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Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec

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Abstract

Single-tree selection cutting is sometimes believed to be similar to the natural gap disturbance regime of hardwood forests, but few studies have specifically compared the compositional and structural characteristics of old-growth hardwood stands, undergoing natural gap dynamics and hardwood stands previously subjected to partial cuts. This study characterized and compared the composition (saplings and trees) and structure (gaps, foliage distribution, tree diameter and density, snags and coarse woody debris) of old-growth stands (OG), 12-year-old selection cuts (SC), and 28–33-year-old diameter-limit cuts (DLC) in sugar maple (*Acer saccharum*)-dominated northern hardwood stands.

Results showed marked structural differences between OG and harvested stands, with stronger differences between DLC and OG than between SC and OG. The synchronized formation of numerous canopy openings in harvested stands induced a massive post-harvest recruitment of advance regeneration in both SC and DLC that created a dense foliage layer in the understory. Large living trees (dbh $>$ 39.1 cm) and defective trees were less numerous in SC than OG, which can have a detrimental impact on species dependent on these structural elements, and on the future availability and characteristics of coarse woody debris. Relatively few compositional differences were noticed among stand types, although a greater proportion of mid-tolerant species was found in the post-harvest recruitment cohorts of harvested stands compared to OG, and a lower proportion of beech (*Fagus grandifolia* Ehrh.) saplings was observed in DLC compared to OG and SC.

We argue that even if selection cutting is closer to the natural disturbance regime of hardwood forests than diameter-limit cutting, and therefore representing progress toward the development and implementation of a natural-disturbance-based management, a recurring application of selection cutting might lead to a homogenization of forest structure and composition, a reduction of key structural features and a reduction in biological diversity at both the stand and landscape scales. Some management recommendations are proposed.

Keywords: Northern hardwood; Old-growth; Selection cut; Diameter-limit cut; Natural disturbance; Gaps; Foliage cover; Snags; Coarse woody debris

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1. Introduction

One of the approaches proposed for implementing ecosystem management is to learn from the study of natural disturbance regimes and to use that knowledge for managing forests in order to minimize the ecological "distance" between managed and natural systems. It is thought that the probability of conserving the majority of the attributes, processes and species characteristic of natural ecosystems would be enhanced by the development and implementation of a natural-disturbance-based approach to forest management (Attiwill, 1994).

If compared to natural disturbance regimes, disturbances associated with forest management differ in their rate of occurrence, extent, severity (Bergeron et al., 2002) and synchronicity. In natural systems, disturbances are known to play a major role in determining patterns of recruitment, growth and mortality, as well as associated structural patterns observed in forests (e.g. Bormann and Likens, 1979; Runkle, 1984, 1985a,b).

In the hardwood forests of northeastern North America, the natural disturbance regime is mainly characterized by the regular death and fall of branches, and single canopy trees or small groups of trees that create gradual or sudden openings in the canopy, (Bormann and Likens, 1979; Runkle, 1985a). This disturbance regime is known as the micro-gap regime. Runkle (1982, 1985a) reported that the average rate of gap creation in old-growth mesic forests of the eastern United States was about 1% of total land area per year, ranging from 0.5 to 2%/year.

In the hardwood forests of Quebec, single-tree selection cutting has been the most widely used harvesting system since the early 1990s (Bédard and Majcen, 2003). It is believed that this silvicultural system is similar in some ways to the natural micro-gap regime (Majcen, 1994; Jones and Thomas, 2004) since it creates single- and multiple-tree canopy openings affecting approximately 30% of the initial basal area, with a return interval of approximately 25 years, i.e. a mean rate of harvest equivalent to the expected periodic net increment.

Many recent studies have assessed the impact of partial harvesting in hardwood stands, by focusing on particular features such as: snag and coarse woody debris (CWD) abundance (Gore and Patterson, 1986; Goodburn and Lorimer, 1998; Doyon et al., 1999; Hale et al., 1999; McGee et al., 1999; Fraver et al., 2002); tree size and structure (Hale et al., 1999; McGee et al., 1999; Solomon and Grove, 1999); gap characteristics (Kimball et al., 1995; Beaudet and Messier, 2002), light profiles (Beaudet et al., 2004); tree species composition (Majcen, 1995; Hale et al., 1999; Solomon and Grove, 1999); tree growth (Majcen, 1995; Bédard and Majcen, 2003; Jones and Thomas, 2004); the biodiversity of various groups of organisms (Bourque and Villard, 2001; DeBellis et al., 2002; Moore et al., 2004). In this study, a more global approach was used to characterize and compare many structural and compositional features of old-growth hardwood stands (OG) modeled under the micro-gap regime, and two types of partially cut stands. Since selection cutting has only relatively recently been widely implemented in Quebec, diameter-limit cuts (DLC), a form of partial cutting that has been widely used in the past (Bédard and Majcen, 2003), were also included in our comparison. This allowed us to assess the forest characteristics most susceptible to recover in the mid-term, and the compositional and structural legacies from that former type of harvesting.

Compared to the natural micro-gap regime, partial harvesting systems imply, among others: (1) a temporal synchronization of canopy opening and (2) a removal of large quantities of wood. The regeneration process driving the future stand composition and dynamics is influenced by canopy openings (Runkle, 1984). The rate of canopy gap formation and gap characteristics (size and spatial distributions) will thus influence the structure and successional path of the future stand (Runkle, 1985b). The micro-gap regime is a type of small-scale disturbance that induces local changes in resource availability, including light conditions, thereby promoting the recruitment and growth of regeneration in a particular location, at a particular moment. At the stand scale, this process of gap formation and regeneration response increases the structural heterogeneity through the formation of a mosaic of patches of vegetation at various ages and growth phase (Runkle, 1984). The harvesting-intensity-to-return-interval ratio of the current selection cutting regime in Quebec is similar to the natural gap formation rate (about 1% area/year). However, harvesting simultaneously affects large expanses of forests and therefore results in the synchronized formation of numerous canopy openings. Such a phenomenon does not correspond to the spatio-temporal pattern of gap formation under the natural micro-gap regime. It should be noted, however, that some natural disturbances, such as heavy ice storms, moderate blowdowns or low-severity fires might possibly impact the forest canopy and influence the regeneration dynamics similar to partial cutting. These more intense disturbance events occur in northeastern hardwood forests and play an important role in their natural dynamics (Lorimer and Frelich, 1994), but are far less frequent and/or affect relatively smaller fractions of the landscape compared to the micro-gap regime. The focus of this study were forests shaped by the micro-gap regime in their recent history.

Large and defective living trees as well as dead wood, whether standing (snags) or downed (stumps, coarse woody debris (CWD)), have been recognized as key structural features for numerous species in all forest ecosystems (Harmon et al., 1986; Hunter, 1990). Their roles are almost as diverse as their users; in the North American Northeast, more than 25% of forest wildlife species are associated with or dependent on some of these structural elements (DeGraaf et al., 1992). In addition to being involved in carbon budgets and nutrient cycling, dead wood provides nesting, denning, perching, sheltering, breeding and foraging sites for many vertebrates and invertebrates, as well as germination and growth substrate for many fungi, bryophytes and vascular plants (Harmon et al., 1986).

The main objective of this study was to compare OG and harvested northern hardwood stands to determine to what extent managed stands differ from unmanaged stands in terms of tree species composition and structural characteristics. More specifically, it was hypothesized that, compared to OG, managed stands would have a greater fraction of their area under gaps, a higher proportion of shade-intolerant and mid-tolerant species, and a more homogeneous horizontal distribution of foliage cover associated with a higher density of saplings. Also, because logging involves the removal of live trees that would potentially become

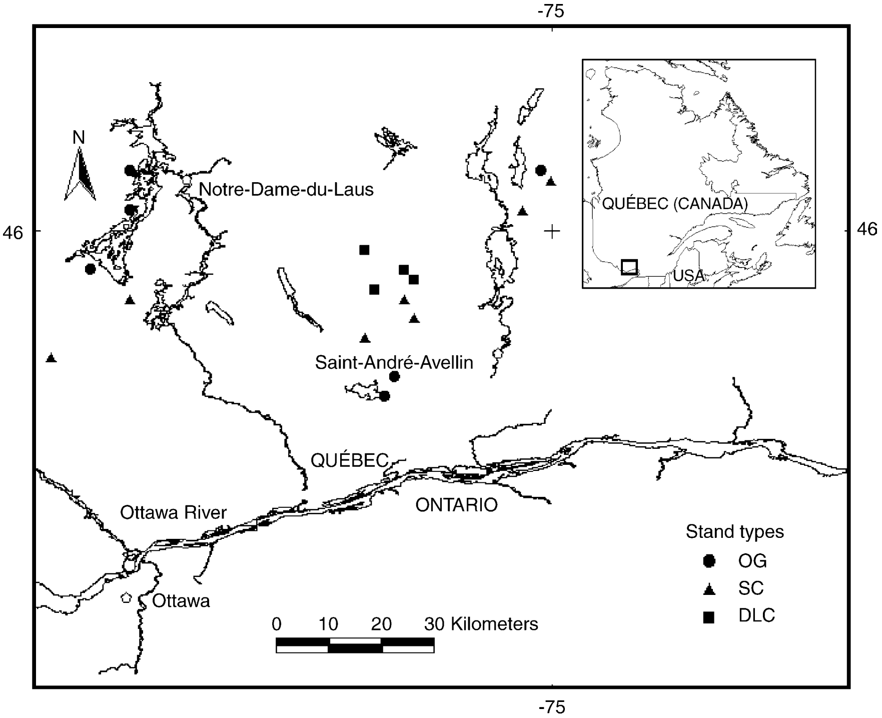


Fig. 1. Study area showing location of old-growth (OG, $n = 6$), selection cut (SC, $n = 7$) and diameter-limit cut stands (DLC, $n = 6$). Since DLC were very close to each other, they do not all appear separately on the map.

large and/or defective trees, and eventually snags and CWD, it was also hypothesized that these structural elements would be less abundant in harvested stands.

2. Methods

2.1. Study area and site selection

Sampling was carried out from June to August 2002 in the Outaouais region, in southwestern Quebec, Canada (45°43′–46°06′N; 75°00′–75°51′W) (Fig. 1). The region is mantled by thin glacial till deposits and bedrock outcrops are common. Relief ranges from 350 to 400 m above sea level (Robitaille and Saucier, 1998). Mean annual temperature ranges from 2.5 to 5 °C, and mean annual precipitation is about 1000 mm, of which 25% falls as snow (Robitaille and Saucier, 1998). Stands were dominated by sugar maple (*Acer saccharum* Marsh) and American beech (*Fagus grandifolia* Ehrh.) with varying but small amounts of yellow birch (*Betula alleghaniensis* Britton), ironwood (*Ostrya virginiana* Mill.), basswood (*Tilia americana* L.) and eastern hemlock (*Tsuga canadensis* Marsh).

Nineteen study sites were chosen: six OG, seven selection cut stands (SC) harvested in 1990 and six diameter-limit cuts (DLC) harvested at different times between 1969 and 1974 (Fig. 1). To counteract the possible bias that would have been induced by a geographic gradient among stands (Hale et al., 1999), representative sites were chosen that were as close as possible to each other. None of the study stands had experienced any recent and obvious large-scale natural disturbances. According to aerial surveys from 1987, sugar maple decline have had a minor importance in those study sites, with 0–25% of crown defoliation (SPIM, 1988). Even though the number of available sample sites for each stand type was limited, an attempt was made to select stands with similar environmental characteristics (deposit, drainage, slope, aspect) (Table 1).

Old-growth stands, defined as ecosystems where dominant trees exceed well beyond their biological maturity age and that have been very slightly affected by human-induced disturbances in recent history (Villeneuve and Brisson, 2003), were selected with the help of the ‘‘Groupe de travail sur les écosystèmes forestiers exceptionnels’’ or GTEFE (freely translated as the Exceptional Forest Ecosystems Working Group), a governmental division that defines, locates, surveys and protects old-growth forests in Quebec. The sampled OG stands were mostly part of relatively large old-growth forest patches and were representative of the environmental conditions of the region. The mean age of dominant trees ranged from 200 to 325 years (Villeneuve, pers. comm.).

Selection cuts had all been completed at the end of 1990 or beginning of 1991. Guidelines recommended harvesting approximately 30% of the basal area, with a planned harvesting interval of approximately 20 years and a minimum residual basal area of 16 m^2/ha (Majcen, 1994). No guidelines were planned for snag or cavity tree retention. No pre-treatment information

Table 1
Characteristics of study sites

Stand types	n	Composition[a]	Parent material[b]	Drainage[c]	Slope[d]	Year of last known harvest	Area under gaps[e] (%)	Nb sampled points	Transect length sampled (m)[f]
Old-growth	6	SM or SMTH	R-1a	2–3	B–D	–	3–15	16–20	740–795 (225–250)
Selection cuts	7	SM or SMTH	R or 1aR	2–3	C–D	1990	22–48	15–20	707–795 (225–250)
Diameter-limit cuts	6	SM or SMTH	1a-1aR	2–3	C	1969–1974	2–10	17–20	685–795 (190–250)

[a] According to the Quebec’s MNR classification rules. SM, sugar maple occupies ≥66% of the basal area; SMTH, sugar maple and shade-tolerant hardwoods, sugar maple is the main species (33–66% of the basal area) and shade-tolerant hardwood species occupy 33–50% of the basal area.

[b] R, no or very thin glacial till; 1aR, thin glacial till (<50 cm); 1a, thick glacial till (>1 m).

[c] 2, Well drained; 3, moderately well drained (six classes total).

[d] B: 4–8%; C: 9–15%; D: 16–30%.

[e] Percentage of transect length located under gaps.

[f] Actual length of the transect sampled was sometimes less than the planned 795 m due to the exclusion of some transect portions located under extreme environmental conditions. Transect length sampled specifically for CWD and gaps are shown in parentheses.

was available, but various harvesting intensities were likely used since the harvested basal area, estimated from cut stumps and using diameter at stump height–diameter at breast height (dsh–dbh) conversion table (MRNFP, 2003), ranged from 6.8 to 13.2 m^2/ha (mean ± S.E.: 8.7 ± 0.8 m^2/ha). All selection cut stands had probably been subjected to some form of high grading in the past, but no records are available.

In DLC, timbered during the late 1960s–early 1970s (Table 1), no records of volume or species harvested were available, and most stumps had decayed. Diameter-limit cuts led to high grading since they were not performed following any strict rule (Bédard and Majcen, 2003). Typically, only large merchantable timber trees or certain high value species, such as white pine (*Pinus strobus* L.), red oak (*Quercus rubra* L.), yellow birch and sugar maple, were removed, and poor quality trees were left behind (Majcen, 1994; Bédard and Majcen, 2003). As the authorities exerted very little control (Majcen, 1994), DLC resulted in a highly variable harvest regime.

2.2. Sampling design and data collection

2.2.1. Sampling design

At each site, a sampling design consisting of four transects of 190–205 m and 50 m apart, in staggered rows, was established. The 50 m distance between transects was selected to make it highly improbable of sampling the same gap twice given the range of gap sizes reported in the literature for northern hardwoods (see Table 2 for a review). Each site was examined before installing the transects to avoid patches of undesirable environmental conditions such as humid or coniferous zones, steep slopes, or rocky outcrops, and to make sure that there was no particular orientation in CWD. Along each transect, 5 sampling points were established 45, 50 or 55 m apart, for a total of 20 sampling points per site.

2.2.2. Foliage cover profile

At each sampling point, a 3.57 m radius circular plot was established and the species of every sapling (1.1 cm ≤ dbh ≤ 9.0 cm) was identified and its dbh was assessed in 2 cm classes. Within the same radius, the vertical profile of foliage cover was visually assessed, always by the same person, using 5 foliage cover classes representing the horizontally projected percentage of foliage cover (1: 0–5%, 2: 5–25%, 3: 25–50%, 4: 50–75%, 5: 75–100%) in four vertical layers (0.1–2 m, 2–5 m, 5–10 m, >10 m aboveground).

2.2.3. Trees

For sampling trees (dbh ≥ 9.1 cm), an adaptation of the point-centered quarter method was used (Cottam and Curtis, 1956; Upton and Fingleton, 1985; Leduc and Bergeron, 1998). Two sections were defined at each sampling point using the transect line. In each section, the nearest tree to the sampling point was selected. From each of these two trees, within the same pre-defined sections, the nearest neighbour was also selected, for a total of four trees per sampling point (80 sampled trees per site). The distances from point to tree and tree to tree were noted, as well as the dbh, species and defect class, the latter being used as an indicator of potential use or colonization by organisms that utilize decaying wood. The defect classes were based on the following criteria (adapted from Hale et al., 1999): class 0 (no defects), class 1 (localized, minor: small to medium knot or canker, small lesion with exposed rot, small holes), class 2 (localized, moderate: large knot or canker, small open split, small to medium healed split, medium lesion with exposed rot), class 3 (extensive, spreading: large knot or canker, medium open split, medium cavity, medium to large lesion with exposed rot, presence of fungi), class 4 (hollow or moribund tree: part of the bole visibly hollow and/or part of the crown dead).

2.2.4. Snags and CWD

Within a 4 m wide continuous strip along each transect, all snags (dead standing trees ≥1.3 m tall with dbh ≥ 5 cm) and stumps (cut or broken trees <1.3 m tall, with diameter at stump height ≥5 cm) were sampled. Any dead portions of live trees were not measured. Species, origin (cut, natural), diameter (diameter at 30 cm for stumps and at dbh for snags) and decay stage were recorded, the latter according to the following criteria (adapted from Goodburn and Lorimer, 1998; Doyon et al., 1999): class 1 (recent death or fall, buds and twigs still intact, tight bark and hard wood), class 2 (fine parts such as buds and twigs lacking, bark loose, wood still hard), class 3 (bark mostly gone, bole periphery softened; a blade can penetrate the outer layer; in snags, tree top is often

Table 2
Structural characteristics in North America's northeastern hardwoods from published literature (OG, old-growth; SC, selection cut; UN, unmanaged)

Reference	Region, stand type	Mean ± 1S.E. (range)
Mean individual gap size		
This study[a]	Southwestern Quebec, OG	36.5 ± 6.0 m^2 (2.3–154.2 m^2)
Runkle (1985a) [a]	Eastern US, OG and mature	≈31 m^2 (1–1490 m^2)
Krasny and Whitmore (1992) [a]	New York, mature	42.8 ± 6.7 m^2
Dahir and Lorimer (1996) [b]	Northwestern Michigan, OG	44.8 m^2
Percentage of land area under gaps		
This study[a]	Southwestern Quebec, SC vs. OG	SC: 32 a ± 3.0% (23.4–48.2) OG: 9.4 b ± 1.7% (3.5–14.6)
Krasny and Whitmore (1992) [a]	New York, mature	8.4 ± 0.8%
Runkle (1985b) [c]	Eastern US, OG	10.1 ± 0.7% (3.3–26.1%)
Runkle (1990) [a]	Ohio, OG	7.0%
Snags (density and size)		
This study	Southwestern Quebec, SC vs. OG	SC: 43.9 a ± 4.9 ha^{-1} (18.9–59.7) OG: 49.3 a ± 6.7 ha^{-1} (20.1–64.2)
McComb and Muller (1983) [d]	Eastern Kentucky, OG	OG: 42.8 ha^{-1}
Forrester and Runkle (2000) [d]	Northeastern Ohio, OG	OG: 27.5 ha^{-1}
Runkle (1991) [e]	New-York, OG	OG: 54–73.8 ha^{-1}
Doyon et al. (1999) [f]	Southwestern Quebec, SC	SC: 94 ± 8.8 ha^{-1}
Hale et al. (1999) [d]	Minnesota, SC vs. OG	SC: 24 ha^{-1} a (0–88) OG: 34 ha^{-1} a (0–75)
McGee et al. (1999) [d]	New-York, SC vs. OG	SC: 42.8 ± 25.3 ha^{-1} (16.7–71.7) OG: 59.7 ± 21.7 ha^{-1} (35.0–80.0) Lower density in ≥25 cm in SC
Goodburn and Lorimer (1998) [d]	Wisconsin and Michigan, SC vs. OG	SC: 38 ha^{-1} a OG: 39 ha^{-1} a Lower density in ≥30 cm in SC
Stewart et al. (2003) [d]	Nova Scotia, OG	OG: 11–100 ha^{-1}
Coarse woody debris (volume and size)		
This study[f]	Southwestern Quebec, SC vs. OG	SC: 100.9 a ± 8.5 m^3/ha (62.5 OG: 93.4 a ± 11.9 m^3/ha (39.5
Doyon (2000) [f]	Southwestern Quebec, SC	SC: 60.7 ± 7.1 m^3/ha
Hale et al. (1999) [g,h]	Minnesota, SC vs. OG	SC: 40 a m^3/ha (12–89) OG: 55 b m^3/ha (12–121)
Goodburn and Lorimer (1998) [i]	Wisconsin and Michigan, SC vs. OG	SC: 61.3 a ± 6.3 m^3/ha OG: 102.2 b ± 6.4 m^3/ha Lower volume in ≥40 cm in SC
Leduc and Bergeron (1998) [i]	Southeastern Quebec, OG	OG: 40.4–84.1 m^3/ha
Forrester and Runkle (2000) [i]	Northeastern Ohio, OG	OG: 80.2 m^3/ha
McGee et al. (1999) [j]	New-York, SC vs. OG	SC: 69.1 a ± 16.7 m^3/ha (55.3 − 100.9) OG: 138.5 b ± 22.0 m^3/ha (120.6 − 180.9) Lower volume in ≥25 cm in SC
Gore and Patterson (1986)	New-Hampshire, SC vs. OG	Lower proportion in ≥15.2 cm in SC
Stewart et al. (2003) [d]	Nova Scotia, OG	OG: 45–58 m^3/ha

Note: Different letters (a and b) indicate significantly different values among stand types at $P < 0.05$ according to respective authors. For dead wood, only studies using a dbh cutoff similar to the one used in this study are presented.

[a] According to the canopy gap definition.
[b] Original canopy gap area.
[c] According to the line intersect method.
[d] Snags ≥ 10 cm dbh.
[e] Snags ≥ 11 cm dbh.
[f] Snags ≥ 5 cm dbh.
[g] Logs only.
[h] CWD ≥ 15 cm.
[i] CWD ≥ 10 cm.
[j] CWD ≥ 1 cm.

broken), class 4 (little to no bark remains, bole periphery well rotten and extends in the core; a blade can easily penetrate; in snags, bole is broken) and class 5 (CWD only, well-decayed wood, incorporating into the forest floor, vegetation has colonized).

Since CWD abundance may exhibit a high spatial variability (Harmon et al., 1986; Hale et al., 1999), the line intersect sampling method was used (Van Wagner, 1968). Ten 25 m transect sections were randomly selected, (250 m sampled at each site), along which all intersecting CWD $\geq$5 cm at line intercept were sampled. Cross diameter at intersection, largest and smallest end diameter, length and decay class were measured and species was recorded.

2.2.5. Gaps

The length of all transect portions found under gaps was measured. A clinometer was used to assess the vertical projection of gap border. The canopy gap definition was used (Runkle, 1982, 1991, 1992), whereby the vertical projection of the canopy opening is defined by the crowns of adjacent trees (dbh $\geq$ 9.1 cm). To be considered as a gap, the regeneration under the opening had to be less than half the height of the dominant trees, and evidence of gap maker(s) (stump, snag or fallen branch or log) had to be present. Edaphic conditions creating temporary or permanent openings were not considered as gap makers, except if a gap had mixed origins including edaphic conditions.

The same transect sections used in CWD sampling were also employed for characterizing gaps. Using a technique inspired from Runkle (1985b, 1992), only gaps which had more than 50% of their vertical projection along a transect section were characterized. This characterization was done in OG and DLC only, since the spatial pattern of openings in SC consisted of a complex network of multiple interconnected gaps, too complicated to be sampled in a meaningful way, a phenomenon also observed by Kimball et al. (1995) and Crome and Richards (1988). The longest axis, as well as perpendicular axes at every 3 m along the longest axis, were measured. When the gap was less than 3 m wide, the perpendicular axis was taken in the middle of the longest axis.

Although every attempt was made to avoid heterogeneous patches and extreme conditions, this was at times unavoidable. In these instances, the corresponding transect sections and points were excluded from the analysis, but at least 15 points per site were sampled (Table 1).

2.3. Data analysis

Tree density was calculated using an adaptation by Pollard (1971) of Moore (1954) estimator (T) based on the distance (r) from a randomly chosen point (n points) to the nearest plant (n = 15–20 trees sampled per site):

$$T = \frac{n-1}{\pi \sum_{i=1}^{n} r_i^2}$$

Since this estimator is known to be very sensitive to deviation from random distribution of plants (Pollard, 1971; Upton and Fingleton, 1985), the random distribution assumption was verified using Eberhardt's E statistic (Upton and Fingleton, 1985):

$$E = \frac{n \sum_{i=1}^{n} r_i^2}{\left(\sum_{i=1}^{n} r_i\right)^2}$$

For each stand, mean dbh and tree species composition were calculated using the four trees sampled per point (n = 60–80 trees per site). Stand basal area was estimated using density and dbh average.

The fraction of area under gaps was calculated as the sum of the lengths of transect portions under gaps, divided by the total transect length (Runkle, 1985b). Individual gap areas were calculated using the ellipse formula (Runkle, 1985b, 1992).

To compare the spatial variability in foliage cover among stand types, a heterogeneity index (H), inspired from Dale (1999), was developed to characterize the heterogeneity of foliage cover for each height class, within a stand:

$$H = \sum \frac{(|c_{xy} - c_{x,y+1}|) + (|c_{xy} - c_{x+1,y}|) + (|c_{xy} - c_{x+1,y+1}|) + (|c_{xy} - c_{x+1,y-1}|)}{n}$$

where c_{xy} is the foliage cover at grid position (x,y), and n is the number of possible pairs (n = 39–55 possible pairs per stand). Since foliage cover was estimated by classes, we used the median cover value of a class for calculation. For instance, if foliage cover was estimated to be between 0 and 5% (class 1) at a given grid

Table 3
Comparison of various structural features among old-growth (OG), selection cut (SC) and diameter-limit cut (DLC) stands

Variables	Old-growth ($n = 6$) Mean ± S.E. (Range)	Selection cuts ($n = 7$) Mean ± S.E. (Range)	Diameter-limit cuts ($n = 6$) Mean ± S.E. (Range)	P	Transformation used
Gaps					
Area under gaps (%)	9.4 ± 1.7 a (3.5–14.6)	32.0 ± 3.0 b (23.4–48.2)	4.4 ± 1.3 c (1.8–10.3)	<0.001	Log
Proportion of gaps of natural origins (% gap area)	100 a	29.8 ± 4.5 b (11.4–49.5)	76.1 ± 9.6 c (45.8–100)	<0.001	Rank
Gap size (m^2)	36.5 ± 6.0 a (2.3–154.2)	–	17.4 ± 6.9 b (2.2–58.5)	0.044	Log
Vertical foliage profile					
Foliage cover heterogeneity index (H) 0.1–2 m[a]	24.8 ± 1.2 a	19.6 ± 1.1 b	25.4 ± 1.2 a	<0.001	Rank
H 2–5 m	22.7 ± 1.1 a	20.4 ± 1.2 a	12.7 ± 0.3 b	<0.001	Rank
H 5–10 m	27.1 ± 1.3 a	26.2 ± 1.2 a	29.7 ± 1.4 a	0.071	Rank
H >10 m	26.8 ± 1.3 a	29.9 ± 1.3 a	32.3 ± 1.6 a	0.076	Rank
Saplings					
Total density (stems/ha)	2919 ± 184 a	6310 ± 330 b	1491 ± 112 c	<0.001	Log
Density dbh 1.1–3.0 cm	2263.2 ± 179.1 a	5090.4 ± 298.0 b	576.4 ± 67.4 c	<0.001	Rank
Density dbh 3.1–5.0 cm	392.5 ± 34.8 a	921.2 ± 71.2 b	472.2 ± 49.7 a	<0.001	Rank
Density dbh 5.1–7.0 cm	177.6 ± 20.8 a	196.2 ± 25.3 a	310.2 ± 34.5 b	0.010	Rank
Density dbh 7.1–9.0 cm	85.5 ± 14.2 a	101.9 ± 16.3 a	131.9 ± 18.2 a	0.116	Rank
Trees (dbh ≥ 9.1 cm)					
Density (stems/ha)	438.0 ± 18.0 a (392.1–511.5)	334.9 ± 41.7 a (250.2–554.8)	578.5 ± 41.9 b (429.9–691.5)	0.001	None
Basal area (m^2/ha)	27.1 ± 2.1 a (20.1–35.4)	16.2 ± 1.7 b (11.5–24.6)	20.2 ± 2.3 ab (13.6–30.5)	0.005	None
dbh (cm)	28.0 ± 0.7 a (9.1–89.0)	24.9 ± 0.5 a (9.1–65.4)	21.0 ± 0.5 b (9.1–58.8)	<0.001	Rank
Proportion of stems ≥29.1 cm dbh (%)	41.2 ± 2.7 a (32.9–50.0)	36.4 ± 1.1 a (31.3–39.7)	22.3 ± 2.2 b (17.5–29.3)	0.001	None
Proportion of stems ≥39.1 cm dbh (%)	23.5 ± 2.3 a (17.1–30.3)	13.4 ± 2.7 b (3.8–22.2)	6.9 ± 1.9 b (1.4–13.3)	<0.001	None
Proportion of stems ≥49.1 cm dbh (%)	11.3 ± 2.0 a (6.6–18.4)	4.1 ± 1.3 b (0–8.3)	1.2 ± 0.45 b (0–2.9)	<0.001	None
Defect class 0 (%)	25.1 ± 2.1 a (17.1–30.0)	17.3 ± 1.3 a (12.5–23.8)	20.8 ± 3.3 a (10.3–31.6)	0.086	None
Defect class 1 (%)	27.7 ± 1.1 a (23.4–31.3)	33.9 ± 2.2 a (26.3–44.4)	30.1 ± 1.5 a (27.6–34.2)	0.065	None
Defect class 2 (%)	17.3 ± 2.6 a (7.9–26.3)	21.5 ± 1.1 a (17.5–25.0)	18.1 ± 1.4 a (13.8–23.6)	0.221	None
Defect class 3 (%)	13.5 ± 1.7 a (8.8–19.7)	20.3 ± 0.9 b (17.5–23.8)	16.9 ± 3.8 b (7.7–35.3)	0.013	Rank
Defect class 4 (%)	16.4 ± 2.4 a (11.3–27.6)	7.0 ± 1.1 b (2.5–10.3)	14.0 ± 1.9 a (9.7–22.5)	0.002	Log
Snags (1.3 m tall with dbh ≥ 5.0 cm)					
Density (stems/ha)	49.3 ± 6.7 a (20.1–64.2)	43.9 ± 4.9 a (18.9–59.7)	118.1 ± 19.8 b (60.8–173.0)	0.001	Square root
dbh (cm)	24.6 ± 1.8 a (5.4–68.0)	26.6 ± 1.4 a (6.6–74.5)	14.0 ± 0.9 b (5.0–101.0)	<0.001	Rank

Table 3 (*Continued*)

Variables	Old-growth ($n = 6$) Mean ± S.E. (Range)	Selection cuts ($n = 7$) Mean ± S.E. (Range)	Diameter-limit cuts ($n = 6$) Mean ± S.E. (Range)	P	Transformation used
Density $\geq$ 49.1 cm dbh (stems/ha)	7.6 ± 2.3 a (0–13.5)	1.4 ± 0.6 a (0–3.2)	4.9 ± 1.8 a (0–10.1)	0.069	Rank
Coarse woody debris (CWD) (dbh $\geq$ 5.0 cm)					
CWD volume (without stumps) (m^3/ha)	78.4 ± 9.6 a (33.0–96.6)	72.7 ± 6.4 ab (43.9-96.2)	41.6 ± 12.0 b (27.3–101.5)	0.037	None
Stumps volume (m^3/ha)[b]	15.0 ± 2.7 a (6.6–20.2)	29.3 ± 2.4 ab (18.6–37.3)	35.7 ± 7.5 b (11.4–57.6)	0.020	None
Total volume (CWD and stumps) (m^3/ha)	93.4 ± 11.9 a (39.5–120.3)	100.9 ± 8.5 a (62.5–133.7)	77.3 ± 17.3 a (43.5–150.0)	0.424	None
Large end diameter (cm)	19.5 ± 0.9 a (5.0–61.0)	17.8 ± 0.7 a (5.4–66.0)	18.5 ± 1.0 a (5.4-56.0)	0.635	Log
Mean piece volume (cm^3)	24.7 ± 3.1 a (0.1–343.3)	19.0 ± 2.4 a (0.1–346.9)	15.3 ± 2.1 a (0.1–140.9)	0.737	Log

Note: Different letters (a–c) indicate significantly different values among stand types at $P < 0.05$.

[a] See methodology for index calculation. Homogeneity was inversely proportional to the index.

[b] Natural and cut stumps.

position and height, the value 2.5% was used for calculation. This index is calculated from the differences of foliage cover between each sampled point and its immediate neighbours on the sampling grid, but because of its formulation this equation prevents any pair repetition. The higher the index, the higher the heterogeneity of foliage cover within a given height class.

Individual CWD volume (V_{ind}) (excluding stumps) was calculated from the formula of a truncated cone. Stand-level CWD volume (V, m^3/ha, excluding stumps) was estimated using Van Wagner's (1968) formula:

$$V = \pi^2 \sum \frac{d^2}{8L}$$

where d is the cross-transect diameter of CWD and L is the transect length sampled. To calculate total CWD volume, the stump volume calculated as a cylinder was added.

2.4. Statistical analysis

For comparing means among the three stand types, one-way analysis of variance (ANOVA) was performed. Some variables were log-, square root- or rank-transformed to meet the assumptions of homoscedasticity and normality. When a significant difference was found among the three stand types, a post-hoc Tukey HSD test was conducted. Statistical analyses were performed using JMP 4.0.2 (SAS Institute, 2000).

For comparing distributions of variables among classes, the chi-square test and the Bonferroni-corrected Freeman–Tukey deviates (Sokal and Rohlf, 1981; Legendre and Legendre, 1998) were used.

3. Results

3.1. Gaps

DLC had the lowest percentage of land area under gaps (4.4 ± 1.3%), followed by OG (9.4 ± 1.7%) and SC (32.0 ± 3.0%), the latter with an average percentage of area under gaps more than three times higher than in OG. All stand types were significantly different from each other (Table 3).

Gap size was only evaluated in OG and DLC, as explained previously. Gaps in OG were 36.5 ± 6.0 m^2 in size on average and their size generally followed an inverse J-shaped distribution characterized by a high proportion of small gaps and few large gaps (Table 3).

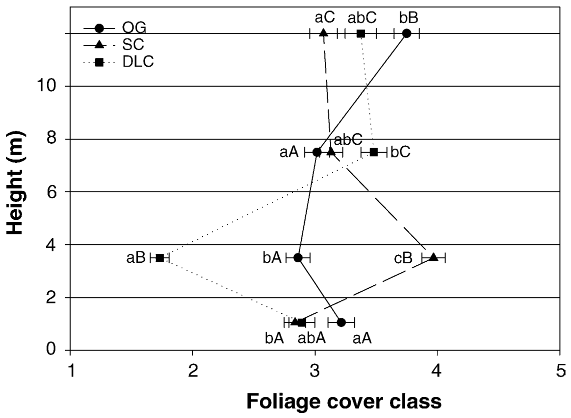


Fig. 2. Vertical distribution of foliage cover in old-growth (OG, $n = 114$ sampled points), selection cut (SC, $n = 130$) and diameter-limit cut stands (DLC, $n = 111$) (mean cover class ± 1S.E.). Cover classes: (1) 0–5%; (2) 5–25%; (3) 25–50%; (4) 50–75%; (5) 75–100%. Different lower-case letters indicate significantly different values among stand types within a given height class while different capital letters indicate significantly different values among height classes within a given stand type. $P < 0.05$.

In DLC, gaps were fewer and smaller. Only eight gaps crossed the total 1390 m section of transects sampled. They were 17.4 ± 6.9 m^2 in size on average, and more than 50% of them were less than 10 m^2 in size.

3.2. Vertical foliage profile

There were marked differences in the vertical distribution of foliage cover among the three stand types, especially at heights between 2 and 5 m (Fig. 2). Overall, OG showed the most even distribution of foliage cover among height classes. Both harvested stand types were characterized by having their highest values of foliage cover in layers located right above height classes showing the lowest values of foliage cover (SC: highest cover at 2–5 m, lowest at 0.1–2 m; DLC: highest cover at 5–10 and >10 m, lowest at 2–5 m).

A greater homogeneity in foliage cover was not observed in the post-harvest recruitment cohort layers in the harvested stand types compared to OG (Fig. 2; Table 3). However, a greater homogeneity was found in the layer right beneath those recruitment cohort layers (SC: 0.1–2 m, DLC: 2–5 m) (Fig. 2).

3.3. Sapling diameter distribution

Sapling density was significantly different among the three stand types (Table 3), being about twice as high in SC and half as low in DLC compared to OG. Differences among stand types were especially pronounced for sapling density in the first two dbh classes (1.1–3.0 and 3.1–5.0 cm dbh). Both OG and SC showed a similar inversed J-shaped pattern, typical of an uneven-aged structure with a decreasing density of individuals with increasing dbh classes, whereas DLC exhibited a flatter distribution (data not shown).

3.4. Tree species composition

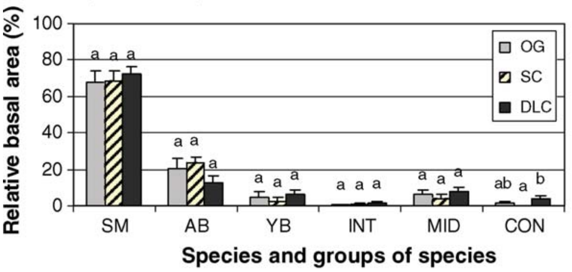
For trees (dbh > 9.1 cm), there were very few differences in species composition among stand types. Sugar maple dominated in all stands, always followed by beech (Fig. 3a). The relative basal areas of these two species, as well as that of yellow birch, were not significantly different among stand types. Since all other species had a mean relative basal area < 5%, no further comparisons were made for individual species. However, the species were grouped according to their shade tolerance (Farrar, 1996), but no significant difference was observed in the relative basal area of shade-intolerant species and mid-tolerant species among stand types. Altogether, coniferous species represented less than 5% of the basal area in every stand type.

About thirty years after DLC, the regeneration cohort constituted much of the young tree stratum. To see if the openings had been important enough to allow the establishment and growth of shade-intolerant species, the composition of trees between 9.1 and 21.0 cm was analyzed. Results showed that there was no greater amount of shade-intolerant species in DLC than in OG ($\text{DLC} = 3.9 \pm 2.1\%$, $\text{OG} = 0\%$), but significantly more mid-tolerant species in DLC than OG ($\text{DLC} = 11.0 \pm 3.3\%$, $\text{OG} = 1.3 \pm 1.3$, $P < 0.01$). In DLC, mid-tolerant species were mostly composed of yellow birch (75% of the mid-tolerant species).

3.5. Sapling species composition

Sapling species composition showed clear differences among stand types (Fig. 3b). As in the tree strata, the two dominant species were still sugar maple

(a) Trees (≥ 9.1 cm dbh)



(b) Saplings (≥ 9.0 cm dbh)

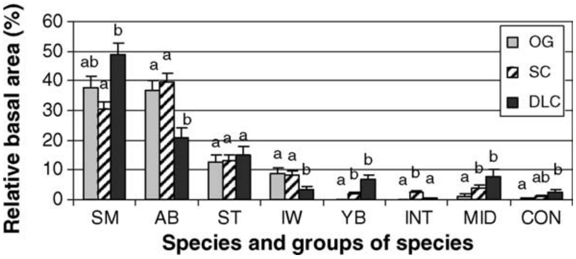


Fig. 3. Relative basal area of main species and groups of species for (a) trees and (b) saplings in old-growth (OG, $n = 456$ trees, 1331 saplings), selection cut (SC, $n = 520$ trees, 3281 saplings) and diameter-limit cut (DLC, $n = 444$ trees, 644 saplings) stands (± 1S.E.). Only species with more than 5% mean relative basal area in at least one stand type are presented. Different letters indicate significantly different values among stand types for a given species or group of species ($P < 0.05$). SM, sugar maple; AB, American beech; YB, yellow birch; ST, striped maple; IW, ironwood; INT, shade-intolerant species: black cherry (*Prunus serotina* Ehrh.), red oak, white birch (*Betula papyrifera* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), bigtooth aspen (*Populus grandidentata* Michx.), trembling aspen (*Populus tremuloides* Michx.) and willow species (*Salix* sp.); MID, mid-tolerant species: yellow birch, red maple (*Acer rubrum* L.), white ash (*Fraxinus Americana* L.), black ash (*Fraxinus nigra* Marsh.) and American elm (*Ulmus americana* L.); CON, coniferous species: eastern hemlock, balsam fir (*Abies balsamea* (L.) Mill.) and spruce species (*Picea* sp.).

and beech. However, the proportion of beech, relative to sugar maple, was greater among saplings than trees. For each of these two species, no significant difference in relative basal area ($P > 0.05$) was observed between OG and SC, but the proportion of these two species differed between SC and DLC. Sugar maple had a higher relative basal area in DLC compared to SC ($P < 0.01$), whereas beech showed the reverse trend, with a lower relative basal area in DLC than SC and OG ($P < 0.01$) (Fig. 3b). In contrast to the main tree composition, some minor species (yellow birch, ironwood and striped maple (*Acer pensylvanicum* L.)) had a mean relative basal area higher than 5% in at least one stand. Yellow birch regeneration was very scarce in OG and its relative basal area was significantly lower than in SC and DLC ($P < 0.01$).

OG and DLC had a similar low relative basal area of shade-intolerant species compared to SC (Fig. 3b) ($P < 0.01$). Results are slightly different when looking at mid-tolerant species: the relative basal area in OG was significantly lower ($P < 0.01$) than in SC and DLC, with no difference between the latter two stand types.

3.6. Tree diameter distribution

The mean tree basal area differed among stand types with SC having the lowest mean basal area, followed by DLC and OG at 16.2 ± 1.7, 20.2 ± 2.3, 27.1 ± 2.1 m^2/ha, respectively (Table 3). Because of post-harvest regeneration, DLC showed significantly higher tree density and smaller mean tree dbh than OG and SC (Table 3), the latter two being not significantly different from each other for both variables. Compared to OG, there was a greater proportion of small dbh trees in DLC and a lower proportion of large trees in both managed stand types (≥29.1 cm dbh in DLC and ≥39.1 cm dbh in SC, Table 3).

The only significant differences in defect class distributions among stand types were in very defective trees (defect classes 3 and 4). Defect class 4 trees (hollow or moribund trees) were significantly less abundant in SC than in OG and DLC, whereas defect class 3 trees (extensive and spreading defects) were more abundant in managed stand types than OG (Table 3).

3.7. Snags

Density of snags was more than twice as high in DLC than in OG and SC (Table 3). Mean snag dbh was, however, almost reduced by half in DLC compared to OG and SC, because of a significantly higher abundance of small dbh (5.0–9.0 cm) snags (Table 3) in DLC. In SC, as for living trees, the mean snag dbh was not significantly different from OG (Table 3). Even though the proportion of large snags (dbh ≥ 49.1 cm) in SC was five times lower than in

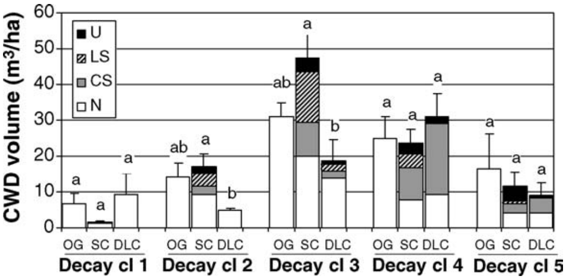


Fig. 4. Distribution of CWD volume (mean ± 1S.E.) by decay class in old-growth (OG), selection cut (SC) and diameter-limit cut stands (DLC) by origin; N, natural; U, unknown; CS, cut stump; LS, logging slash. CWD include fallen woody debris, logging slash and stumps. Different letters indicate significantly ($P < 0.05$) different values among stand types within a given decay class.

OG, there was no significant difference among stand types (Table 3).

3.8. Coarse woody debris

The mean volume of CWD, excluding stumps, was significantly lower in DLC than OG (Table 3). However, mean total CWD volume, including stumps, mean CWD larger end diameter as well as mean piece volume, both excluding stumps, were not significantly different among stand types (Table 3).

In harvested stands, logging debris contributed to a relatively large extent to the overall volume of CWD (Fig. 4). In SC, almost half (44%) of CWD volume originated from harvest (logging slash and stumps), and 23% were stumps. In DLC, approximately 30 years after harvest, slashed debris were very scarce (less than 3%), whereas 36% of the CWD volume was represented by cut stumps.

When looking at the distribution of CWD and stump volume among decay classes (Fig. 4), all stand types showed a roughly normal distribution pattern and OG best showed a typical pattern of continuous input. Harvested stands exhibited less flat distribution than OG, typical of distributions resulting from an increased input of dead wood at one specific moment. These cohorts of harvest-induced dead wood seemed to evolve through decay stages relatively similarly in both types of harvest, with a visible delay corresponding to time spent between treatments (there was more volume of anthropogenic origins in decay class 3 in SC and more of decay class 4 in DLC).

4. Discussion

4.1. Implications of the synchronized opening of the canopy in harvested stands

4.1.1. Gaps

Comparing the fraction of land area under gaps and gap characteristics observed in this study with values reported in the literature is difficult since many different gap definitions and methodologies are used (Runkle, 1992). The results in this study in OG are, however, in general agreement with other studies (Table 2). The inverse J-shaped distribution of gap size was also observed by other authors (Runkle, 1982, 1985a; Payette et al., 1990; Krasny and Whitmore, 1992).

Because of the definition of gap used whereby a gap is delimited by the vertical projection of adjacent tree crowns, results regarding the fraction of the area under gaps suggest that the general canopy structure was similar between DLC and OG, which was not actually the case. In DLC, the strong and synchronized opening of the canopy 30 years ago induced a synchronized closing of the canopy, mainly from below, by young trees that now form a nearly even-sized regeneration structure. The fraction of area under gap was actually lower in DLC than in OG, but, despite that the vertical distribution of foliage cover was not characterized above 10 m, DLC's upper canopy obviously differed from the OG's, with foliage cover in the upper height class (>10 m) being mostly located very low, and being strikingly thinner and more translucent, with almost no tree crowns overlapping. In opposition, canopy above 10 m in OG is characterised by well-developed tree crowns, often overlapping, with tallest trees often reaching 25 m or more. The very low fraction of area under gap in DLC suggests that the gap formation rate is currently very low while canopy is restructuring itself. However, most gaps were of natural origins (76.1%, Table 3), suggesting a return to a natural gap formation process.

In SC, 12 years after harvest, the fraction of land area under gaps was still very high compared to OG. This is probably due to a high harvesting intensity, to the gap dynamics prevailing before logging, and to a high rate of post-harvest mortality among less vigorous trees (Bédard and Brassard, 2002), as suggested by the relatively high proportion of gaps of natural origins (29.8%, Table 3). According to the return interval planned by local authorities, those stands will be harvested again in 15–20 years. Under this recurrent selection cutting regime, the forest canopy will likely never be allowed to recover fully or for a substantial period of time, and species associated with open canopy conditions may be favoured at the expense of closed canopy species (Crome and Richards, 1988; Bourque and Villard, 2001).

In fact, the actual area affected by canopy openings was probably higher than the fraction of land area directly under gaps (as measured in this study) since the latter does not take into account the potentially large area in the vicinity of gaps where the light regime is modified by the presence of canopy gaps, particularly at the relatively high latitudes of our study sites (Canham, 1989). Given that the mean proportion of land area under gaps in SC 12 years after harvesting was 32%, that extended gaps or area under canopy gaps plus the adjacent area extending to the tree trunks surrounding the gaps (Runkle, 1990) are about twice as large as canopy gaps (Runkle, 1984) and that lateral closing probably had occurred since harvest, the actual area where the understory light regime had likely been affected by SC immediately after harvest might have been easily more than 50% of land area. This is in agreement with Beaudet et al. (2004) who observed that in recent (1–4 years) selection cuts, 51% of sampled microsites had light profiles typical of recently disturbed stands.

Studies usually characterize the size distribution of gaps at a given moment in time, which provides a snapshot of the situation but does not take into account the fact that gaps are at various stages in their development or closure process. From a management perspective, it would be more helpful to study the size range of recently formed natural canopy gaps, the annual variability in areas of recently formed gaps and the canopy closure rates to gain greater insight into the natural patterns of gap formation and closure.

4.1.2. Sapling recruitment

Following the presumed strong and synchronized enhancement of the light regime in gaps resulting from harvesting, there seems to have been a strong response of the regeneration in both SC and DLC. In harvested stands, the vertical distribution of foliage cover was characterized by the presence of peaks in foliage cover, probably associated with the post-harvest cohort's crowns (Fig. 2). This pattern in harvested stands differed from the fairly even vertical distribution of foliage cover observed in OG. A very high density of small saplings was also observed in SC compared to OG, as was a high proportion of small trees in DLC (Table 3). A high density of saplings was also observed approximately 10 years after SC by Doyon (2000).

In both types of harvested stands, this dense regeneration layer probably intercepted enough light to disturb the regeneration process in the underlying stratum. This is suggested by the decrease in foliage cover observed in the strata located right below the recruitment cohort in both SC and DLC (Fig. 2) as well as by the very low density of saplings in DLC (where the small tree cohort was very abundant) (Table 3). Inhibition of regeneration recruitment caused by strong light attenuation associated with dense understories has also been reported by several authors, including Roberts (1992), Lorimer et al. (1994), Yanai et al. (1998) and Beaudet et al. (2004). This phenomenon probably also occurs in OG when a gap is formed, but the impact is local and restricted at the gap scale, whereas in harvested stands, the impact is more generalized throughout the stand.

4.1.3. Homogenization of foliage cover

While the smallest fraction of land area under gaps (Table 3) was observed in DLC, DLC still had less foliage cover above 10 m than OG (Fig. 2). This may seem contradictory but, in fact, assessment of foliage cover showed that many of the trees in DLC were young, and their crowns often overlapped the 5–10 m and >10 m height classes. Moreover, those young crowns were fairly open compared to those of older trees. Being thin and distributed in two height classes, the foliage cover >10 m was consequently less in DLC than in OG where much of tree crowns were more opaque and located well above 10 m.

Patterns of foliage cover, as presented in Fig. 2, provide a useful description of stand-level trends but may hide ecologically interesting data about the within-stand variability in foliage cover (Parker and Brown, 2000). The heterogeneity index therefore provides complementary information about the within-stand horizontal variability of foliage cover. Since most of the canopy openings were formed synchronously in the harvested stands, the vegetation response was also expected to be relatively synchronous and uniform and that a greater homogeneity of foliage cover would be observed in the height classes corresponding to the post-harvest recruitment cohort (SC: 2–5 m, DLC: 5–10 and >10 m). However, this was not the case. Some homogenization of foliage cover was detected in the harvested stands, but in the vegetation layers right beneath those associated with the post-harvest recruitment cohorts (SC: 0–2 m, DLC: 2–5 m). The process of homogenization in harvested stands would thus not be a direct result of the opening in the canopy, but an indirect result mediated by the response and effect of post-harvest recruitment cohort. The formation of dense subcanopies, following the opening of the canopy by various types of harvests or natural disturbances, has been reported on several occasions and has been shown to intercept light in a way that homogenizes the light conditions near the forest floor and affects the establishment and survival of the regeneration (Lorimer et al., 1994; Ray et al., 1999; Hane, 2003; Beaudet et al., 2004). The horizontal homogenization of foliage cover in specific strata may, depending on the time elapsed since disturbance, favour or inhibit the growth of species that require specific densities of foliage in specific strata (Bourque and Villard, 2001). These results contradict those of Doyon (2000) who found no difference between SC and unmanaged stands in horizontal heterogeneity of foliage cover within each regeneration layer. However, this might be explained by the less intense harvesting in the SC studied by Doyon (15–30% removal of basal area) which may have contributed to maintaining a more natural level of heterogeneity in foliage cover within stand.

4.1.4. Composition

Industrial forestry is relatively recent and has probably not been performed over a long enough period to significantly modify the tree species composition in northern hardwood stands in Quebec. However, the characteristics of the regeneration niches created by harvesting might differ from those resulting from the micro-gap natural regime. This is suggested by the higher relative basal area of shade-intolerant species observed among saplings in SC, of mid-tolerant species observed among saplings in SC and DLC stands and among small trees in DLC (trees of dbh $\leq$ 21 cm), corresponding to the post-harvest recruitment cohort. The relative basal area of shade-intolerant species was lower than expected in harvested stands, particularly in DLC where harvesting intensity was higher. This might be due to the scarcity of these species among mature trees. In regions where the shade-intolerant species tree component is higher, the post-harvest sapling composition might be different. As reported in the literature comparing the species composition of logged versus presettlement hardwood forests (Siccama, 1971; Brisson et al., 1988), a higher relative basal area of sugar maple saplings and a lower relative basal area of beech saplings in DLC stands compared to OG was also observed in this study.

In both harvested and OG stands, sugar maple was far less represented among saplings than among trees, whereas beech was more abundant (in terms of relative basal area) among saplings than trees. Assuming that the composition of saplings should be representative of a stand's future tree composition, at least for shade-tolerant species, the observed pattern suggests a shift in dominance between sugar maple and beech towards a higher proportion of beech. Since this trend was also observed in OG stands, harvesting might not be the causal factor. Over the last decade, a pronounced decline in sugar maple saplings survival and a major increase in beech saplings abundance has been observed in unmanaged stands throughout Quebec by Duchesne et al. (2003), who have suggested soil acidification and reduction in soil nutrients as potential causes.

4.2. Implications of wood removal in harvested stands

Relatively few differences were noted in trees, snags and CWD characteristics among OG, SC and DLC. However, the differences noted regarding the size, quality and recruitment of these elements reveal trends in stand evolution that might become major issues with repeated interventions.

4.2.1. Abundance of large trees and snags

Many authors agree that large living and dead trees have a higher biological value than small ones (Evans and Conner, 1979; Harmon et al., 1986). Not only is large stem size necessary for large vertebrates, but large trees, snags and CWD provide unique microhabitats, persist longer in the ecosystem and may thus be used more extensively than smaller ones (Harmon et al., 1986; Doyon et al., 1999; Hale et al., 1999; Fraver et al., 2002). The high density of snags created by self-thinning of the post-harvest cohort or by the death of short-living species in DLC is thus of low biological interest since most of those snags were less than 10 cm in dbh.

Given the actual return interval for selection cutting, trees will probably not be allowed to develop beyond their dbh of commercial maturity, and the future recruitment in large stems might not be ensured. After a single entry, the reduction of large living trees in harvested stands and the trend towards a decrease of large dbh snags in SC is evidence of a tendency that could lead to a more pronounced reduction in the availability of these elements with the following cutting rotations. Indeed, many authors have already reported a reduction in size and abundance of large trees, snags and CWD following a number of rotations of SC (Table 2).

4.2.2. Trees and dead wood quality

The reduction in the proportion of highly defective stems (defect class 4) in SC compared to the other two stand types was likely due to the preferential removal of defective and low-vigor trees or to their hastened death following harvesting. In DLC, defective trees were often left behind during harvesting, and this might explain the similar abundance of highly defective stems in DLC and OG. As old remnant trees from DLC will die and as selection cutting will be applied in those stands, highly defective trees and trees with potential to move from defect class 3–4 will likely become more scarce in these forests. The combination of a lower abundance of large living trees in harvested stands and of highly defective trees in SC may result in a reduced availability of habitat for species requiring these structural features (Evans and Conner, 1979; Hagan and Grove, 1999; Hale et al., 1999).

Regarding CWD, the overall normal distribution among decay classes observed in OG, and to a lesser extent in harvested stands, is a typical result of a continuous input in dead wood (Fig. 4), also observed by Hale et al., (1999), McGee et al. (1999) and Fraver et al. (2002). Residence time is actually known to be much longer in decay classes 3 and 4 than in other classes because of rapid decay in the earliest and latest phases of the dead wood decay process (Harmon et al., 1986). Also, low CWD volumes in the first two decay classes can be explained by the fact that CWD often come from snags breakdown, with the wood already partly decayed when it becomes CWD.

CWD of anthropogenic origin, particularly in the form of stumps, were prominent in harvested stands. If logging residues were absent, the volume of CWD in each decay class, as well as the total CWD volume, would be lower in harvested than OG (except for decay class 1 in DLC) (Fig. 4).

4.2.3. Dead wood recruitment

The similar abundance of snags in SC and OG might be explained by the presence of existing snags at time of harvest, but also by a high recruitment of snags after harvest. Indeed, Bédard and Brassard (2002) reported that post-harvest tree mortality was higher than expected following selection cutting. Soil compaction, mechanical injuries (Hale et al., 1999), and water shortage due to canopy opening may have affected residual trees and hastened tree death. If the high density of snags observed in SC is partly due to a high post-harvest rate of tree mortality, and if this rate of mortality decreases over time, this might lead to a future decrease in snag recruitment. Furthermore, selection cutting aims at minimizing tree mortality through the preferential harvest of low-vigor trees that are likely to die in the following rotation (Bédard and Majcen, 2003). Reduction in mortality, and consequently in both quantity and quality of dead woody materials were observed in regions that experienced several rotations of selection cutting (Goodburn and Lorimer, 1998; McGee et al., 1999; Table 2).

Since harvesting might affect the natural mortality process, the recruitment dynamics of dead wood might be shifting from a relatively continuous input of dead wood, typical of natural conditions, to a harvested-induced periodic input. Rotation length and harvesting intensity will likely influence the rate and size of harvest-related input in dead wood. For instance, with long rotations, such as with DLC, dead wood recruitment eventually only depends on natural tree mortality, whether through the death of a few old and large residual trees or to self-thinning among young poles. As decay progresses, however, the continuity in the recruitment of large, poorly decayed CWD might not be ensured in DLC, as suggested by the very low amounts of CWD in decay class 2, and the very high proportion of small woody debris found in decay class 1. This gap in recruitment of CWD in DLC might be dragged through the succeeding decay stages as time goes on until natural mortality or selection cut occurs.

In SC, because of the recent application of the treatment and of the delay in transition from standing dead wood to CWD, few differences between SC and OG were found in terms of CWD characteristics. However, lower amounts of CWD were found in SC in decay class 1, probably indicating a possible interruption in the continuity of the recruitment process. Further research on degradation rates and residence time through decay classes are needed to find out if occurrence of CWD in all decay stages will be ensured in stands submitted to repeated harvests over relatively short rotations, such as with SC. This is important since different species use different stages of wood decay (Harmon et al., 1986; Runkle, 1991) or a combination of many stages for different life-history functions (McComb and Muller, 1983), and they would be temporarily deprived of habitats if continuity in dead wood recruitment was modified by harvesting.

4.3. Potential implications at the landscape scale

In unmanaged northeastern hardwoods, the micro-gap regime disturbance interval is long relative to the recovery time and only a small fraction of land is affected at any one time by such disturbance (i.e. gap scale) (Turner et al., 1993). The different phases of stand development (recently disturbed, recovering, etc.) are in equilibrium at the landscape scale (Turner et al., 1993). However, in the SC studied here, it seems highly unlikely that the old-growth characteristics would have recovered before the next entry.

One of the major consequences of this discrepancy between recovery time and logging return interval might be an excess of relatively open stands and a deficit in structural characteristics typical of mature and old-growth stands at the landscape level (Turner et al., 1993; Haeussler and Kneeshaw, 2003), especially if selection cutting is the main harvesting system used. Tolerance elasticity of some disturbance-sensitive species might be shorter than the time required by a forest stand to recover. Therefore, if no adequate habitat is readily available, given the life history traits of a species (e.g. dispersal abilities, home range), such species may be temporarily or permanently eliminated from the system (Siitonen and Martikainen, 1994).

The process of regulating stand age-class distribution in a managed territory has been recognized as problematic in boreal forest even-aged management since it does not allow for the maintenance and development of overmature or old-growth stands (Haeussler and Kneeshaw, 2003). This is less evident in an uneven-aged management context since forest cover is maintained through time, but the same concept does apply. Given that about 30% of the basal area is harvested at each entry using a selection cutting system, all trees will theoretically have been harvested within four entries, which does not allow for trees to grow beyond their size or age of commercial maturity. In its actual version, selection cutting may be threatening the long-term integrity of the forest through repeated small cumulative effects.

4.4. Management recommendations

Even if the DLC studied here had been performed approximately 30 years earlier than the SC, more striking compositional and structural differences were observed between DLC and OG than between SC and OG. In other words, this suggests that the ecological distance between DLC and OG is larger than between SC and OG. However, many important differences remain between SC and OG, in terms of structure and composition. From a management perspective, the issue is therefore to propose mitigation measures considering the likely long-term impact of such a silvicultural practice.

To address the issue of logging intervals being probably shorter than recovery time, we recommend, given the current practice, allowing portions of forest to undergo greatly extended logging return intervals. This would provide continuous supply in old-growth characteristics in the landscape by maintaining relatively closed conditions in some areas and ensuring that larger living trees, and eventually larger snags and coarse woody debris, are continuously produced.

To mitigate the likely shortage in large trees and highly ecologically valuable dead wood, we recommend implementing some variants of the tree retention approaches advocated in clearcut systems, either by leaving some existing snags and large living trees dispersed within stands (Goodburn and Lorimer, 1998; Hale et al., 1999; McGee et al., 1999; Fraver et al., 2002) or by leaving small patches of intact forest within harvested areas that allow conservation and production of these structural elements (Hagan and Grove, 1999). To prevent the homogenization of understory stand structure over large areas, we recommend varying the intensity level of partial cutting both within and among stands to maintain a certain level of heterogeneity.

In this article, the focus has been on a comparison between the effects of harvesting regimes and a natural micro-gap regime, at the stand scale. Small-scale gap disturbance is the main natural disturbance in northeastern hardwoods, but other types of less frequent but more intense and larger-scale natural disturbances also occur in these forests (e.g. ice storms, fires, windstorms). Trying to incorporate some aspects of those larger-scale disturbances in our management would help to preserve landscape diversity as it naturally occurs. However, given that most of these moderate and severe disturbances are uncontrollable, managers should ensure that the natural level of representation is not excessively multiplied in management practices.

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