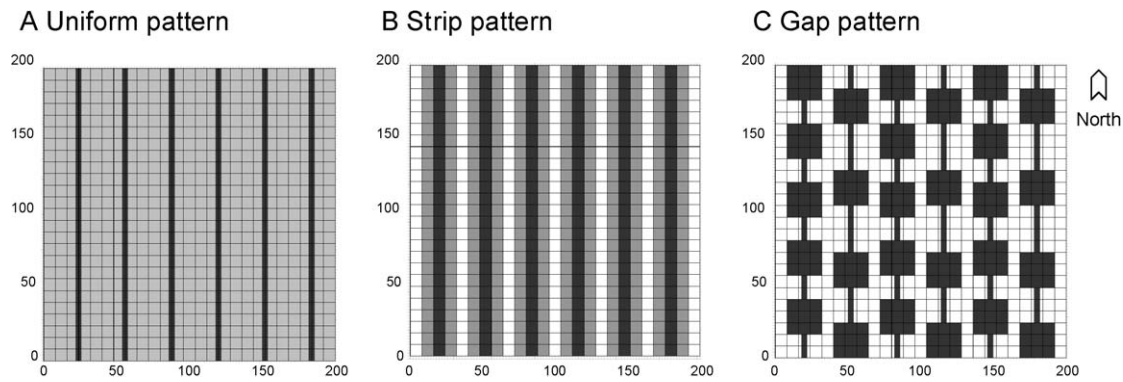
Table 3
Parameter values (C_2, b) and their 95% confidence intervals for the crown depth vs. tree height relationship (Eq. (3)). Also presented are the sample size, range of and mean height and crown depth observed among sampled trees, R^2 values (mean corrected), and predicted crown depth for a 5 m and a 15 m tall individual of each species. Species are listed in order of increasing shade tolerance based on Harvey et al. (2002).

Species	n	Height (m) min–max (mean)	Crown depth (m) min–max (mean)	Parameter C_2	95% C.I. (min–max)	Parameter b	95% C.I. (min–max)	R^2	Crown depth (m) of a 5 m tall tree	Crown depth (m) of a 15 m tall tree
Aspen	249	2.8–30.8 (19.1)	1.1–13.9 (6.9)	0.200	0.107–0.293	1.196	1.046–1.347	0.568	1.37	5.10
Jack pine	79	14.5–27.5 (21.8)	3.3–15.9 (7.2)	0.036	0.028–0.099	1.720	1.145–2.295	0.315	0.57	3.79
Paper birch	129	3.9–27.2 (13.9)	1.4–17.1 (6.8)	0.739	0.410–1.069	0.847	0.686–1.008	0.512	2.89	7.32
White spruce	92	4.1–28.3 (17.3)	2.0–24.5 (11.2)	0.630	0.382–0.877	1.010	0.881–1.139	0.812	3.20	9.71
White cedar	210	2.0–19.6 (9.0)	1.3–15.5 (5.7)	0.652	0.509–0.794	0.982	0.895–1.070	0.764	3.17	9.31
Balsam fir	194	1.8–23.9 (10.5)	0.6–19.8 (5.8)	0.345	0.252–0.437	1.188	1.091–1.284	0.826	2.33	8.61

Fig. 1. Schematic representation of the three patterns of tree removal, here illustrated for a removal rate of 45% BA. (A) Uniform partial cut (with 4-m skid trails); (B) strip pattern comprising 8-m wide trails, 8-m wide partially cut strips, and 8-m wide uncut strips; (C) gap pattern in which 4-m wide skid trails are locally enlarged to form $24\,m \times 24\,m$ openings ($576\,m^2$) in which a 100% removal is performed, with no harvest between trails and gaps. Gap size differs for the stand-level 30% and 60% removal rates (see text). Areas in white, grey and black indicate no harvest, partial harvest and 100% removal, respectively.

growing season were April 15th and September 15th, respectively. The modelled sky hemisphere was subdivided into 18 azimuthal and 12 altitudinal divisions, and the minimum solar angle was set to 45° from horizontal.

2.3. Model evaluation

2.3.1. Test #1: prediction of understory GLI in mapped stands

Gap Light Index (GLI) values predicted by SORTIE-ND (GLI_{pre}) were compared to light measured in three mapped plots. We used plots established in mixedwood stands (%BA ranging from 47% to 66% for aspen, 5% to 27% for paper birch, 4% to 28% for white spruce, and 4% to 11% for balsam fir) originating from fire in 1823 (plot 1) and 1847 (plots 2–3). Trees with DBH > 10 cm were mapped in plots 1 and 2, and DBH > 2 cm in plot 3. In plot 1, an experimental gap ($20\,m \times 20\,m$) was created in 1990. Fisheye photographs were taken along a $5\,m \times 5\,m$ grid over a $20\,m \times 20\,m$ (plots 1 and 2) and a $40\,m \times 80\,m$ area (plot 3). A buffer area at least 20 m wide was mapped around the sampled grids. Fisheye photographs were taken at ~3.5 m in plot 1 (above shrubs), and at ~1.5 m in plots 2 and 3. Although fisheye photographs were generally taken under overcast conditions, some photographs were overexposed and could not be used. In all, 60 fisheye photographs were analysed with GLA (v.2) to obtain observed GLI values (GLI_{obs}). To generate corresponding GLI_{pre} values for the test, SORTIE-ND was initialized with allometric parameters and crown openness values obtained in this study, a tree map for each plot, and the coordinates (x, y, z) at which

the fisheye photos had been taken. Note that we multiplied the C_1 parameter (Eq. (2), Table 2) by a scaling factor of 0.5, as suggested by Canham et al. (1999) since preliminary tests showed that this provided a better fit than an unadjusted C_1 value. We calculated the linear regression between GLI_{pre} and GLI_{obs} and used t-tests to determine if the slope and intercept differed significantly from 1 and 0, respectively.

2.3.2. Test #2: prediction of mean stand-level GLI in un-mapped stands

In this test, GLI_{pre} were compared to GLI_{obs} values obtained from fisheye photographs taken in stands that had been submitted to a wide range of harvest intensities (0%, 33%, 61%, and 100%) as part of the SAFE ("Sylviculture et aménagement forestier écosystémique") project in the LDRTF (Brais et al., 2004). This silvicultural trial was performed in aspen stands originating from a 1923 fire. Before harvesting, the mean BA was $43.1\,m^2\,ha^{-1}$ with 92.6% aspen and 3.3% of conifers. Five permanent plots were established per treatment, and a forest inventory of all stems (DBH > 2 cm) was performed before and after harvesting, which took place during the winter of 1998–1999 (Brais et al., 2004). Fisheye photographs were taken in September 1999, under overcast conditions at a height of 3 m (above the shrub layer) in each plot (Brais et al., 2004). We used the five GLI_{obs} values for each treatment in Block 1 (Brais et al., 2004). SORTIE-ND was initialized using parameters in Tables 1–3 and crown openness values, as well as with post-harvest tree density per species and DBH class from the above-mentioned sampling

Table 4
Pre- and post-harvest characteristics of the modelled stands.

Harvest pattern	Pre-harvest	Uniform			Strip			Gap		
Harvest rate (target) (%BA[a])	0	30	45	60	30	45	60	30	45	60
Overstory (DBH ≥ 9 cm)										
BA ($m^2\,ha^{-1}$)	39.3	27.7	21.6	15.5	28.1	21.7	18.1	28.0	21.1	16.7
Density ($n\,ha^{-1}$)	1424	1199	1096	937	1075	971	836	1025	751	604
Species composition (% BA)										
Aspen	63.3	53.7	40.8	17.3	60.3	48.6	38.5	62.4	64.6	63.2
Paper birch	1.7	2.1	2.7	3.8	1.9	2.4	2.9	1.7	1.7	1.7
White spruce	35.0	44.1	56.5	79.0	37.8	49.0	58.6	35.9	33.7	35.0
Understory (0 cm < DBH < 9 cm)										
BA ($m^2\,ha^{-1}$)	1.1	1.0	1.0	1.0	0.8	0.8	0.8	0.7	0.5	0.4
Density ($n\,ha^{-1}$)	826	732	732	732	635	635	635	578	435	340
Species composition (% BA)										
Aspen	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Paper birch	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.0
White spruce	67.0	66.6	66.6	66.6	67.3	67.3	67.3	67.0	68.6	66.6
Balsam fir	32.8	33.1	33.1	33.1	32.4	32.4	32.4	32.7	31.0	33.3

[a] BA: Basal area.

plots. Random coordinates were assigned to trees by SORTIE-ND. For the two partial cut treatments, we simulated skid trails by removing all trees in 4-m wide strips, one every 30 m, similar to Brais et al. (2004). For each treatment, SORTIE-ND generated GLI$_{pre}$ at 3 m and these GLI$_{pre}$ were compared to field-based GLI$_{obs}$ using t-tests.

2.4. Simulations varying the intensity and spatial pattern of harvest

An initial tree map file was created for a 4 ha plot (200 m × 200 m) based on inventory data from a mixedwood stand situated 25 km south of the SAFE research site. The initial BA was 39 m^2 ha^{-1}, with deciduous (mainly aspen) and coniferous species (mainly white spruce) accounting for 65% and 35% of the overstory BA, respectively (Table 4). The understory was almost exclusively comprised of conifers, mainly white spruce. Tree densities by DBH class and species were specified to SORTIE-ND, with tree positions randomly determined by the model.

The resulting tree map file was then modified according to nine silvicultural treatments resulting from the combination of three harvest rates (30%, 45% and 60% BA removal) and three harvest patterns (uniform, strips, gaps) (Fig. 1). In all cases, skid trails were explicitly located every 32 m. In the uniform partial cuts, all trees and saplings were removed in 4-m wide skid trails, and a partial cut of aspen (DBH > 9 cm) was performed between skid trails (Fig. 1A). A narrow strip harvest was simulated with 8-m wide trails in which all trees and saplings were removed, flanked by two 8-m wide strips in which aspen was partially harvested (Fig. 1B). An 8-m wide strip was also left uncut (Fig. 1B). A gap pattern was also tested in which 4-m wide skid trails were locally enlarged to form square or rectangular openings (Fig. 1C) (Robert, 2010). These openings were 256 m^2 (16 m × 16 m), 576 m^2 (24 m × 24 m), and 768 m^2 (24 m × 36 m) in size for the 30%, 45%, and 60% BA harvests, respectively. In simulated gap cuts, all saplings and trees were removed in skid trails and gaps, with no harvest in between. SORTIE-ND was used to predict GLI at 3 m above-ground along a 2 m × 2 m grid covering the entire 4 ha plots. We modelled light at 3 m because it reflects conditions that should influence post-harvest response of saplings. This choice is also supported by the fact that the tests of the model (Sections 2.3.1 and 2.3.2) mainly involved light conditions at such a height.

3. Results and discussion

3.1. Inter-specific variation in allometry and crown openness

Asymptotic height (H_1, Eq. (1)) ranged from 18.8 m for white cedar to 34.6 m for white spruce (Table 1). Aspen and jack pine had the highest predicted heights at both small and larger DBH, while white cedar had the lowest predicted heights at the same DBH (Table 1). The three intolerant species, jack pine, aspen and paper birch, had the three highest B values, indicating a faster approach to asymptotic height than for the more tolerant conifers (Table 1 and Fig. 2A). Such a trend was also reported by Canham et al. (1999) for species in British Columbia (BC). Rank order of species in terms of predicted height at various DBH (Fig. 2A) were in agreement with Sharma and Parton's (2007) and Peng's (2001) height vs. DBH models for boreal species in northern Ontario.

The two deciduous shade-intolerant species, aspen and paper birch, had the widest crowns, while shade-tolerant conifers had relatively wide crowns at small DBH, but narrower crowns than deciduous species at larger DBH (Table 2 and Fig. 2B). In contrast, Canham et al. (1999) reported that more shade-tolerant conifer species had overall wider crowns than intolerant species.
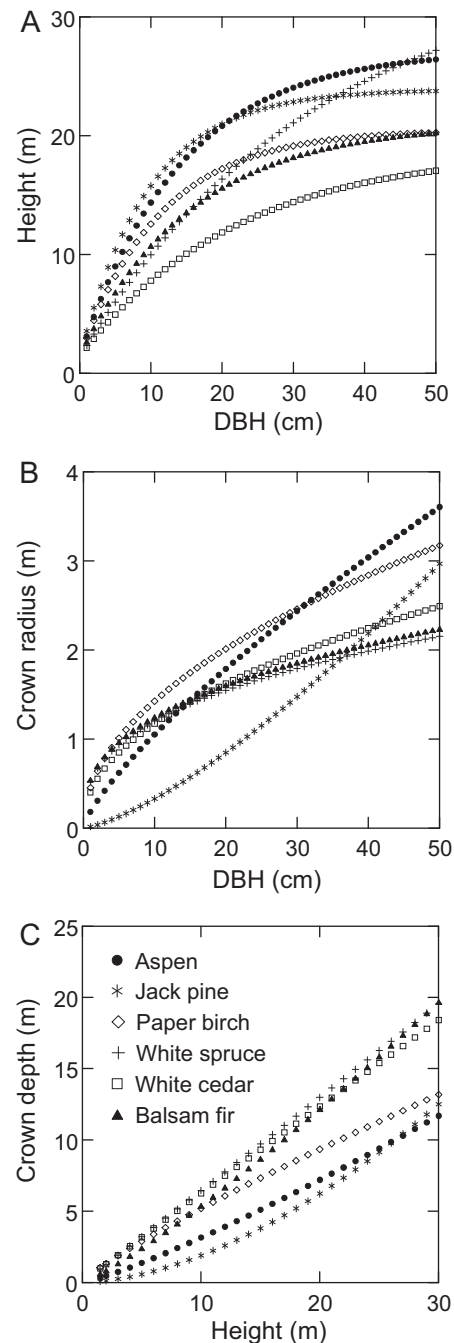

Fig. 2. Predicted (A) tree height as a function of DBH (Eq. (1), parameters in Table 1); (B) crown radius as a function of DBH (Eq. (2), parameters in Table 2); and (C) crown depth as a function of tree height (Eq. (3), parameters in Table 3) for six tree species in the Lake Duparquet Forest study area.

Less shade-tolerant species (mainly jack pine and aspen, but also paper birch) tended to have a lower crown depth than more tolerant conifers (Table 3 and Fig. 2C). The tendency for tolerant species to have deeper crowns than shade-intolerant species has also been observed for northern hardwood species (Canham et al., 1994; Beaudet et al., 2002), but not among BC species (Canham et al., 1999).

Crown openness differed among species (ANOVA: $P < 0.001$, $F = 10.692$, df = 5, $n = 206$) with mean values ranging from 0.101 for paper birch to 0.163 for aspen (Fig. 3). These values are in the same range as those reported in studies that used a similar methodology to quantify crown openness (Canham et al., 1999; Beaudet
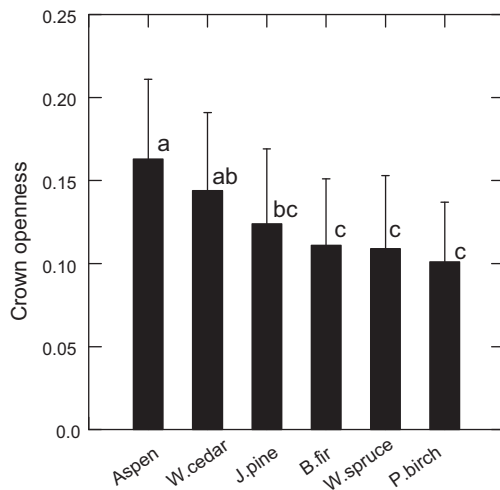
Fig. 3. Mean (±1 SD) crown openness for trembling aspen (mean = 0.163; $n = 38$), white cedar (0.144; $n = 31$), jack pine (0.124; $n = 36$), balsam fir (0.111; $n = 33$), white spruce (0.109; $n = 37$), paper birch (0.101; $n = 31$). Different letters indicate significant differences ($P < 0.001$) based on an ANOVA and a Tukey HSD test.

et al., 2002; Astrup and Larson, 2006). However, unlike elsewhere (Canham et al., 1994, 1999; Beaudet et al., 2002), crown openness did not vary with shade tolerance (Fig. 3).

3.2. Model evaluation

In mapped plots (test 1), we found a significant relationship ($P < 0.001$) between GLI_{pre} and GLI_{obs} (Fig. 4A). However, although the intercept was clearly not different from 0 (*t*-test, $P = 0.182$), the slope coefficient of 1.271 was only marginally not different from 1 (*t*-test, $P = 0.051$). Under higher light conditions, a few points occurred above the 1:1 expectation (Fig. 4A) suggesting that SORTIE-ND might tend to overestimate light levels above ~30% in the study stands. However, most of these points corresponded to locations in plot 1, a 400 m^2 artificial gap created >10 years prior to taking the photographs and mapping the trees. Since only trees >10 cm in DBH were mapped in that plot, it is possible that several small trees may have intercepted light in the gap without being represented in the simulated plot. We therefore suggest that the discrepancy between predictions and observations above 30% GLI may partly be attributable to an incomplete sampling of the trees that would have intercepted light in plot 1. This explanation is supported by the fact that SORTIE-ND did not overestimate light transmission above ~30% in our second validation test.

The R^2 of 0.6 for the relationship between predicted and observed GLI (Fig. 4A) was similar to that reported by Beaudet et al. (2002) in an earlier test of SORTIE in northern hardwood forests. While this may not be considered an excellent fit, it is probably unavoidable given the simplified, cyclinder-shaped tree crowns represented in SORTIE-ND and the relatively narrow light range simulated. Using radially symmetric crowns in a light model prevents capturing the asymmetry of natural crowns, and this has been shown to impact on the accuracy of light predictions (Piboule et al., 2005). Another source of error results from tree and crown dimensions in the simulated plots being derived from allometric equations rather than being measured for each tree (e.g., Koop and Sterck, 1994). This implies that deviation of individual crowns from average allometry cannot be accounted for in light simulations (Vieilledent et al., 2010), nor than the presence of tree lean or branch breakage. Gersonde et al. (2004) explicitly tested the effect of using crown radius, crown length and tree height derived from DBH rather than measuring values for each tree. They showed that with the tRAYci model this led to a decrease in R^2 from approxi-

mately 0.75 to 0.6, the latter being equivalent to the fit obtained in this study. Finally, the crown radius and crown depth models (Eqs. (2) and (3)) are relatively simple and do not account for the influence of neighborhood characteristics (e.g., density) on crown dimension (Thorpe et al., 2010).

In the un-mapped plots (test 2), SORTIE-ND light predictions (GLI_{pre}) did not differ from observations (GLI_{obs}) in three of the four treatments (Fig. 4B). In the control stand, however, SORTIE-ND underestimated light levels with a mean GLI_{pre} of 5.0% compared to a mean GLI_{obs} of 15.6%. Note that the GLI_{obs} were obtained from fisheye photos taken in late September (Brais et al., 2004). Although we found no clear evidence of it in the fisheye photographs, it remains possible that at that time of the year, leaves may have started to discolour and fall.

Despite the non-negligible difference between GLI_{pre} and GLI_{obs}, the light levels predicted in the control stand are not completely
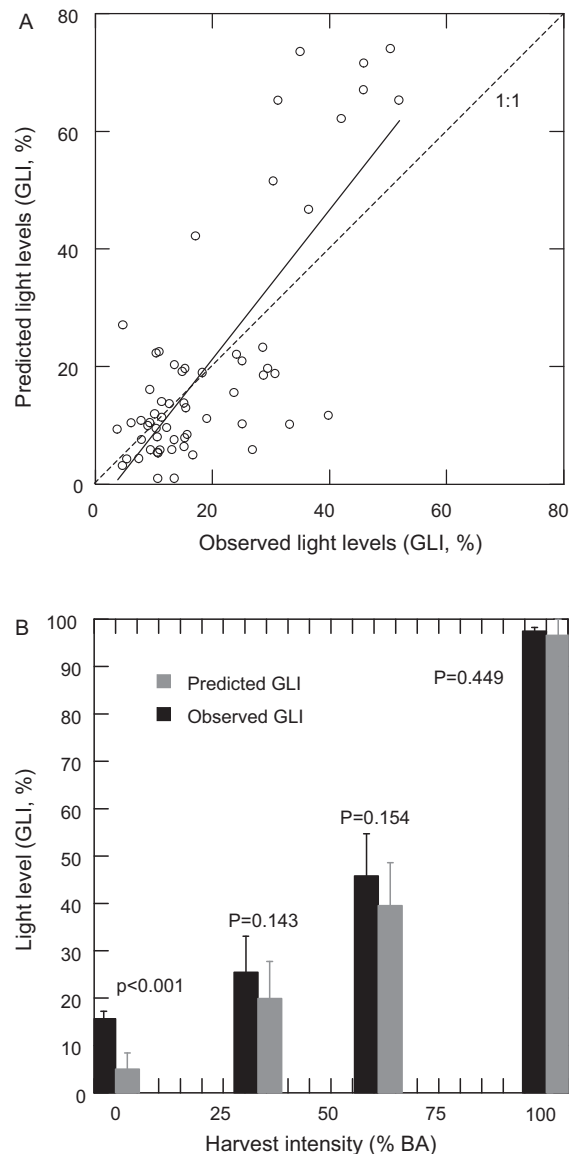

Fig. 4. Results of the two validation tests: (A) Relationship between predicted light levels (GLI_{pre}) and light levels estimated from fisheye photographs taken in three mapped plots (GLI_{obs}). The dotted line corresponds to a 1:1 relationship, while the full line corresponds to the regression $GLI_{pre} = 1.27\,GLI_{obs} - 4.18$, $R^2 = 0.600$, $n = 60$; (B) Comparison of predicted light levels (mean ± 1SD) (GLI_{pre}) and light levels obtained from fisheye photographs (GLI_{obs}) taken in four un-mapped plots. The four treatments were a control, a 33% and 61% partial cut, and a clearcut.
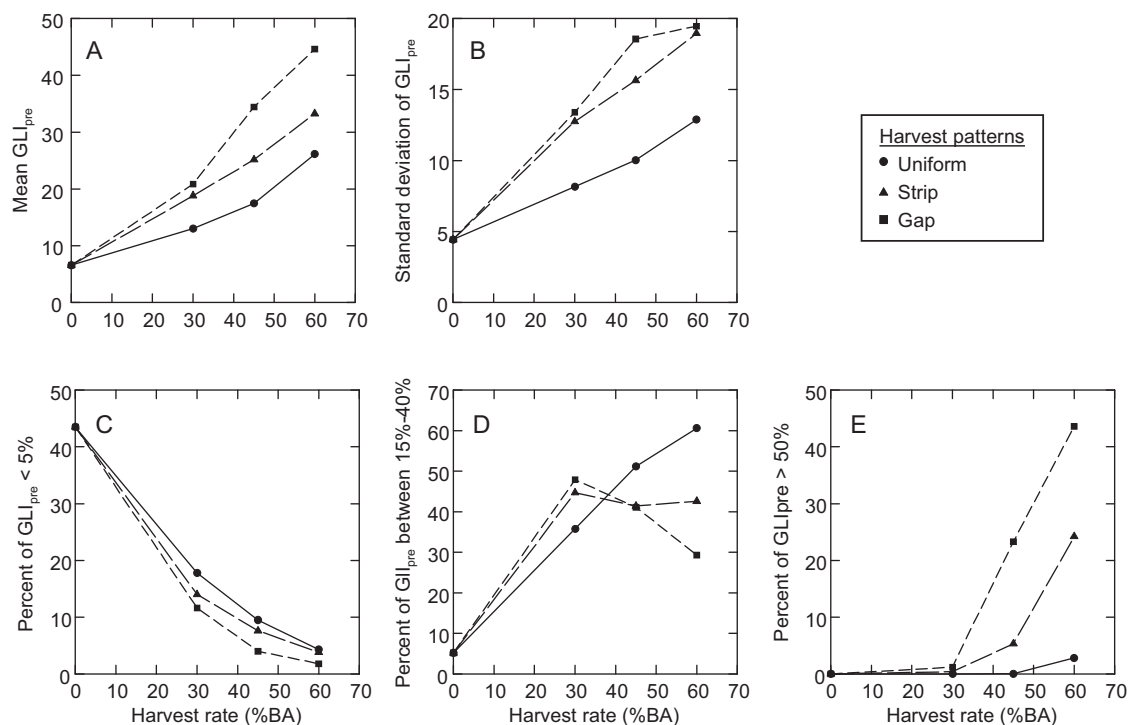
Fig. 5. Variation in (A) the mean predicted light levels (GLI$_{pre}$); (B) standard deviation of GLI$_{pre}$, (C) percentage of microsites with GLI$_{pre}$ < 5%; (D) <15% GLI$_{pre}$ < 40%; and (E) GLI$_{pre}$ > 50%, as a function of the intensities and spatial patterns of harvest.

unreasonable. For instance, Lapointe et al. (2006) reported an average light transmission of 7.7% at the same site, for measurements made at 0.75 m above-ground. Messier et al. (1998) and Aubin et al. (2000) also reported lower light levels than in Brais et al. (2004), i.e., on average 9–10% in closed-canopy aspen-dominated stands from the same area. An alternative explanation to the discrepancy between GLI$_{pre}$ and GLI$_{obs}$ is that the simplified representation of tree crowns in SORTIE-ND – with dimensions derived from allometric relations – might have contributed to a possible underestimation of light conditions under closed canopy conditions. Vieilledent et al. (2010) showed that individual variability in tree allometry has a substantial impact on light transmission in forest understories; when it was ignored (i.e., when average allometry was used to model individual trees—as was the case in our simulations), it led the light model SamsaraLight (Courbaud et al., 2003) to underestimate light levels under closed canopy conditions. Nevertheless, since the simulations in this study focus on partial cuts, i.e., conditions under which SORTIE-ND predictions were accurate, we proceeded with the simulations. However, further testing would be relevant to better understand the cause of the discrepancy between GLI$_{pre}$ and GLI$_{obs}$ in the uncut treatment.

3.3. Simulations varying the intensity and spatial pattern of harvest

3.3.1. Effect on light conditions

Prior to harvesting, GLI$_{pre}$ were low in the modelled stand, i.e., on average 7% (Fig. 5A) with ~45% of values <5% (Fig. 5C). The maximum GLI$_{pre}$ was 29%, and the frequency distribution of GLI$_{pre}$ was markedly right-skewed (Fig. 6A). Light levels predicted by SORTIE-ND in the pre-harvested stand were similar to those reported by Messier et al. (1998) for mixed stands in the same region (i.e., on average 7.2%), and in the same range as those observed by Lieffers and Stadt (1994) in western aspen-spruce mixedwood stands with a 20–80% deciduous proportion (i.e., ~5–12%).

Even the lowest level of removal (30% BA) markedly affected light conditions, with mean GLI$_{pre}$ ranging from two to three times greater than in the pre-harvest stand, depending on harvest spatial pattern (Fig. 5A). The 30% removal cuts, regardless of harvest pattern, substantially decreased the proportion of microsites with GLI$_{pre}$ < 5%, from 45% pre-harvest to less than 18% post-harvest (Fig. 5C), however, the 30% removal cuts created virtually no microsites with GLI > 50% (Fig. 5E).

As expected, given the well-known negative relationship between stand BA and light transmission (e.g., Palik et al., 1997; Comeau, 2001; Sonohat et al., 2004; Comeau et al., 2009; Hale et al., 2009), mean light levels increased with increasing rate of tree removal (Fig. 5A). However, mean light levels also clearly varied as a function of the harvest pattern for a given harvest rate, and this variation tended to increase in magnitude with increasing rate of removal (Fig. 5A). Overall, increasing the removal rate had less impact on light conditions with a uniform harvest, and a more marked effect in the gap cuts (Fig. 5). Conditions created by a narrow strip cut were generally situated between the two other types of cuts (Fig. 5).

The amount of variability in light levels was also affected by the rate and spatial pattern of harvest (Fig. 5B). Variability increased with increasing rate of removal, but the magnitude of the increase was lower in uniform cuts than in gap and strip cuts which were similar (Fig. 5B). The tendency for light levels to increase and become more variable with increasing harvest aggregation (i.e., from uniform to gap cuts) corroborates field observations in Battaglia et al. (2002). A greater amount of variance associated with decreasing canopy cover and increasing aggregation has also been reported by Martens et al. (2000).

The frequency distributions of light levels differed markedly depending on the rate and pattern of harvest (Fig. 6). Uniform cuts led to narrower distributions of light levels than strip and gap cuts, and had a right-skewed distribution under all harvest rates (Fig. 6). The strip harvests had distinctly bimodal distributions with the left peak (corresponding to more shaded conditions) more pronounced
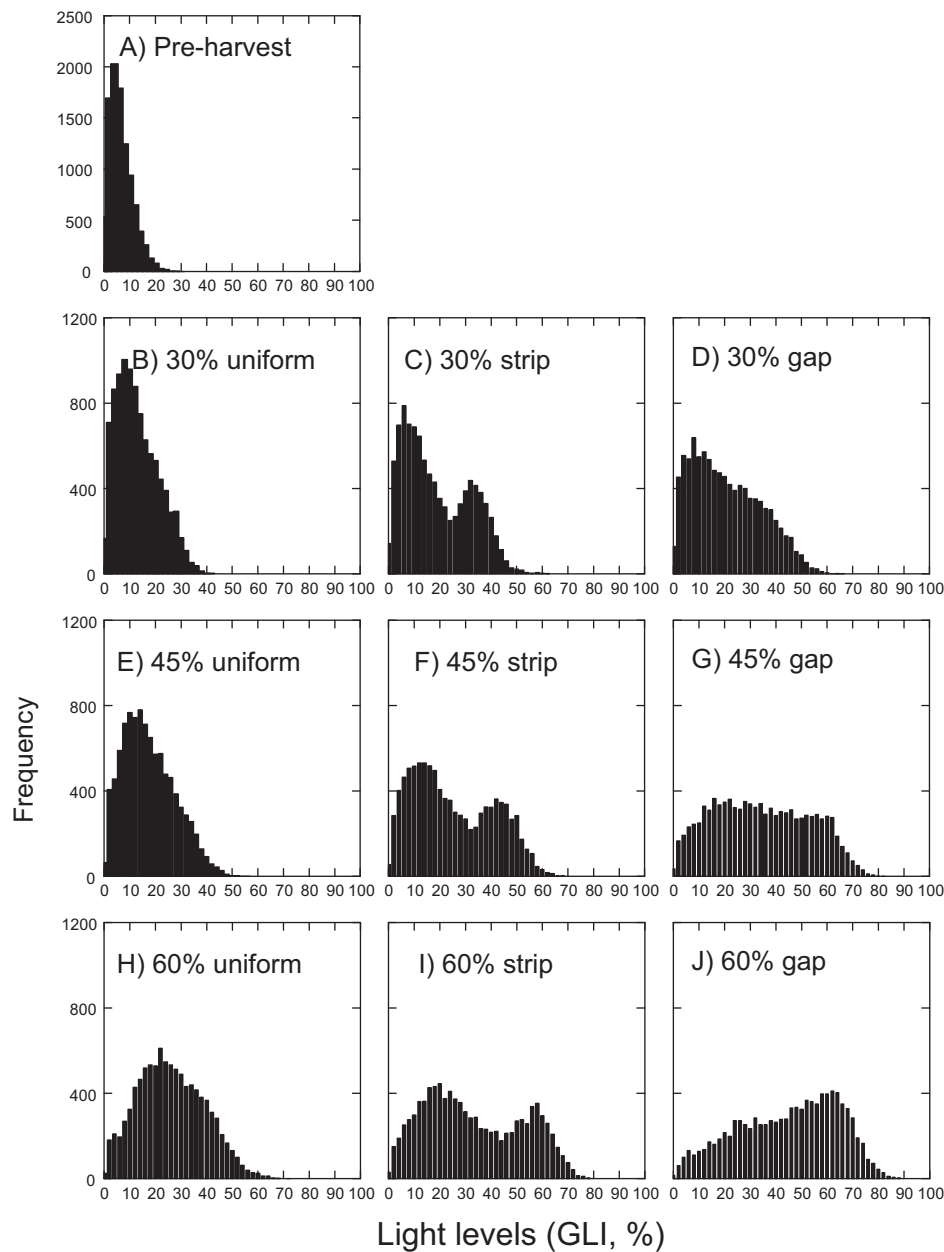
Fig. 6. Frequency distribution of light levels predicted at 3 m above-ground under the pre-harvest and nine post-harvest scenarios that resulted from the combination of three harvest rates, expressed in %BA, and three spatial patterns of tree removal (see Fig. 1). Light levels were predicted by SORTIE-ND along a 2 m × 2 m grid covering 4 ha-modelled plots. Note that the scale of the *y*-axis is different for panel A (pre-harvest) compared to other panels.

than the right-one (corresponding to higher light conditions) in the lower intensity cuts (Fig. 6). In the gap cuts, the frequency distribution of light levels varied from a right-skewed distribution for the 30% cut, to a left-skewed distribution for the 60% cut (Fig. 6).

The spatial distribution of light levels was clearly influenced by the harvest pattern (Fig. 7). In the uniform partial cuts, the relatively narrow 4-m wide skid trails had a noticeable impact on light conditions (Fig. 7). They allowed light levels to locally reach GLI of 15–35% in the 30% cut, GLI of 20–40% in the 45% cut, and GLI of 40–50% in the 60% cut (Fig. 7). Skid paths are almost inevitably present in the field, but only rarely represented in modelled harvested stands (e.g., Sprugel et al., 2009). In gap cuts, the expected north–south variability in light conditions (Canham, 1988) is observable in the simulated gaps, with higher light levels in the northern than in the southern part of gaps (Fig. 7). Light levels reached >45% in the north-central part of most of the ~250 m^2 gaps in the 30% gap cut; they

reached >60% in most of the ~575 m^2 gaps in the 45% gap cut; and >70% of the ~770 m^2 gaps in the 60% gap cut (Fig. 7).

3.3.2. Management implications

Post-harvest regeneration depends on multiple environmental factors including the availability of light, water, and soil nutrients, micro-climatic conditions, and seedbeds (Blanco et al., 2009; Martin-DeMoor et al., 2010). While light conditions alone clearly do not determine regeneration response following harvesting, they remain a key factor (e.g., Lapointe et al., 2006), and a factor that can be manipulated through silvicultural interventions (Lieffers et al., 1999). Because of inter-specific differences in response to light, managing light intensities through variations in the intensity and patterns of tree removal can create conditions that will favour the recruitment, growth and survival of some species more than others (Messier et al., 1999). It is therefore possible to identify intervals
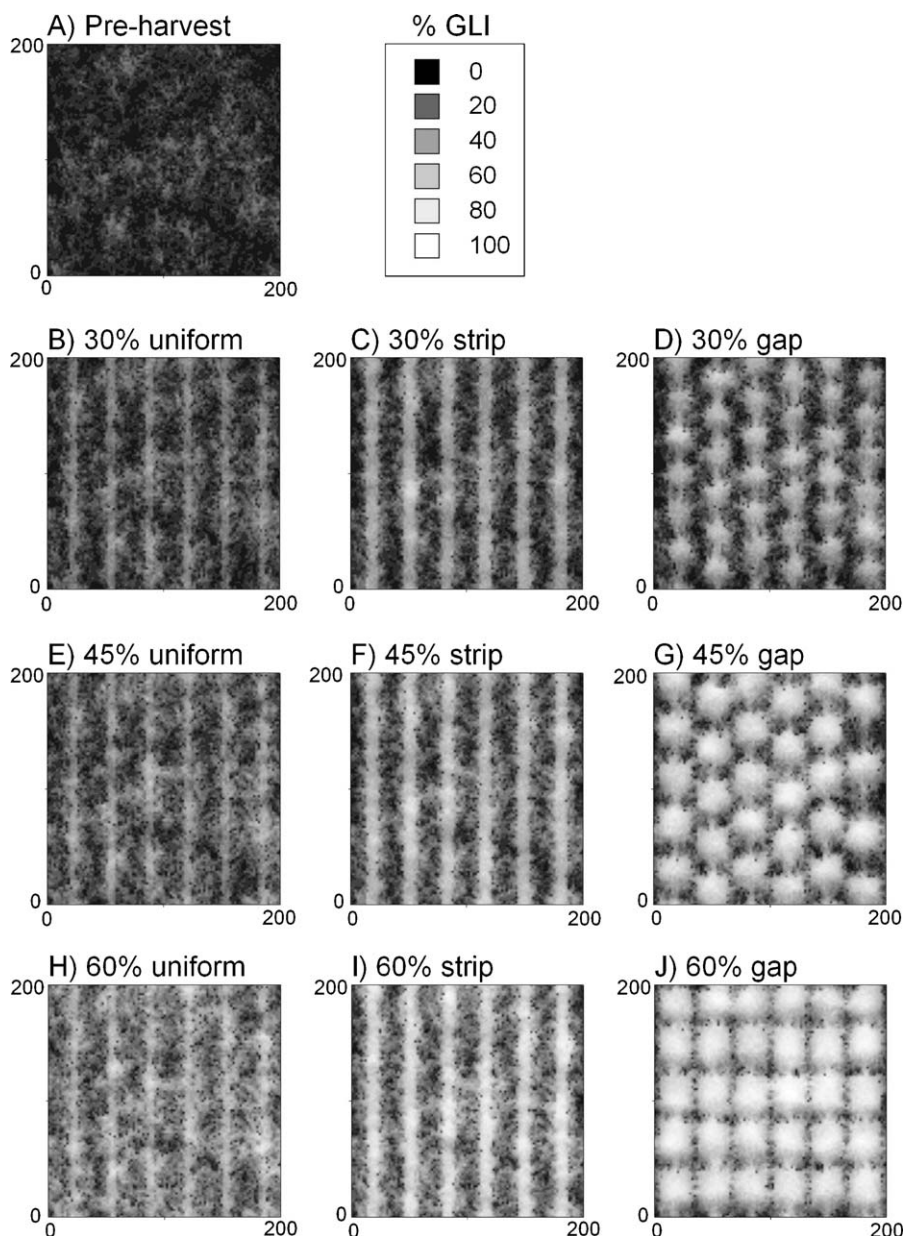
Fig. 7. Spatial distribution of light levels (%GLI) predicted at 3 m above-ground along a 2 m × 2 m grid in the pre-harvest (A) and nine post-harvest modelled plots (4 ha) resulting from the combination of three harvest rates: 30% (B–D), 45% (E–G), and 60% (panels H–J); and three spatial patterns of harvest: uniform with skid trails (B, E and H), strip (C, F and I), and large gaps (D, G and J).

of light conditions that provide an environmental advantage for some species over others, and to use light model simulations to determine which silvicultural treatments best generate the desired light conditions (Comeau, 2001; Mizunaga, 2007). We illustrate this below with examples relevant to boreal mixedwood silviculture.

If the silvicultural objective is to accelerate the transition from an early-successional aspen stand to a later-successional mixedwood stand with a harvest removal rate in the range of 45–60% BA, then our results suggest that uniform cuts might be more appropriate than the more aggregated strip and gap cuts to favour spruce and fir over aspen. Among all treatments, the 45% and especially the 60% uniform cuts were those which generated the greatest proportion of microsites receiving moderately low light conditions (here defined as GLI$_{pre}$ between 15% and 40% based on Lieffers and Stadt, 1994) (Figs. 5 and 6). These light conditions would be high enough to allow a noticeable increase in growth among shade-tolerant conifers, while not being elevated enough to trigger high densi-

ties and growth of aspen suckers (Lieffers and Stadt, 1994; Messier et al., 1999; Gendreau-Berthiaume, 2010). Our simulations indicate that the proportion of microsites with light conditions within such a range (i.e., 15–40%) was greatest in the 60% uniform cut, followed by the 45% uniform cut (Fig. 5D). Moreover, the uniform partial cuts almost never created high light conditions (GLI$_{pre}$ > 50%, Fig. 5E), which are expected to be more favourable to shade-intolerant species. For instance, sapling radial growth data from our study area indicate that aspen starts to outgrow white spruce and balsam fir above ∼50% GLI (Poulin and Messier, 2006). Chen and Popadiouk (2002) suggested that light levels higher than 40% are required for aspen establishment and Bourgeois et al. (2004) concluded that a ∼60% removal rate, through a uniform harvest pattern, could contribute to accelerate the transition from aspen toward mixedwood stands.

If a lower removal rate is to be used (e.g., 30% BA) to accelerate the transition from an aspen to a mixedwood stand, then

our results indicate that strip and gap cuts might be preferable to a uniform partial cut. Certainly at such low removal rates, some kind of gap or strip cutting approach presents fewer operational constraints than a diffuse, uniform harvest. With a 30% removal rate, strip and gap cuts generated the greatest proportions of GLI$_{pre}$ between 15% and 40% (Fig. 5D). The 30% uniform partial cut created slightly more shaded conditions (Figs. 5 and 6), less favourable to increased growth among pre-established shade-tolerant conifers (Parent and Messier, 1995; Claveau et al., 2002). More shaded conditions might even compromise regeneration survival for some species (e.g., below 8% for white spruce: Lieffers and Stadt, 1994), especially among larger saplings (Kneeshaw et al., 2006). Moreover, at such a low removal rate (i.e., 30% BA), the more aggregated strip and gap harvests did not generate light conditions >50% (Fig. 5E), and are therefore not expected to be overly favourable to the development of intolerant competitors such as aspen.

Although the general trends that emerge from our simulations regarding the effect of variation in the rate and spatial pattern of harvest would be expected to hold among similar stands, the specific recommendations we present should be considered with the following points in mind. First, mixedwood stands are diverse by nature and often structurally complex, and light conditions may vary greatly among stands due to differences in stand structure and species composition (Barkman, 1992; Messier et al., 1998). Second, our simulations are believed to be representative of the light conditions immediately after harvest, but they do not account for the dynamic vegetation response that is generally observed over time after harvesting (Brais et al., 2004; Man et al., 2008). Finally, the specific light values that were used as thresholds to identify the intervals of light conditions to be promoted or avoided through silvicultural interventions were selected based on specific publications. These thresholds could arguably differ somewhat as a function of a number of factors including site productivity and region (Wright et al., 1998), and depend on the variable considered (e.g., photosynthetic response, height growth, radial growth, biomass increment) (Messier et al., 1999).

4. Conclusions

Our study demonstrates that spatially explicit light models can be useful tools to improve our understanding of how different silvicultural prescriptions can influence post-harvest light regimes, and ultimately, regeneration success. More specifically, the simulations performed in this study allowed quantification of the impact of a range of harvest intensities on understory light conditions, but perhaps more importantly highlighted the marked differences that are generated in terms of understory light levels when the spatial pattern of tree removal is modified in a partial harvest. Our results clearly showed that harvesting in a stand does not necessarily increase light transmission proportional to the reduction in BA; the spatial arrangement of the residual trees (and hence the spatial pattern of harvest) also plays a very important role (Battaglia et al., 2002; Sprugel et al., 2009). Overall, simulation results indicated that increasing the removal rate had less impact on light conditions with a uniform harvest, and a more marked effect in the more aggregated harvests. This suggests that higher harvest rates can be applied in uniform harvest patterns while still maintaining light levels below a threshold preferred by shade-intolerant species (e.g., aspen). Although uniform or dispersed partial harvesting is more difficult operationally, the higher volume removals may compensate for potentially higher harvest costs. This illustrates how a better understanding of the interactions between spatial patterns of harvest and rates of tree removal can affect light conditions (and subsequent stand development) and provide opportunities for designing silvicultural prescriptions that are better suited to meet a variety of management objectives.

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