A comparison of forest structure among old-growth, variable retention harvested, and clearcut peatland black spruce (*Picea mariana*) forests in boreal northeastern Ontario[1]

by Aaron M. Deans[2,3], Jay R. Malcolm[2], Sandy M. Smith[2] and Terance J. Carleton[2]

Harvesting techniques that retain structural elements of the original forest may help to preserve the characteristic ecological features and biological diversity of old-growth forests. Harvesting with advance regeneration protection (HARP) is one such technique practised in the Lake Abitibi Model Forest of northeastern Ontario on peatland sites. In this system, winter harvesting operations clear trees in strips about 5–7 m wide and using a minimum diameter limit cut extract trees from the adjacent residual forest rows, 5–9 m wide. In order to assess the effectiveness of HARP in retaining forest structure, we quantified forest and understorey structural features in 24 1.65-ha plots spanning a wide range of forest retention, including clearcuts, three levels of HARP, and the edge and interior of unharvested forest (logging had occurred 2.5–3.5 years before the study). Mean tree age, diameter, and height in HARP forests in all cases exceeded 68% of the mean values found in unharvested forest, which was strikingly higher than the percent retention of basal area (20–43%). Also, unlike clearcuts, HARP forests retained the inverse-J curves between stem density and size class observed in unharvested forests, although stem densities in all size classes were lower. The percentage of black spruce regeneration originating from seed versus vegetative layering was directly related to the amount of forest basal area retained, averaging 2–5% in unharvested forests, 9–38% in HARP forests, and 67% in clearcuts. Many understorey characteristics closely followed the harvest intensity gradient, with amounts of moss, lichen, and *Ledum* highest at the unharvested end of the gradient and amounts of decaying moss, coarse and fine downed woody debris, exposed soil, and sedge highest at the clearcut end of the gradient. When the structural features were combined into a single composite variable using Principal Components Analysis (PCA) and the scores plotted against basal area, the relationship was curvilinear, with HARP treatments retaining greater amounts of structural characteristics than expected based solely on the basal area of wood harvested. This research suggests that the retention and redevelopment of old-growth features in peatland black spruce forests will be better under a HARP system than under a traditional clearcut system. Longer-term research, specifically on the edge habitats created by the HARP system, is required.

Key words: boreal, peatland, black spruce, alternative harvesting methods, forest ecology

Les techniques de récolte conservant les éléments structuraux de la forêt d'origine peuvent aider à préserver les caractéristiques écologiques et la diversité biologique des vieilles forêts. La récolte accompagnée de la protection de la régénération préexistante (RPRP) est l'une de ces techniques appliquées dans les stations à tourbières de la forêt modèle du lac Abitibi, dans le Nord-Est de l'Ontario. Elle consiste à couper, l'hiver, les arbres à partir d'une limite minimale de diamètre, sur des bandes de 5 à 7 m de largeur et à extraire les arbres des bandes résiduelles contiguës, qui ont de 5 à 9 m de largeur. Afin d'évaluer l'efficacité de cette méthode pour le maintien de la structure de la forêt, nous avons quantifié les caractéristiques structurelles de la forêt et du sous-étage sur 24 placettes de 1,65 ha se trouvant dans des peuplements soumis à une large gamme de régimes de conservation, notamment des coupes à blanc, trois niveaux de RPRP et la lisière et l'intérieur d'une forêt non exploitée (la coupe avait eu lieu de 2,5 à 3,5 ans avant l'étude). L'âge moyen des arbres, leur diamètre et leur hauteur, dans les forêts soumises à la RPRP, excédaient dans tous les cas 68 % des valeurs moyennes observées dans la forêt non exploitée, ce qui, de façon frappante, était supérieur au pourcentage de conservation de la surface terrière (20–43 %). En outre, contrairement aux coupes à blanc, les forêts soumises au RPRP ont conservé les courbes en J inversé entre la classe de densité des tiges et la classe de tailles observées dans les forêts non soumises à la récolte, bien que la densité des tiges ait été inférieure dans toutes les classes de tailles. Le pourcentage de régénération de l'épinette noire provenant de semences, par opposition au marcottage, était directement proportionnel à la surface terrière de la forêt conservée, s'établissant en moyenne de 2 % à 5 % dans les forêts non soumise à la récolte, de 9 % à 38 % dans les forêts soumises à la RPRP et à 67 % dans les coupes à blanc. Beaucoup de caractéristiques du sous-étage coïncidaient fidèlement avec le gradient d'intensité de la récolte, les quantités de mousses, de lichens et de lédons étant maximales à l'extrémité du gradient correspondant à l'absence de récolte et les quantités de mousses en décomposition, de débris ligneux grossiers et fins jonchant le sol, de sol exposé et de carex étant maximales à l'autre extrémité du gradient. Après réunion des caractéristiques de la structure en une simple variable composée, à l'aide de l'analyse en composantes principales, et report, sur un graphique, des pointages en fonction de la surface terrière de la forêt, on constate que la relation est curviligne, les traitements sous le régime de la RPRP conservant plus de caractéristiques structurales que prévu, uniquement d'après la surface terrière du bois récolté. Cette recherche porte à croire que la conservation et l'évolution ultérieures des caractéristiques de la vieille forêt dans les forêts d'épinettes noires des tourbières seront meilleures dans un système de RPRP que dans un système traditionnel de coupe à blanc. Il faut poursuivre une recherche à plus long terme, plus précisément dans les habitats créés à la lisière des peuplements soumis à la RPRP.

Mots clés : boréal, tourbière, épinette noir, modes alternatifs de récolte, écologie forestière

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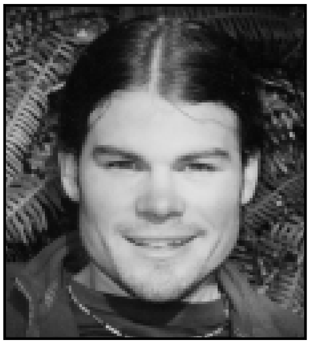
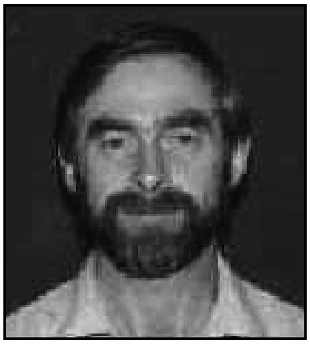
[2] Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, Ontario M5S 3B3

[3] Corresponding author. E-mail: aaron.deans@utoronto.ca


Aaron M. Deans


Jay R. Malcolm


Sandy M. Smith


Terance J. Carleton

Introduction

Old-growth forests are important for a wide range of organisms, in part because of their unique structural characteristics such as large-diameter trees (living and dead), relatively closed and multi-layered canopies, and abundant decaying coarse woody material (e.g., Welsh 1987, Crow 1990, Thompson 1994, Okland 1996, Spence *et al.* 1996). In the boreal forest, where disturbance-initiated succession is an intrinsic feature of the forest ecosystem and is widely regarded as a key influence in forest development (Larsen 1980, Heinselman 1981, Wein and MacLean 1983, Pickett and White 1985, Payette 1992, Attiwell 1994, McCullough *et al.* 1998, Bergeron *et al.* 2001, Churcher 2001), these old-growth forests are a self-perpetuating, late-seral stage that is characterized by single-tree replacement processes rather than by stand-replacing events such as wildfire or clearcut logging (Burton *et al.* 1999).

It is generally acknowledged that secondary forests originating from clearcuts differ from old-growth forest with respect to both the spatial arrangement of seral stages and many stand-level attributes (e.g., Kimmins 1997). These differences are of special concern in the boreal forest of Canada, where industrial clearcut logging has become an increasingly common land use (Jackson *et al.* 2000). Anthropogenic disturbances such as logging typically result in the loss of old forests from the landscape and a truncation of the characteristic post-fire stand age distribution (Bergeron *et al.* 2001). In addition, the development of structural diversity within stands may differ following anthropogenic and natural disturbances; for example, the accumulation of downed woody debris may differ significantly between forests originating from clearcut logging versus those initiating from fire, resulting in a simplified forest structure (Sturtevant *et al.* 1997, Sippola *et al.* 1998).

Better characterization of old-growth structural elements and their responses to disturbance may allow for development of harvesting methods that retain more elements of old-growth ecological diversity (Haila 1994, Noss and Cooperrider 1994, Niemelä 1999). Several methods have been developed that attempt to maintain the structural heterogeneity of old-growth forests into the post-harvest condition. One approach is to leave a significant portion of the original forest behind in what is known as variable retention (VR) harvesting (Franklin *et al.* 1997). Variable retention harvesting systems retain structural elements of the harvested stand for at least the next rotation, in part to retain ecological characteristics associated with structurally complex forests. This structural retention may provide refugia for elements of biological diversity that otherwise might be lost from the harvested area, either by fulfilling habitat/microclimate requirements and/or by retaining structures that reduce the physical changes accompanying forest removal. However, the extent to which such harvesting will ameliorate the net loss of old-growth forests is poorly understood. Of particular importance is an understanding of the relationship between the amount and spatial configuration of the retention and subsequent changes in structural and biological diversity (Franklin *et al.* 1997).

In peatland black spruce (*Picea mariana* [Mill.] B.S.P.) forests of the Lake Abitibi Model Forest (LAMF) in northeastern Ontario, the importance of retaining structural elements in the harvested stand has been recognized for a number of reasons. The advance regeneration in the forest understorey represents the next cohort of merchantable black spruce trees, which may require less time to reach maturity than aerially seeded or planted seedlings. Retention of this advance growth has the potential to reduce the need for costly restocking of harvested stands, which is not always successful. Furthermore, the retention of residual seed-producing trees in the harvested stand offers the possibility of regeneration of adjacent harvested areas by natural processes.

In order to take advantage of these possibilities, a form of VR harvesting known as "harvesting with advance regeneration protection" (HARP) has been widely implemented on LAMF peatland sites (MacDonell and Groot 1997). HARP is a method of strip harvesting wherein the principle aims are to: (1) maintain an intact forest floor and organic layers by using winter harvesting and by restricting the movement of harvesting equipment, (2) ensure the preservation of advance regeneration of black spruce, and (3) conserve some of the natural structural heterogeneity of the stand by leaving residual rows of non-merchantable seed trees (Groot and Horton 1994, Tallman 1998). Under this system, harvesting operations clear trees in strips approximately 5–7 m wide and extract trees from the adjacent residual forest rows using a minimum diameter limit cut. The residual rows of cone-producing subcanopy trees and advance regeneration are 5–9 m wide. Retaining this residual structure is thought to decrease the time to the next harvest and to reduce costly regeneration expenses (MacDonell and Groot 1996). It may also result in the retention and/or rapid redevelopment of habitat features important for old-growth species.

The objective of this study was to compare the structural characteristics of these HARP stands with those of two other forest types: old-growth peatland black spruce forests and traditional clearcut stands. Because the amount of structural retention varied considerably among HARP stands, we were able to investigate a full gradient of structural retention at the

LAMF site. We were particularly interested in the degree to which stand structural features (including the diameter distribution of black spruce trees, advance regeneration, understorey cover types, and downed woody debris) were maintained as a function of the total basal area removed. Was the change in stand structure in proportion to the amount of basal area removed, or did the HARP system allow for more old-growth characteristics to be preserved than might be expected based on the amount of wood harvested?

Methods

Study area: the Lake Abitibi Model Forest

Throughout the boreal zone of Canada, peatlands often support black spruce forests (Ketcheson and Jeglum 1972). In the Clay Belt region of northeastern Ontario and Quebec, half the black spruce forests are found on peatlands (MacDonell and Groot 1996). Typically, peatland black spruce trees grow very slowly and form multi-aged cohorts of trees (Groot and Horton 1994). In contrast to even-aged upland sites, where stand-replacing fires are prevalent, peatland black spruce stands are less prone to fire (Vincent 1965, Johnson 1992, Payette 1992). In the LAMF, the average age of black spruce trees on peatland sites is 172 years. In some cases, the time since fire can be greater than 500 years (Bergeron *et al.* 2001), which is considerably longer than the normal longevity of black spruce (200–350 years) (Farrar 1995, Greene *et al.* 1999). Peatland black spruce forests that escape fire beyond maturity typically have an uneven-aged and size-class structure and demonstrate an inverse-J relationship between the abundance and diameter distribution of stems (MacDonell and Groot 1996, Smith *et al.*1997). In these peatland forests, mortality of old trees creates light gaps in the canopy and offers opportunities for growth of trees in the previously light-deprived understorey. Black spruce has effective vegetative reproduction (via layering), is moderately shade tolerant, and can remain suppressed in the understorey for long periods of time (Vincent 1965, Groot and Hokka 2000). The resulting structure of old-growth peatland black spruce forests is a multi-storeyed forest with many openings in the canopy, diverse microclimatic conditions, and abundant advance regeneration.

The Lake Abitibi Model Forest (LAMF), located in the Clay Belt of northeastern Ontario, includes a mosaic of forest types and stand ages across its million-hectare landscape. Black spruce is the dominant tree species in the peatlands (Groot and Horton 1994, Farrar 1995), however larch (*Larix laricina* Du Roi) may also be found on boggy sites and occasionally balsam fir (*Abies balsamea* L.) on fresh to moist sites (Lagacy *et al.* 1995). The climate of the Clay Belt is continental, although modified by the presence of the Great Lakes to the south and Hudson and James Bays to the north (Rozee and Wolfe 1982). The mean annual temperature is between –1.1 and 1.7°C, with an average growing season of 140–169 days (Lagacy *et al.*1995). The frost-free period is typically from June to mid-September. Mean annual precipitation averages 66–76 cm, of which approximately 20–25 cm is as summer rain. Snowfall is heavy, with an annual mean accumulation of 280 cm (Brumelis and Carleton 1988).

Site selection

To aid in site selection, Forest Resource Inventory (FRI) maps (Ontario Ministry of Natural Resources, unpublished) were overlaid onto information on harvesting operations in the area. Only stands that were classified in the FRI as 100% black spruce were considered for this study. All sites were in two Forest Ecosystem Classification (FEC) Operational Groups: *Ledum* (OG11) and *Alnus* herb-poor (OG12) (Jones *et al.* 1983). The two dominant vegetation types (McCarthy *et al*. 1994) were V25 (labrador tea–sphagnum) and V24 (speckled alder–sphagnum–Schreber's moss). Only sites of moderate productivity (FRI site classes 2 and 3; Plonski 1974) were selected for study. Stands were visited on the ground to visually verify stand compositional information in the FRI. In a few cases, some of the chosen sites stands were only 80–90% black spruce, with balsam fir, larch and, to a lesser degree, eastern white-cedar (*Thuja occidentalis* L.) making up the remainder.

Five levels of forest retention were selected, ranging from intact, unharvested forests, through three levels of HARP retention, to clearcut areas. Within unharvested forest, we selected two treatments: areas within 150 m of harvested forests (unharvested edge = UE) and areas greater than 150 m from any harvesting in some of the few remaining large contiguous uncut forests in the region (unharvested interior = UI). We chose these two treatments in part to strengthen our baseline observations of unharvested peatland black spruce forests, but also to test whether edge effects from nearby harvesting influenced the insect communities of uncut forests (Deans *et al.* in prep.).

Because HARP harvesting is based on a minimum diameter limit cut, the amount of forest retention in a stand depended in part on the initial distribution of tree sizes (another factor was the efficacy of the machine operator in following the harvest prescription). If all trees were above the diameter limit, the result was a clearcut, whereas if many trees were below the limit, the result was a strip cut. The amount of retention thus varied from stand to stand across the landscape, which allowed us to sample a full range of harvest intensities. In HARP areas, three levels of forest retention were selected based on *a priori* visual assessments of the amount of forest clearing in a local 1.65-ha harvested area. They were: low-retention HARP areas (which were usually close to cleared areas) (= HL), medium-retention HARP areas within the interior of contiguous HARP (strip-cut) forests (= HM), and high-retention HARP areas at the edge of unharvested forests (= HH). Clearcut areas were those with very little to no retention of trees (= CC). All harvesting occurred in 1995–1996 or 1996–1997, 3.5–2.5 years before the study. In total, 24 sites (four per treatment) were selected for study based on the above criteria and upon ease of access. All plots were within the rectangle 49.48–49.70° N latitude, 80.28–80.84° W longitude.

Study plot design

In each selected area, a 110 × 150-m (1.65-ha) study plot was delineated. Centred within that plot was a 10 × 50-m subplot (Fig. 1). In HARP-harvested forests, plots were located such that the subplot was oriented parallel to the axis of the strip cutting and such that 5 m of the subplot extended into the cut corridor and 5 m into the residual strip of trees. At HARP sites, the subplot sampled an area where strip cutting was evident, whereas in other areas of the plot, strips might not have been evident (such as in HL and HH sites). At HH sites, the plot was positioned such that the subplot was within HARP forest, but at the edge of unharvested forest. The centres of the plots were at least 75 m from waterways, forest edges along roads,

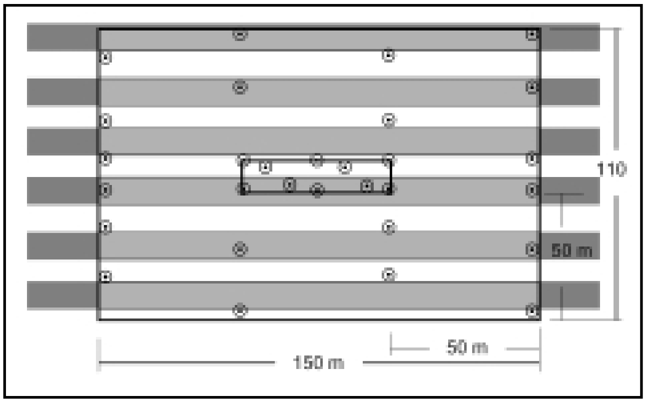


Fig. 1. Schematic representation of a study plot (110 × 150 m) and a nested subplot (10 × 50 m) used to sample forest structure in 24 stands of the Lake Abitibi Model Forest. ⊙ = 2-m radius sampling station. White stripes represent cleared corridors and grey stripes represent residual leave strips.

and edges of neighbouring study plots. The average nearest neighbour distance between plot centres was 420 m. Because of the pattern of road access, most of the study sites were grouped into three main research areas (of about 3000 ha each). To the extent possible, treatments were randomly interspersed within each area.

Within each plot, sampling took place in 30 stations that were 2 m in radius and were systematically placed throughout the plot (Fig. 1). The density of stations was higher in the subplot than elsewhere because of insect sampling there (Deans *et al.* in prep.). Although systematic, the stations were spaced irregularly to ensure representative sampling over the range of forest conditions in each plot.

Data collection

In 1999, numerous structural characteristics of the forest and understorey were measured in the 2-m radius sampling stations. Here, we define "structure" in a broad sense to include a wide variety of potentially important old-growth habitat features, including structural characteristics of the tree community itself as well as substrate characteristics in the forest understorey. The diameters of all live and standing dead black spruce trees whose stems originated within the sampling station were measured. Abundance of black spruce stems was determined in four regeneration height classes: < 10 cm, 10 – < 30 cm, 30 – < 150 cm and 150 – < 300 cm. Regenerating stems < 30 cm high were further categorized by propagation type (seed versus vegetative layering).

The percentage and type of ground cover under a 2-m measuring pole was assessed to the nearest 10%. One end of the pole was held at the station centre and measurements were taken in each of the four cardinal directions for a total of 8 m of line-transect per station. Ground cover types were: dead moss, live moss, fine downed woody debris (< 4 cm in diameter), coarse downed woody debris (> 4 cm, including stumps), lichen, sedge, water, bare soil, and conifer needles. Stumps, which provide a source of the decaying wood in the understorey, were measured across their top surface and decay class was assessed from one to five (recent = 1; highly decayed = 5; see Maser *et al.* 1979). Abundance of understorey shrub plants used to define FEC stands (labrador tea and speckled alder) was also measured with respect to percentage ground cover along the line transects and number of stems > 30 cm high.

Increment cores were taken at breast height from a minimum of five codominant or dominant residual standing trees in each subplot (except at clearcut sites). Height and diameter at breast height (dbh) of the cored trees also was recorded. In the lab, cores were sanded to increase the visibility of rings and ages were determined using a microscope-and-computer-based measurement system.

Data analysis

Study plots were the unit of replication; hence, means were calculated across the 30 sampling stations per plot. Comparisons among treatments were performed using analysis of variance (SAS v. 8.01) with Tukey's test as a multiple range test. Relationships between structural variables and basal area were examined using Spearman's rank correlation coefficients (STATISTICA 5.1). A Bonferroni-adjusted probability level ($P < 0.00125$) was used to control for the large number of comparisons and the resulting high probability of type-I errors. Because of the large number of habitat variables (30), Principal Components Analysis (PCA; Jongman *et al.* 1995) on the correlation matrix was used to summarize major patterns of variation in the data set. The analysis was conducted using CANOCO for Windows, v. 4.0 (ter Braak and Smilauer 1997). Habitat variables that demonstrated a non-normal distribution were transformed by natural logarithms [$\ln(x + 1)$] before ordination. Only those variables that showed significant Spearman correlations ($P > 0.05$) with basal area were included in the PCA. Principal component scores along the first axis were used to provide an overall measure of structural variation among the study plots and were subsequently plotted against basal area. In addition to the structural variables, we included basal area itself in the PCA because we were not only interested in structural retention as a function of basal area, but also in patterns of correlation among the various variables.

Results

Tree characteristics

Although greater tree basal area was found in the UI plots compared to the UE plots, the difference was not significant (Table 1). Similarly, the diameter, height, and age of dominant and codominant black spruce trees were slightly greater in UI than UE sites, but the differences again were not significant.

As expected given the experimental design, mean basal area was ranked in the sequence CC, HL, HM, HH, UE, UI (Table 1). Most other tree characteristics could also be ranked in the same sequence; the exceptions were average tree height and dbh, which were approximately equal in the HL and HM treatments. The HARP sites tended to show greater similarity to each other than to the unharvested forests, as evidenced by the fact that only two of 15 possible pair-wise comparisons were significant among the HARP stands, whereas six of 10 possible comparisons between HH and the two unharvested treatments were significant.

To directly compare retention of structural features between unharvested and harvested forests, we expressed means in the harvested treatments as percentages of the unharvested mean (Table 2). Given the lack of significant differences in tree characteristics between UE and UI sites, these treatments were com-

Table 1. Characteristics of black spruce trees in six treatments in the Lake Abitibi Model Forest of northeastern Ontario. Means (± SEM) are shown for the four replicate plots per treatment

	Treatment [5]						**ANOVA**	
Stand characteristic	CC	HL	HM	HH	UE	UI	F$_{1,23}$	P
Advance regeneration								
< 10 cm (trees/ha)	2499^{a} ± 739.7	1862^{b} ± 131.3	1816^{b} ± 447.6	849^{c} ± 221.6	1299^{bc} ± 157.8	1074^{c} ± 404.9	6.56	<.0001
10 – < 30 cm (trees/ha)	3693^{a} ± 653.7	3865^{a} ± 659.0	4568^{ab} ± 737.7	4853^{ab} ± 337.3	5403^{b} ± 440.3	3772^{a} ± 497.9	5.14	0.0001
30 – <150 cm (trees/ha)	1352^{a} ± 511.1	2466^{b} ± 310.7	2579^{b} ± 315.9	3076^{b} ± 359.9	3069^{b} ± 357.5	2168^{b} ± 369.6	7.59	<.0001
150–<300 cm (trees/ha)	444^{c} ± 29.3	643^{bc} ± 180.4	815^{ab} ± 117.4	988^{a} ± 90.9	1100^{a} ± 182.6	948^{a} ± 106.2	5.99	<.0001
% from seed[1]	67.3^{a} ± 14.3	38.0^{b} ± 6.4	35.4^{b} ± 9.8	8.5^{c} ± 5.1	5.1^{c} ± 4.4	2.0^{c} ± 1.8	47.7	<.0001
Trees								
Basal area (m^2/ha)	1.07^{a} ± 0.1	4.68^{b} ±0.3	6.31^{b} ± 0.7	9.75^{b} ± 1.3	19.49^{c} ± 3.3	26.32^{c} ± 3.1	27.6	<.0001
Density (trees/ha)[2]	212^{a} ± 39.0	855^{b} ±27.4	1114^{c} ± 133.1	1379^{c} ±151.0	2246^{d} ± 213.4	2394^{d} ± 258.6	91.2	<.0001
Height (m)	–	9.5^{a} ± 0.5	9.4^{a} ± 1.0	10.7^{b} ± 0.8	12.0^{b} ± 1.3	13.9^{b} ± 1.1	21.1	<.0001
Dbh (cm)[3]	–	11.8^{a} ± 0.7	11.7^{a} ± 0.7	13.0^{ab} ± 1.3	14.4^{c} ±1.5	16.6^{c} ± 2.0	12.9	<.0001
Age (years)[4]	–	95.7^{a} ± 27.8	99.0^{ab} ± 20.0	115.0^{abc} ± 25.2	131.2^{bc} ± 18.8	148.3^{c} ± 16.4	5.77	0.0003

[1] Percentage of black spruce advance regeneration (< 30 cm) originating from seed.

[2] Density of stems > 4 cm dbh.

[3] Diameter of tree measured at breast height.

[4] Based on mean ages of five dominant or codominant trees per plot.

[5] CC = Clearcut forest; HL = Low-retention HARP; HM = Medium-retention HARP; HH = High-retention HARP; UE = Unharvested forest < 150 m from harvest; UI = Unharvested contiguous forest > 150 m from harvest). Means followed by the same letter were not significantly different at $\alpha = 0.05$ (Tukey's test).

Table 2. Percentage retention of structural elements in harvested forests of the Lake Abitibi Model Forest relative to unharvested forest sites (UI+UE; *n* = 8)

		Harvested areas [1]			
Forest structural variables	Unharvested (± SEM)	HH	HM	HL	CC
Advanced regeneration					
< 10 cm (trees/ha)	1186.5 ± 557.0	71.5 %	153.0 %	156.9 %	210.6 %
10 – < 30 cm (trees/ha)	4587.5 ± 1816.7	105.8 %	99.6 %	84.2 %	80.5 %
30 – < 150 cm (trees/ha)	2618.5 ± 1151.2	117.5 %	98.5 %	94.2 %	51.6 %
150 – 300 cm (trees/ha)	1024.0 ± 311.7	96.5 %	79.6 %	62.8 %	43.3 %
Trees					
Basal area (m^2/ha)	22.91 ± 6.99	42.6 %	27.5 %	20.4 %	4.7 %
Age (years)	139.8 ± 36.9	82.3 %	70.8 %	68.4 %	–
Diameter (cm)	15.5 ± 4.0	83.9 %	75.5 %	76.1 %	–
Height (m)	12.9 ± 3.0	82.6 %	72.6 %	73.4 %	–
Density (trees > 4 cm dbh/ha)	2320.0 ± 438.4	59.4 %	48.0 %	36.8 %	9.1 %

[1] HH = High; HM = Medium; and HL = Low-retention HARP forests; CC = Clearcut forests.

bined into a single category (= UN), representing the unharvested (baseline) forest condition.

In all of the HARP treatments, percentage retention of tree age, diameter, and height was strikingly higher than expected based on percentage retention of basal area (Table 2). Although only 43% of basal area was retained under high-retention HARP harvesting, retention of these other variables in all cases exceeded 82%. Similarly, although 28 and 20% of basal area was retained in the HM and HL treatments respectively, retention of the other variables was in the range 68–76%. Not surprisingly, percentage retention of tree density more closely approximated basal area retention, varying in the range 37–60%. Clearcut areas had 95% of the baseline forest basal area removed, corresponding to 91% removal of black spruce stems relative to the baseline forest.

Diameter distributions revealed that the black spruce trees retained in the HARP-harvested forests followed the inverse-J curves typical of the unharvested forests, although stem densities in all size classes were lower in the HARP stands than in the uncut forests (Fig. 2). Clearcut stands failed to show this inverse-J structure.

Black spruce regeneration

Regenerating black spruce seedlings and saplings tended to be more abundant in the understorey of unharvested edge (UE) compared with unharvested interior (UI) forests; however, the difference was only significant for stems in the 10 – < 30 cm size class (Table 1). Of the regeneration assessed in the < 30-cm size class, most arose from vegetative layering. Regeneration arising from seed was relatively rare, averaging only 5% in the UE forest and 2% in the UI forest.

The amount of black spruce regeneration in the understorey tended to be similar among the HARP and unharvested stands (Table 1). In only two of 24 pair-wise comparisons between a HARP treatment and one or the other of the unharvested treatments was the regeneration abundance significantly different. The two exceptions were the number of stems in the largest size class (150 – < 300 cm), which was significantly lower in the low-retention HARP treatment than in both the UE and UI treatments. The smallest regeneration size class (< 10 cm) had the greatest abundance in clearcut areas, with more than twice as many stems than in the old-growth forest (2499 versus 1186 stems/ha). Regeneration in the

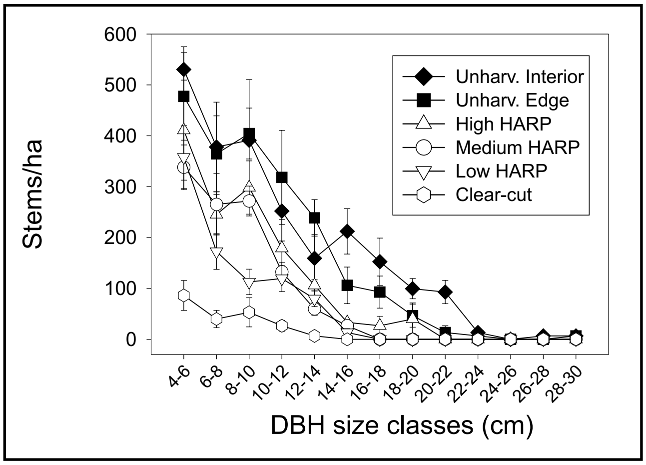


Fig. 2. Stem density of black spruce on peatland study plots in the Lake Abitibi Model Forest area of northeastern Ontario plotted in dbh classes.

other size classes was always lower in the clearcuts than elsewhere, although significantly so only for the 30 – < 150-cm size class.

Percent retention of regeneration relative to the unharvested (UN) forests was much higher than might have been expected based on retention of basal area (Table 2). With the exception of the largest stems in the HL treatment (63%), percentage retention in the HARP areas, relative to unharvested forests, was in the range 79–157%. The abundance of the smallest trees in the clearcuts was 211% relative to the unharvested forest, whereas retention in the larger size classes ranged from 43–81%.

The ratio of black spruce regeneration originating from vegetative layering versus seed appeared to be directly related to the retention of forest basal area (Table 1). On average, less than 5% of advance regeneration < 30 cm tall in unharvested forests was from seed. Conversely, 67% of regeneration in the clearcut plots originated from seed, which was significantly higher than in the other treatments. The low (38%) and medium-retention (35%) HARP plots did not have significantly different proportions of regeneration arising from seed; however, they had significantly greater proportions than in HH and unharvested forests. The proportion of regeneration arising from seed in the high-retention HARP treatment (9%) most closely resembled the unharvested forest.

Ground cover

Many of the understorey characteristics closely followed the harvest intensity gradient and in most cases could be ranked in the sequence CC, HL, HM, HH, UN (Table 3). Where exceptions occurred, they tended to be between treatments that were adjacent to each other in the basal area gradient (such as between HL and HM). Needle and water did not demonstrate significant differences across the treatments. Although the number of *Alnus* stems exhibited significant differences among the treatments, the differences did not appear to be related to the disturbance gradient.

On average, 88% of the ground was covered with mosses in the unharvested forests (Table 3). High- and medium-retention HARP stands retained 74% and 68% of this moss cover, respectively, which was significantly lower than in unharvested forests. Low-retention HARP plots preserved significantly less moss than high-retention HARP, but significantly more than in clearcuts.

In contrast, an inverse relationship between the amount of decaying moss and forest retention was observed (Table 3). Virtually no dead moss was observed in the unharvested study plots. High-retention HARP sites had similarly small proportions of decaying moss ground cover as the unharvested forest. However, medium- and low-retention HARP-harvested plots had significantly greater amounts than unharvested forests, with an average of more than 8% in both. Clearcut sites on average had 23% of their substrate covered with dead moss.

Downed woody debris was more abundant overall in harvested than in unharvested stands. Coarse wood (> 4 cm in diameter) was significantly more abundant in the understorey of low-, medium-, and high-retention HARP-harvested forests than in unharvested forest. Not surprisingly, clearcuts had the greatest amount of coarse woody debris on the ground (approximately three times as much as in unharvested plots). The amount of fine wood (< 4 cm in diameter) was also significantly greater in harvested than in unharvested forests. In high-retention HARP sites, 8% of the ground was covered with fine wood. The percentage cover of fine wood in medium- and low-retention HARP study plots represented the next significant level of the fine downed wood debris. The highest percentage of fine woody debris was recorded in cleared study plots, and was significantly higher than in any other treatment.

The percentage cover of lichens and *Ledum* in the unharvested forest was preserved in similar quantities in the low-, medium-, and high-retention HARP-harvested forests. Clearcut study sites had half as much *Ledum*, however, and lichens only covered 0.3% of the substrate. Virtually no exposed mineral soil or sedge was found in the unharvested plots, whereas clearcut plots had the greatest amount of exposed soil and sedge. Low-, medium-, and high-retention HARP-harvested forests had significantly greater amounts than the baseline forest, although the differences were relatively slight.

In addition to the downed woody debris in the understorey described above, stumps and standing dead trees represented another major source of decaying wood in the forest. Not surprisingly, stump basal area and decay class closely followed the retention gradient. The mean density of standing dead trees was not significantly different among treatments. On average, HARP-harvested forests maintained a similar number of snags as unharvested forest (Table 3).

Correlations with basal area

Spearman's correlations revealed many significant correlations between the structural variables and basal area. Four of 12 stand-level structural characteristics and nine of 18 understorey variables were significantly correlated with forest basal area (Table 4). Among tree characteristics, tree density had the strongest correlation, followed by the abundance of large trees (dbh > 15 cm). Average forest height and age also showed strong positive correlations with basal area.

Other variables that correlated positively with basal area included moss ground cover, the relative abundance of black spruce regeneration arising from vegetative layering, the degree of stump decay, as well as the percentage cover of *Ledum* ground cover. Variables that were inversely correlated to forest

Table 3. Dead wood and ground cover characteristics for five treatments in the Lake Abitibi Model Forest (LAMF) of northeastern Ontario. Means (± SEM) are shown for the replicate plots per treatment

	Treatment [5]					**ANOVA**	
Understorey characteristic	CC	HL	HM	HH	UN	$F_{1,23}$	P
Stumps							
Basal area (m^2/ha)	42.60 ^{a} ± 5.6	25.35 ^{b} ± 2.2	22.80 ^{b} ± 3.0	21.57 ^{b} ± 4.5	7.70 ^{c} ± 3.6	14.96	< .0001
Decay class [1]	2.7 ^{a} ± 0.1	2.7 ^{a} ± 0.1	2.9 ^{a} ± 0.2	2.9 ^{a} ± 0.1	4.2 ^{b} ± 0.2	11.59	< .0001
Snags [2]							
Density (snags/ha)	20 ^{a} ± 12	93 ^{a} ± 8	106 ^{a} ± 54	66 ^{a} ± 28	96 ^{a} ± 73	0.73	0.6123
Substrate [3]							
Moss	41.5 ^{a} ± 5.9	62.6 ^{b} ± 5.4	68.0 ^{bc} ± 7.5	74.3 ^{c} ± 4.9	88.2 ^{d} ± 3.1	93.56	< .0001
Dead moss	22.6 ^{a} ± 4.1	8.7 ^{b} ± 2.8	8.2 ^{b} ± 2.6	4.0 ^{bc} ± 0.5	0.6 ^{c} ± 0.2	53.13	< .0001
Coarse wood	12.0 ^{a} ± 1.6	8.3 ^{b} ± 0.9	7.2 ^{bc} ± 1.3	8.6 ^{b} ± 0.9	4.3 ^{c} ± 2.4	15.63	< .0001
Fine wood	14.9 ^{a} ± 2.6	11.4 ^{b} ± 2.8	12.0 ^{b} ± 2.8	7.9 ^{c} ± 2.0	3.2 ^{d} ± 1.2	36.07	< .0001
Lichen	0.3 ^{a} ± 0.0	3.7 ^{b} ± 1.1	3.1 ^{b} ± 1.2	3.9 ^{b} ± 0.8	4.3 ^{b} ± 1.9	4.24	0.0008
Needle	0.4 ^{a} ± 0.3	0.3 ^{a} ± 0.1	0.1 ^{a} ± 0.0	0.1 ^{a} ± 0.0	0.6 ^{a} ± 0.3	1.08	0.3700
Water	0.3 ^{a} ± 0.2	1.1 ^{a} ± 0.1	0.2 ^{a} ± 0.0	0.4 ^{a} ± 0.1	0.8 ^{a} ± 0.3	1.51	0.1848
Sedge	4.3 ^{a} ± 0.5	0.6 ^{b} ± 0.1	1.1 ^{b} ± 0.1	0.4 ^{b} ± 0.1	0.2 ^{b} ± 0.1	13.89	< .0001
Soil	3.7 ^{a} ± 1.7	3.3 ^{a} ± 0.3	0.1 ^{b} ± 0.0	0.6 ^{b} ± 0.1	0.0 ^{b} ± 0.0	11.69	< .0001
Ledum	15.1 ^{a} ± 4.3	25.4 ^{b} ± 1.7	28.4 ^{bc} ± 2.4	33.0 ^{c} ± 2.7	32.1 ^{bc} ± 3.2	23.41	< .0001
Alnus (stems/ha) [4]	673 ^{a} ± 229.8	269 ^{b} ± 177.8	460 ^{ab} ± 176.3	281 ^{ab} ± 197.1	416 ^{ab} ± 210	3.78	0.0220

[1] Decay class of stump (1 = fresh to 5 = old) based on Maser *et al.* (1979).

[2] Snags = standing dead black spruce trees.

[3] Percentage ground cover measured along 8 m of line transect per station.

[4] Number of speckled alder (*Alnus rugosa*) stems > 30 cm in height.

[5] CC = Clearcut forest; HL = Low-retention HARP; HM = Medium-retention HARP; HH = High-retention HARP; UN = unharvested forest (UI+UE; *n* = 8).). Means followed by the same letter were not significantly different at $\alpha = 0.05$ (Tukey's test).

basal area included dead moss ground cover, abundance of seedlings from seed, fine woody debris, stump basal area, and sedge ground cover.

Multivariate analysis of forest structure

The first PCA axis, which accounted for 51.7% of the total variance in the data, was influenced primarily by the forest removal gradient (Fig. 3). Clear separation of unharvested forest sites on the left half of the ordination and clearcut forests on the far right is seen along this axis. HARP-harvested forests are centrally located, with high-retention HARP forests closest to unharvested sites. Most variables loaded negatively on the first axis, with unharvested forests having the greatest density, height, and diameter of trees, as well as the largest proportion of the understorey covered with moss. The degree of stump decay, the amount of *Ledum* in the understorey, and sapling abundance in the 30–150 cm and 151–300-cm size classes were all greatest in high-retention forests. Clearcut sites had abundant regeneration (< 10 cm) originating from seed, dead moss, sedge, fine and coarse woody debris, and stump basal area. The second axis (13.2% of the total variance) was related to the total amount of regeneration in the understorey, especially in the 10 – < 30 cm and 30 – < 150 cm size classes. Little evidence of separation among treatments was shown along this axis (Fig. 3).

We used the principal component scores along the first axis as an overall measure of structural retention. When plotted against basal area, principal component scores of HARP treatments were below a line joining points for the clearcut and unharvested treatments, indicating a non-linear relationship between structural and basal area retention (Fig. 4). This suggests that HARP retained greater amounts of structural characteristics than might have been expected based solely on the basal area of wood harvested.

Table 4. Spearman rank correlations of stand and understorey characteristics against forest basal area[1]. Only variables with significant correlations based on a Bonferroni-adjusted level of significance ($p < 0.00125$) are shown

Habitat variable	R_S	**P**
Stand-level variables		
Tree density (trees/ha)	0.9726	< 0.0001
Trees > 15 cm diameter at breast height (dbh)	0.9150	< 0.0001
Stand height	0.8922	< 0.0001
Forest age	0.6546	0.0005
Understorey variables		
Moss ground cover	0.9058	< 0.0001
Ratio of regeneration from vegetative layering	0.8847	< 0.0001
Dead moss ground cover	–0.8522	< 0.0001
Seedling abundance[2]	–0.8376	< 0.0001
Fine woody debris	–0.8356	< 0.0001
Stump basal area	–0.7643	0.0001
Stump decay	0.7563	0.0002
Sedge ground cover	–0.7054	0.0001
Ledum groenlandicum cover	0.6478	0.0006

[1] Forest basal area (m^2/ha) was calculated using tree diameters (> 4 cm) measured at breast height and subsequently averaged for each of the four replicates in each treatment.

[2] Abundance of regenerating stems arising from seed.

Discussion

The natural variability of unharvested peatland forests was incorporated into this study by selecting unharvested sites from eight different forested areas across the managed landscape, including areas relatively close to (< 150 m) and far from (> 150 m) harvesting activities. These two landscape contexts showed similar structures on average, suggested that proximity to the harvested edge had little effect on structural or natural regeneration features of the forest, and warranting the

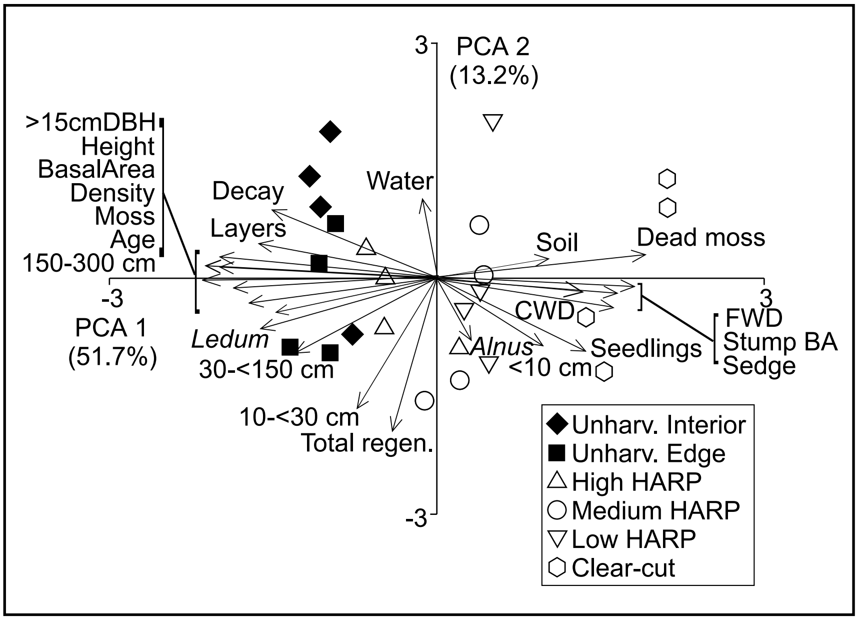


Fig. 3. Principal Components Analysis of structural variables measured in 24 peatland black spruce study plots in the Lake Abitibi Model Forest area of northeastern Ontario. The variables include tree characteristics (basal area, age, height, density, density of trees > 15 cm dbh), advance regeneration variables (density in regeneration height classes [< 10, 10 – < 30, 30 – < 150, 150–300 cm], total regeneration density, density of regeneration from seeds (seedlings), ratio of regeneration arising from vegetative layering (layers)), ground cover characteristics (moss, *Ledum*, *Alnus*, sedge, coarse woody debris (CWD), fine woody debris (FWD), dead moss, soil, and water), and stump characteristics (mean decay class (decay) and basal area (stump basal area). See text for details.

combination of the eight sites into a benchmark for comparison with harvested forests.

The importance of retaining old-growth forests in the landscape includes the preservation of genetic reservoirs of species and genes, and habitat refuges for shade-tolerant organisms, and as an ecological baseline for comparison with the regenerating forest (Hansson 1992). The abundance of some species may be directly dependent on microclimate conditions and indirectly dependent on the forest structures that define old-growth forests (e.g., Okland 1996). Short of preserving areas of contiguous unharvested forest, HARP harvesting represents a focused attempt to preserve old-growth forest structures and characteristic natural regeneration.

The retention of large numbers of trees in the HARP stands, especially of older trees, offers the possibility of regeneration of cleared travel corridors by natural processes. HARP-harvested forests had 70% of the baseline basal area removed on average; however, all three HARP treatments retained greater densities of trees (> 4 cm) per hectare as well as greater mean diameter, height, and age of trees than would be expected based on the amount of basal area removed. The silvics of black spruce suggest that the retention of cone-bearing trees in the HARP stands may be a viable option for promoting natural regeneration of harvested peatland forests (Groot and Hokka 2000). Black spruce starts seed production after 15–30 years and the seed supply is abundant and dependable, with substantial cone crops occurring every four years on average (Vincent 1965, Groot 1984). Cones are persistent and seeds are released gradually over a period of years. Seeds are wind-dispersed, often being scattered a distance as much as twice that of the height of the tree (Payandeh and Haavisto 1982).

In addition to providing a seed source, the HARP system was successful in retaining advance regeneration, as evidenced by retention of the inverse-J size class distribution that is characteristic of the unharvested old-growth forest. Black spruce is a moderately shade-tolerant species that is able to respond to increased light availability even after long periods of suppression (Morin and Gagnon 1992, Greene *et al.* 1999, Paquin *et al.* 1999, Groot and Hokka 2000). Light travelling into the forest understorey promotes the generation of new propagules of black spruce by vegetative layering of the lower sphagnum-submerged branches. As described by Groot (1984) and observed in this study, the predominant method of natural regeneration of black spruce in peatland sites is by vegetative reproduction. Research has suggested that even though there appears to be a “growth lag” of the advance growth following canopy removal, the height advantage of preserved advance regeneration justifies the application of harvesting methods that protect it regardless of its origin (Morin and Gagnon 1992, Pothier *et al.* 1995, Paquin *et al.*1999, Groot and Hokka 2000).

HARP appeared to effectively preserve characteristic densities of most advance regeneration compared with the unharvested forest, despite the harvesting of considerable amounts of the forest basal area. In part, this retention arose because machine movement was restricted to the travel corridors, but also because harvesting activities occurred primarily during the winter, when snow cover and frozen soil protected the substrate (Groot 1987, MacDonell and Groot 1997, Tallman 1998). Moreover, the creation of openings in the canopy appeared to have initiated regeneration in the understorey, as demonstrated by the relatively high densities of both the 10 – < 30 cm and 30 – < 150 cm size classes in the HARP-harvested forests. Results from a 10-year study on advance regeneration in black spruce clearcut strips in Quebec suggested that seedlings in cleared corridors are more likely to be evenly distributed and at higher densities than in large clearcuts (Pothier 2000). In our study, only the low-retention HARP-harvested forest had a significantly lower abundance of the largest size-class (150–300 cm) saplings compared with the baseline forest. Clearcut areas, in addition to the large size-class saplings, also had significantly lower abundance of medium size-class saplings (30 – < 150) per hectare than the baseline unharvested forest.

The proportion of moss (*Sphagnum* spp.), *Ledum*, and lichen cover preserved by the HARP method was significantly greater than that preserved by the traditional clearcuts. Although the amount of moss cover was significantly less than in unharvested peatland forests, the conversion of growing moss to decaying moss in harvested forests potentially represents an

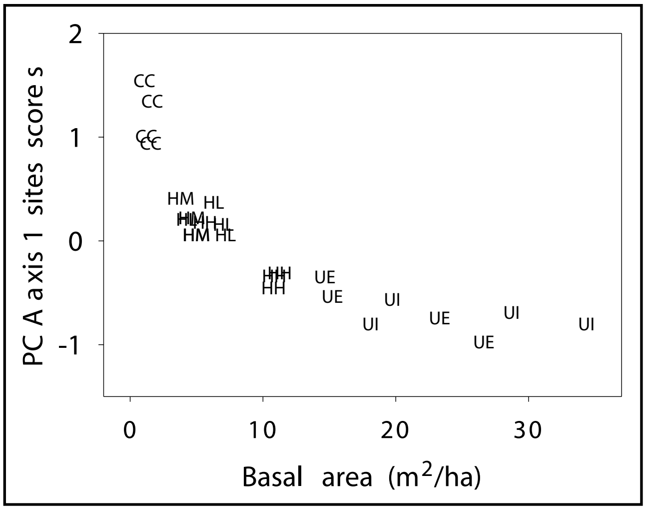


Fig. 4. Scores on the first principal component axis plotted against stand basal area for stands in the Lake Abitibi Model Forest (LAMF) area in northeastern Ontario. CC = Clearcut forest; HL = Low-retention HARP; HM = Medium-retention HARP; HH = High-retention HARP; UE = Unharvested forest < 150 m from harvested areas; UI = Unharvested contiguous forest > 150 m from harvested areas.

increased receptivity of the seedbed. As shown in previous studies, the most receptive seedbeds for black spruce on peatlands are poorly decomposed sphagnum peat, sheared sphagnum, and living, compact sphagnum moss (Groot 1988, Groot and Adams 1994). The greatest abundance of seedlings (< 10 cm) was found in clearcut forest areas followed by low- and medium-retention HARP, suggesting that a receptive seedbed was maintained and that aerial seeding was successful in these sites (Groot and Adams 1994).

Concerns for the reduction in the amount of coarse downed woody debris in managed stands, often cited as a key problem following harvesting activities (e.g., Hansen *et al.* 1991), does not seem to be important here in these HARP-harvested forests, at least in the short term. The removal of large-diameter "legacy" trees in these forests may eventually erode the amount of coarse downed woody debris; however, the reduction will evidently be much slower than in regenerating clearcuts. An important additional factor is the moss layer of the forest floor, which in old growth and presumably HARP stands will rapidly cover downed wood. The retention of standing dead trees does not appear to be changed by HARP harvesting, with similar abundance retained in HARP and unharvested forests.

The PCA on the various structural variables supported the possibility of greater retention of structural features than might be expected based on basal area removal, with potentially positive implications for both black spruce regeneration as well as the many organisms that use (and in some cases may rely upon) these old-growth forests. However, two important caveats must be kept in mind: the short-term nature of this study, which studied HARP stands at only 2.5–3-5 years following harvest, and the unusual juxtaposition of cleared and residual forest created by the HARP system.

The intimate juxtaposition of cleared and residual forests in the HARP stands on one hand raises the possibility of a rapid recovery of old-growth features in the regenerating cleared strips through the emulation of gap-phase dynamics in old-growth forests, but it also raises concerns about the long-term structural integrity of the residual strips due to edge effects. Creation of increased amounts of edge alters abiotic conditions in the forest, including sunlight, humidity, moisture, and wind, raising the possibility of increased susceptibility to windthrow in HARP stands, especially in low-retention HARP-harvests, which because of low tree densities, may be particularly prone to windthrow (Smith *et al.* 1987, Groot 1984, Ruel 1995). Edge effects are suggested to extend about three times the canopy height into the forest (Harris 1984), although they may extend less in black spruce forests. The average width of residual strips of trees retained by HARP was less than one tree height. Although a travel corridor is certainly a much smaller clearing than a clearcut, the high concentration of travel corridors may mean that virtually all residual forest is subjected to additive edge effects (see Malcolm 2001). What was once interior forest is now exposed to a different surrounding matrix. The edges impose both direct and indirect biological impacts on the ecosystem, by potentially altering species richness and the abundance of various taxa, as well as by potentially interfering with biological interactions such as predation, parasitism and herbivory (e.g., Helle and Muona 1985, Murcia 1995, Schowalter 1995, Roland and Taylor 1997, Deans *et al.* in preparation). Although HARP effectively increases the local structural heterogeneity retained in harvested forests by retaining late-successional forest characteristics in residual leave strips, these strip are immediately adjacent to early successional cleared corridors. Certainly, HARP increases locally available microclimates and habitats for elements of the biota that may otherwise be lost from the harvested forest. However, edge effects have the potential to erode these benefits. A critical contribution will be to monitor the long-term effects of the HARP harvesting and, in particular, the evolution of any such edge effects through time.

Conclusions

The HARP system of harvesting maintained greater amounts of advance regeneration and late-seral-stage structural characteristics than traditional clearcutting. Moreover, HARP forests appear to show greater retention of old-growth structures than might be expected based solely on amount of basal area removed. This is presumably due to two features of the harvesting system that reduced the damage to the forest floor: restriction of machine movements to the cleared travel corridors and winter harvesting. Logging-related disturbances to the forest floor can have important effects on the understorey plant communities; for example, frequently leading to dominance by fast-growing deciduous tree species on upland sites (Hearnden *et al*. 1992, Carleton and MacLellan 1994). The HARP system thus has the potential to offset these negative effects of mechanized clearcutting; a conclusion also supported by research on understorey plant communities at this site (Ramprasad 2001).

Acknowledgements

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