Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: initial response of aspen stands to different levels of harvesting[1]

S. Brais, B.D. Harvey, Y. Bergeron, C. Messier, D. Greene, A. Belleau, and D. Paré

Abstract: The SAFE (sylviculture et aménagement forestiers écosystémique) project was set up in 1998 in the Lake Duparquet Research and Teaching Forest to test stand-level silvicultural treatments designed to reflect different aspects of natural forest dynamics. In the winter of 1998–1999, four levels of forest harvesting, including a no-harvest and a clearcut treatment, were applied to even-aged trembling aspen (*Populus tremuloides* Michx.) stands according to a complete block design with three replications. Two partial cut treatments removed 33% and 61% of the stand basal area. During the first growing season, harvesting induced a large increase in indigenous understorey biomass that paralleled changes in the canopy opening. Aspen sucker density increased from 4916 stems/ha in the control to 28 751 and 63 333 stems/ha in the one-third and two-thirds harvesting treatments and 102 916 stems/ha in the clearcut. Most changes in nutrient cycling occurred in the second year and included an increase in forest floor organic C, total N, and base cation availability and a decrease in microbial C/N ratio. These changes may have occurred in response to reduced vegetation uptake and woody debris abundance.

Résumé : Le projet SAFE (sylviculture et aménagement forestiers écosystémique) a débuté en 1998 dans la Forêt d'enseignement et de recherche du lac Duparquet afin de tester différents traitements sylvicoles inspirés de la dynamique naturelle des peuplements. Quatre intensités de récolte, incluant la coupe totale, la récolte de 33 et 61% de la surface terrière totale et un traitement témoin non coupé, ont été appliquées à des peuplements équiennes de tremble (*Populus tremuloides* Michx.) au cours de l'hiver 1998–1999, selon un plan en block complet avec trois répétitions. La végétation de sous bois a répondu par une augmentation de sa biomasse proportionnelle à l'ouverture du couvert. Au cours de la première année, la densité des drageons de tremble était de 4916 tiges/ha dans le traitement témoin, 28 751 et 63 333 tiges/ha dans les coupes partielles et 102 916 tiges/ha dans la coupe totale. La plupart des changements observés dans le cycle des nutriments sont survenus dans la couverture morte pendant la deuxième année suivant la coupe. Parmi ceux-ci figurent une augmentation du C organique, du N total et des cations basiques échangeables et une diminution du ratio C/N de la biomasse microbienne. La diminution du prélèvement par les plantes et les changements dans l'abondance des débris ligneux expliqueraient ces changements.

Introduction

Fundamental ecological research conducted in the boreal mixedwood forest of northwestern Quebec has led to a good understanding of the natural disturbance regime, succession dynamics, and other ecosystem processes in this region (Bergeron 1991; Dansereau and Bergeron 1993; Morin et al. 1993; Bergeron et al. 1995; Brais et al. 1995*a*; Paré and Bergeron 1996). An ecosystem management model based on natural dynamics has been developed for the region

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(Bergeron and Harvey 1997; Harvey et al. 2002; Bergeron et al. 2002). Key forest-level objectives are to maintain forest composition and general age structure characteristics of the natural forest mosaic. These objectives are derived from studies of regional natural disturbance history, forest ecosystem classification, and stand dynamics (Bergeron and Dansereau 1993; Gauthier et al. 1996).

At the stand level, natural dynamics on upland mesic sites can be characterized by successive rotations of intolerant hardwood, mixedwood, and softwood dominance (Bergeron and Dubuc 1989; Bergeron 2000). The transition from hardwood to mixedwood is dependent on the rate at which hardwood stands are invaded by softwood species from nearby seed sources (Galipeau et al. 1997). As the proportion of balsam fir (*Abies balsamea* (L.) Mill.) increases with time since disturbance, species replacement toward coniferous dominance can be set back to a mixed composition, particularly in large gaps created during spruce budworm (*Choristoneura fumiferana*) outbreaks (Morin et al. 1993; Kneeshaw and Bergeron 1998). To integrate these notions into silvicultural and management objectives, stands have been associated with cohorts of different successional status based on time since disturbance and stand structure and composition. Operationally, the ecosystem management model relies on varying silvicultural treatments to more closely reflect different aspects of natural dynamics: clear-cutting or other even-aged harvesting systems are employed to recruit first-cohort stands, a surrogate for stand reinitiation by fire, partial cutting is used to modify stand composition and structure and move stands more rapidly into second- and third-cohort stand types, similar to the process of natural succession from intolerant hardwoods to mixedwood and conifer-dominated stands, and selection cutting is intended to mimic gap dynamics (Bergeron et al. 2002; Harvey et al. 2002).

Management of these complex biological systems towards ecological, social, and economic ends requires a good understanding of the relationships between natural disturbances and disturbances induced by silvicultural practices, resource availability, and species silvics supported by well-structured and conducted experiments (MacDonald 1996). The SAFE project, the French acronym for “sylviculture et aménagement forestiers écosystémique” or ecosystem management and silviculture, is such an experiment set up in 1998 in the Lake Duparquet Research and Teaching Forest in the southern part of the eastern boreal forest. The first phase of the SAFE project involved first-cohort, even-aged aspen (*Populus tremuloides* Michx.) stands. The objective of this paper is to report on the first 2 years of response of these stands to four levels of harvesting intensity. More specifically, it describes the relationships between canopy opening, resource availability, and understorey biomass increment. Our hypothesis was that resource availability and soil processes would be controlled by residual ecosystem structures (living trees, coarse woody debris (CWD), and soil organic matter) and that vegetation would respond to an overall increase in light, water, and nutrients.

Materials and methods

Study area

The study area is located in the Lake Duparquet Research and Teaching Forest in the Abitibi region of northern Quebec 45 km northwest of Rouyn-Noranda, Que. (48°86′N–48°32′N, 79°19′W–79°30′W). The region is situated in the mixedwood zone of the boreal shield. The climate is continental with a mean annual temperature of 0.6 °C. Annual precipitation is 823 mm, of which 639 mm falls as rain from April to November. The mean frost-free period is 64 days (Environment Canada 1982). Soils are Grey Luvisols (Canada Soil Survey Committee 1987) originating from glaciolacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy 1977). Soil texture is that of heavy clay (>75% clay) and the forest floor is a thin mor of 2–7 cm.

Experimental design and treatments

Phase 1 of the SAFE study is conducted in aspen-dominated stands (Fig. 1) of fire origin dating from 1923 (Dansereau and Bergeron 1993). Stands were healthy; rotation age for aspen on rich sites is between 90 and 100 years and stands were not affected by insect outbreaks during the study period. In the winter of 1998–1999, four levels of forest harvesting, including one no-harvest and one clearcut treatment, were applied according to a complete block design with three replications of each treatment (Fig. 1). Two partial cut treatments were aimed at removing one third and two thirds, respectively, of the merchantable basal area. Treatments were assigned randomly, but some minor adjustments were made so that partial cut treatments were assigned to areas where softwood understorey regeneration was present. Experimental units ranged from 1 to 2.5 ha.

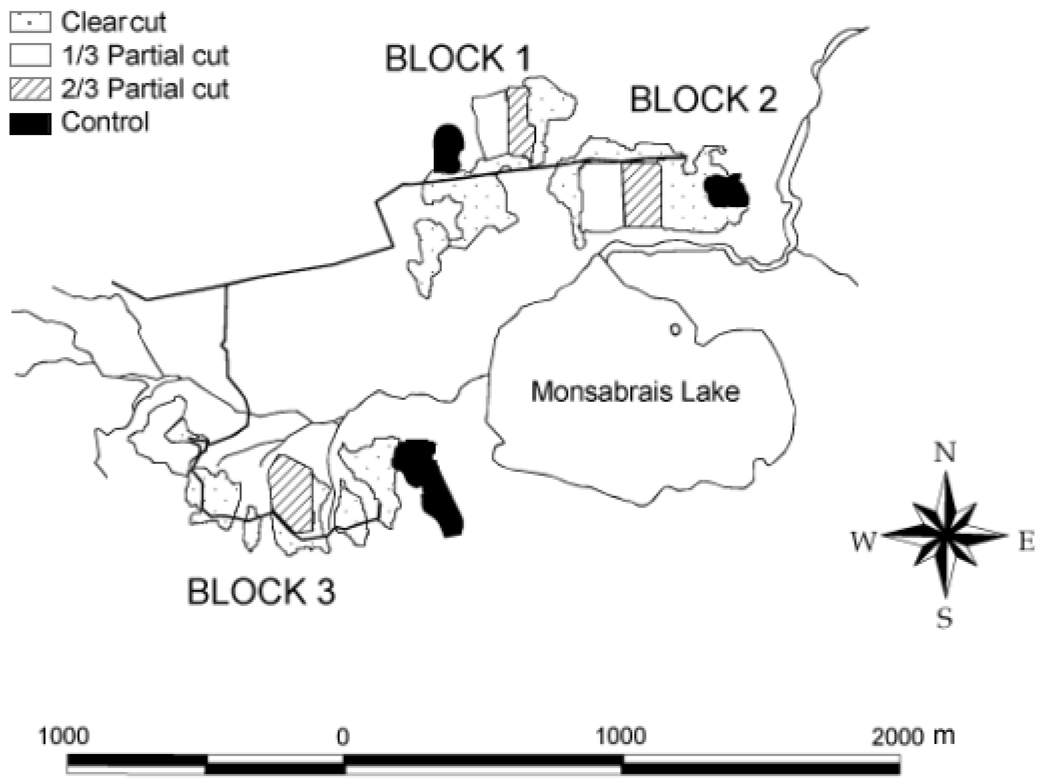
In partial cuts, trees to be removed were marked prior to harvesting. Stands in the one-third removal treatment were low thinned with nonvigorous stems removed, while stands in the two-thirds removal treatment were essentially crown thinned with larger, vigorous stems preferentially selected. Harvesting was done manually in all treatments. Stems were delimbed on site and hauled full length in the clearcut treatment, whereas in the partial cuts, stems were generally bucked in 2.5, 5, or 7.5 m lengths before removal to the roadside to avoid damage to residual stems and regeneration. In the partial cut treatments, trees were hauled using small cable skidders; skid trails in these treatments averaged 4.5 m in width, and distance between trails averaged 30 m. In the clearcut treatment, stems were skidded using larger size cable skidders. Trails and between-trail width averaged 5 and 10 m, respectively. The ground was snow covered at the time of harvesting; physical soil disturbances (rutting or scarification) were minimal in all treatments.

Sampling design

Forest inventory

Before harvesting and in all experimental units, five permanent circular (radius = 11.28 m) sampling plots were located. All stems (trees and high shrubs) greater than 5.0 cm diameter at breast height (DBH) were identified, tagged, and measured (DBH). In a 100-m^2 quarter of each plot, all stems between 2.0 and 4.99 cm DBH were also tagged and measured (DBH). After harvesting, three sampling plots out of 60 had to be relocated because of modification of the limits of the experimental units during harvesting operations. A tally of remaining stems was conducted in all sampling plots

Fig. 1. Experimental treatments were control (no harvest), one-third partial cut (33% basal area removed), two-thirds partial cut (61% basal area removed), and clearcut repeated three times according to a complete block design. Experimental units ranged from 1 to 2.5 ha.



of the partial cuts to estimate the residual basal area and change in stem density and diameter distribution.

Most nondestructive sampling (soil temperature and moisture, understorey vegetation inventory, fisheye photography, decomposition bags, and mineralization rates) was done within the five permanent plots of each experimental unit. CWD inventory and light attenuation measurements were conducted over the entire area of each experimental unit. Destructive sampling (soil and vegetation biomass) was conducted close to but outside each of the five permanent sampling plots.

Soil moisture and temperature

Soil was sampled for moisture content once every 2 weeks during the growing season. Bulk samples were taken from the forest floor and the 0–10 cm mineral soil. Soil temperatures were measured at the same time and for the same soil layers. Air temperature 1 m aboveground was measured as well.

Canopy openness

In September 1999 before leaf fall, hemispherical (fisheye) canopy photographs were taken above (3 m height) the high shrub canopy within each sampling plots. Photographs were taken with the top of the image to the north during uniform overcast days or when the sun was below the skyline on clear sunny days. The photographs were scanned and processed with Gap Light Analyzer software (Frazer et al. 1999) yielding a percent canopy openness factor (percentage of open sky seen from beneath the canopy; no influence of the surrounding topography). Under the same conditions and at a 75 cm height, light attenuation measurements were taken using a plant canopy analyzer (LAI-2000; LI-COR, Inc., Lincoln, Nebr.) every metre along two transects in each experimental unit, yielding 100 measurements per experimental unit. A second sensor took simultaneous measurements form a nearby open area. A percentage of sky openness diffuse noninterceptance (DIFN) was derived from the LAI-2000 measurements.

Understory vegetation inventory

Understorey vegetation was sampled in eight 1-m^2 quadrats uniformly dispersed within each sampling plot for a total of 40 quadrats in each experimental unit. Within each 1-m^2 quadrat, aspen stems smaller than 2 cm DBH were identified and measured for height. Density was tallied by height class.

Annual increment of understorey vegetation biomass (aboveground) was estimated from two 0.5-m^2 quadrats located outside each sampling plot (10 per experimental unit). All vegetation within each quadrat was clipped at the base and grouped into the following categories: herbaceous plants, shrub annual growth (stem and branch yearly increment and leaves), and aspen annual growth (stem and branch yearly increment and leaves). Different quadrats were sampled every year. Each category was weighed in the field and a sample was kept for oven dry mass conversion.

CWD inventory

The volume of CWD was estimated by the triangular-transect method in 1999 following harvesting. One triangle (30-m sides (Van Wagner 1982)) was sampled in each experimental plot. Along each transect line, the frequency of CWD was recorded by species, diameter class (5 cm, 2.5–

7.6 cm; 10 cm, 7.6–12.5 cm; 15 cm, 12.6–17.5 cm; 17+ cm, ≥17.6 cm), and five decomposition classes (Daniels et al. 1997). Samples of CWD were brought back to the laboratory to estimate density for each combination of species–decomposition and diameter classes. Density was estimated from volume, determined by water displacement, after immersing samples in hot paraffin, and dry mass.

Litter decomposition rate

To estimate fine litter and wood decomposition rates, five litter bags containing aspen leaves collected on the ground the previous autumn and five litter bags containing aspen wood blocks were set on the ground (Trofymow 1998) in the summer of 1999 in each of the permanent sampling plots. A bag of each litter type was collected 1 year later for a total of five bags for each litter type in each experimental unit.

Soil nutrient concentration and content

In the fall of 1998 (before treatments), 1999, and 2000 and close to each sampling plot, two forest floor samples were collected for nutrient concentration. Three bulk soil samples were taken from the 0–10 cm mineral soil and pooled, leading to one sample per sampling plot for mineral soil nutrient concentrations.

Net mineralization rates and microbial parameters

Nitrogen mineralization rates were estimated by the closed-top cores in situ incubation technique (Raison et al. 1987). Two cores were positioned in pairs in each sampling plot. Soils were incubated from mid-July to late October in 1999 (15 weeks), from late October 1999 to late May 2000 (32 weeks), and from late May 2000 to late October 2000 (23 weeks). ABS cores, 30 cm long and 4.5 cm in diameter, were driven through the forest floor to a depth of 10 cm in the mineral soil. Tubes were covered with plastic to prevent rain from entering. At the beginning of each incubation period, forest floor and 0–10 cm mineral samples were collected beside each pair of cores for determination of initial NO_3^- and NH_4^+ concentrations and, in the fall, for additional laboratory measurements of soil microbial biomass and respiration. At the end of each period, the soil was removed from the core, and forest floor material was separated from the mineral soil. Samples from core pairs were pooled in the field.

Laboratory analysis

Forest floor samples were ground (1.7 mm) and mineral soil samples were sieved (2 mm). Samples were analyzed for Kjeldahl N, including NO_2^- and NO_3^- (Bremner and Mulvaney 1982) and for exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) (inductively coupled plasma atomic emission, Perkin Elmer Plasma 40), and acidity (titration, Metler DL-40) after extraction with NH_4Cl—$BaCl_2$ (Amacher et al. 1990). Effective cation-exchange capacity was estimated by summing base cations and exchangeable acidity. Soil pH was determined in 0.01 mol/L $CaCl_2$ (Hendershot et al. 1993). Organic matter (organic C = 0.58 × organic matter) of forest floor samples was determined by loss on ignition and organic C of ground mineral samples (250 mm) by wet oxidation (Yeomans and Bremner 1988). Forest floor samples were wet digested (Parkinson and Allen 1975) and total cation concentrations (Ca^{2+}, Mg^{2+}, and K^+) measured by inductively coupled plasma atomic emission. Samples from incubation cores were extracted with 2 mol/L KCl. Mineral N concentrations in KCl extractions were determined with an autoanalyzer (Kalra and Maynard 1992).

Microbial N was determined on fresh samples collected in the fall by the fumigation–extraction method (Voroney et al. 1993). Microbial C was determined on K_2SO_4 extracts acidified to a pH of 2 with a Shimadzu C analyzer. Microbial N was determined according to Cabrera and Beare (1993). Correction factors were K_{EC} = 2.86 (Sparling et al. 1990) and K_{EN} = 1.85 (Brookes et al. 1985; Joergensen et Mueller 1996).

Soil basal respiration was estimated in the laboratory on fresh samples. Ten grams of forest floor and 50 g of mineral soil were incubated in closed jars at 21 °C for 24 h. Respiration was estimated from the amount of CO_2 absorbed in NaOH and determined by HCl titration (Skoog and West 1965; Alef and Mannipieri 1995). Jars containing NaOH but no soils were used as a control.

CWD density was estimated from two sections of 330 samples each. The first section was weighed (fresh) and coated in hot paraffin before its volume was measured by water displacement. The second section was weighed (fresh) and oven-dried for moisture content estimation. The density was estimated from the first section after its fresh mass was corrected for moisture content.

Statistical analyses

Data analyses were done using the REG, GLM, MEANS, and CORR procedures of the SAS statistical package (SAS Institute Inc. 1988). Homogeneity of variance between treatments was tested using Bartlett's procedure (Steel and Torrie 1980). Data that did not meet the requirements were log transformed. Parametric analysis of variance was conducted according to a completely randomized design with four treatments and three replications per treatment. Contrasts between treatments were used to answer the following three a priori questions (Steel and Torrie 1980): (*i*) Are the partial cuts different from the unharvested stands? (*ii*) Are the partial cuts different from the clearcuts? (*iii*) Is the one-third partial cut treatment different from the two-thirds partial cut treatment? As we were more interested in tendencies than in the absolute level of probability of the observed differences, a level of significance of 0.1 was retained.

Path analyses (Sokal and Rolph 1981; Legendre and Legendre 1998) were used to summarize results and define relationships between residual structures (residual basal area, CWD, and soil organic matter), changes in resource availability or abiotic conditions (temperature, moisture, incident radiations, and nutrient availability), and stand response variables or soil processes during the first 2 years following harvesting. Causal ordering among variables was determined from ecological theory and was depicted by arrows (Legendre and Legendre 1998). Multiple linear regressions with no intercept were conducted using a stepwise procedure. Levels of significance for addition or deletion of variables were set to 0.05. These contribute to reduce the number of explanatory variables (predictor) for each response variable (criterion). To assess the relative importance of explanatory variables, all variables were first standardized

Table 1. Composition and characteristics of control stands.

Species	Mean density (stems/ha)	Mean DBH (cm)	Mean basal area (m^2/ha)
Tree species (DBH > 2 cm)			
Trembling aspen	848	24.17	39.89
White birch	172	9.08	1.20
Balsam poplar	5	39.20	0.61
Balsam fir	77	11.63	0.37
White spruce	113	9.41	0.80
Black spruce	5	13.13	0.09
Jack pine	3	24.20	0.16
Total	1223		43.12
High shrub species (DBH > 2 cm)			
Mountain maple	1327	2.89	0.86
Speckled alder	97	3.49	0.08
Green alder	27	2.58	0.01
Beaked hazel	13	2.40	0.01
Pin cherry	3	6.60	0.01
American mountain ash	7	2.40	0.00
Total	1474		0.97

using the STANDARD procedure of SAS; hence, correlation coefficients and simple regression coefficients were equal.

Results

Effects of harvesting on sky openness, temperature, and soil moisture

Control stands (Table 1) had a mean basal area of 43.12 m^2/ha, of which aspen represented 92.6% and softwood species only 3.3%. High shrub canopy (stem DBH over 2 cm) was composed mostly of mountain maple (*Acer spicatum* Lamb.), which had a mean density of 1327 stems/ha. Harvesting resulted in a 33% and 61% decrease in basal area in the one-third and two-thirds removal treatments, respectively, and a total removal in the clearcut treatment (Table 2; Fig. 2). Following these treatments, sky openness over the high shrub canopy was increased 1.6, 2.8, and 8.8 times in the one-third, two-thirds, and complete removal treatments, respectively, compared with control stands. The corresponding values at 75 cm aboveground were a little more extreme: for the one-third, two-thirds, and complete removal treatments, they were 3.5, 7.3, and 17.4 times higher, respectively, than control stands values.

The growing season (end of May to the end of September) of 1999 was warmer and dryer than that of 2000, as shown by higher air temperatures and lower forest floor moisture content (see Fig. 3 for exact dates of sampling). The 0–10 cm mineral soil had already reached 12 °C in the control stands at the end of May 1999 when the first measurements were conducted and temperatures of 17, 20, and 19 °C were observed in June, July, and August, respectively, of 1999. In 2000, the highest temperature observed for the 0–10 cm mineral soil in the control stands was 18 °C at the end of July.

Partial harvesting had little impact on daytime soil temperatures and moisture regime compared with those of control stands (Fig. 3), as there were few significant differences in air and soil temperatures between partial cuts and control stands. From mid-August to September 1999, after a hot summer, soil temperatures decreased faster in the control stands than in partial cuts. In 2000, as temperatures gradually increased through the summer, air and soil temperatures increased somewhat faster in partial cuts than in control stands. Significant differences in temperatures ranging between 1.6 and 2.5 °C for air, 1.9 and 2.0 °C for forest floor, and 0.9 and 1.2 °C for the 0–10 cm mineral soil were found in June between partial cuts and control stands. Fewer differences were observed between partial cuts and control stands in terms of soil moisture content (Fig. 3). Starting from similar conditions at the beginning of the 1999 growing season, soil moisture content in partial cuts decreased at a faster rate than that in control stands. Similar values were observed at the end of July 1999 and thereafter.

In May and June 1999, air and soil temperatures increased faster in clearcuts than in partial cuts but remained similar thereafter. In 2000, significant differences between total and partial cuts were found later in the growing season, as soil daytime temperatures were higher in the clearcuts. The most consistent difference between total and partial cuts was found in the comparison between forest floor and mineral soil moisture content. Starting from similar values in May 1999, moisture content remained significantly higher in the clearcut for most of the sampling dates. On only one sampling date did we find a significant difference between the one-third and two-thirds partial harvesting treatments related to temperature and moisture: the two-thirds treatment showed a higher mineral soil temperature in July 1999.

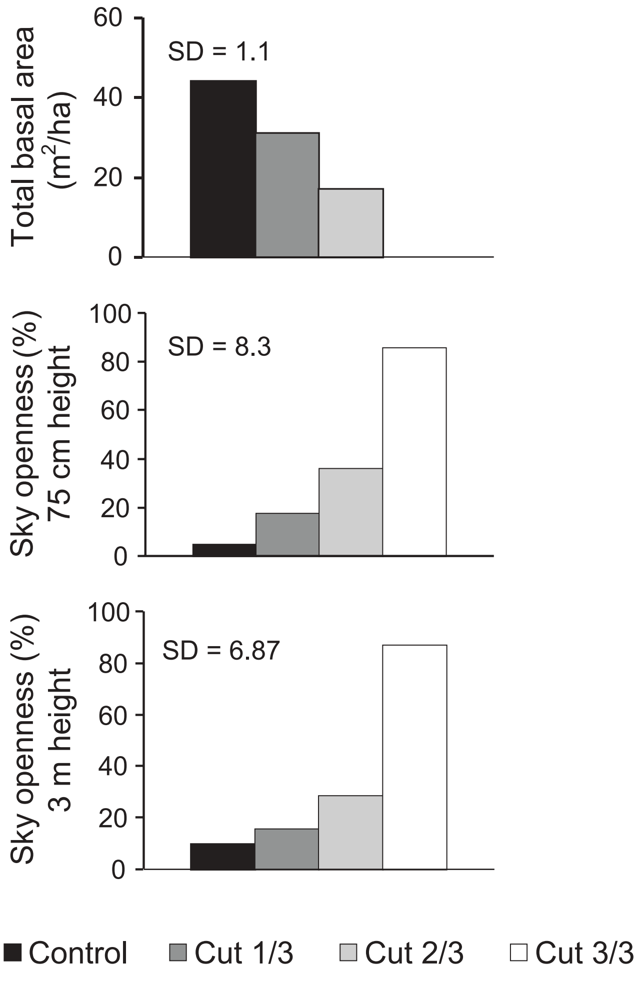
Effects of harvesting on soil nutrient dynamics

CWD was divided in two large decomposition classes: fresh and well decomposed (CWD_F = classes 1 to 3, CWD_D = classes 4 to 5) and summed over all species and diameter classes. Harvesting induced a large input of CWD_F (Fig. 4) but a significant difference was found only between total and partial harvesting treatments (Table 2). CWD_F load in control stands was 13.7 Mg/ha, while total harvesting load

Table 2. A priori comparisons ($p > F$) of harvesting treatment effects on stand characteristics.

Variable	Control vs. partial cuts	Clearcut vs. partial cuts	One-third vs. two-thirds partial cuts
Stand basal area	<0.001	<0.001	<0.001
Canopy openness factor (3 m)	0.049	<0.001	0.067
Canopy openness factor (75 cm)	0.009	<0.001	0.033
Fresh CWD mass	0.182	0.004	0.812
Well-decomposed CWD mass	0.712	0.016	0.338
Fresh CWD mass loss to decomposition	0.156	0.007	0.907

Fig. 2. Basal area and sky openness factors following partial and total harvesting of trembling aspen stands. SD is the standard deviation of the population mean. (Mean comparisons are presented in Table 2.)



was 53.3 Mg/ha. Harvesting also resulted in a decrease in CWD_D in clearcuts compared with partial harvesting treatments (Fig. 4). During the year following harvesting, no significant differences were found between treatments for wood blocks and fine litter lost mass (decomposition rates). Wood and fine litter decomposition rates were 26% and 31%, respectively, in control stands and 32% and 34%, respectively, clearcuts. Wood decomposition rates in experimental plots were applied to their respective CWD_F loads to assess the loss of CWD_F to decomposition (Fig. 4). Loss of fresh wood to decomposition was higher (p = 0.007) following clearcut harvesting (16 Mg/ha) than following partial harvesting (7 Mg/ha).

No differences in soil microbial parameters were found between treatments in the first growing season following harvesting (see Table 3 for first-year control stands values). During the second growing season, forest floor microbial C/N ratio was significantly lower (p = 0.039) in the clearcut harvesting treatment than in the partial cuts: microbial C/N ratios were 5.4 (SD = 1.3) in the total harvesting treatment, 6.9 in the two-thirds treatment, 8.9 in the one-third treatment, and 8.8 in control stands. Also in the second year, significantly higher microbial N values (106 μg N/g soil, SD = 16, p = 0.016) were observed in the 0–10 cm mineral soil of control stands compared with values of 65 and 71 μg N/g soil for the one-third and two-thirds removal treatments, respectively. Microbial N in the 0–10 cm mineral soil of clearcuts was 81 μg N/g soil.

No significant differences were found in in situ net mineralization rates between treatments. Immediately following harvesting (first growing season), high rates of net immobilization were observed in the forest floor (from –7.7 to –83.2 mg N·(kg soil)$^{-1}$·week^{-1} (SD = 55.9) as well as in the 0–10 cm mineral soil (from –2.4 to –8.8 mg N·(kg soil)$^{-1}$·week^{-1} (SD = 6.4). The two-thirds and clearcut harvesting treatments had the highest forest floor net immobilization values: –74.0 and –83.2 mg N·(kg soil)$^{-1}$·week^{-1}, respectively. Net immobilization was still observed in the forest floor during the second growing season (mean value = –5.6 mg N·(kg soil)$^{-1}$·week^{-1}, SD = 3.7) and low rates of net mineralization were measured in the 0–10 cm mineral soil (mean value = 0.03 mg N·(kg soil)$^{-1}$·week^{-1}, SD = 0.24).

During the course of the first growing season, clearcut harvesting significantly increased concentrations of forest floor organic C (p = 0.086) and available P (p = 0.017) compared with partial cuts (Fig. 5). During the second growing season, forest floor available P was highly variable and no significant trend was found. Forest floor organic C concentrations were still higher in the clearcut harvesting treatment compared with partial harvesting treatments, although not significantly so (p = 0.121), as organic C increased in the two-thirds harvesting treatment as well. Harvesting treatments had no effects on forest floor exchangeable base cations in the first growing season (see Table 3 for first-year control stands values), but during the second growing season, exchangeable Ca and Mg increased following harvesting, while exchangeable K decreased (Fig. 6). Significant differences in forest floor exchangeable Ca and K were found between control stands and partial cuts (p = 0.090 and p = 0.047, respectively) as well as between clearcuts and partial cuts (p = 0.050 and p = 0.068, respectively). Signifi-

Fig. 3. Air temperature and soil temperature and moisture 1 and 2 years following partial and total harvesting of trembling aspen stands. SD is the standard deviation of the population mean by sampling date. *1, significant contrast (p = 0.100) between control and partial cuts; *2, significant contrast between partial cuts and clearcut; *3, significant contrast between partial cuts. Sampling dates: 31 May, 21 June, 21 July, 28 August, and 28 September 1999 and 24 May, 20 June, 31 July, 16 August, and 20 September 2000.

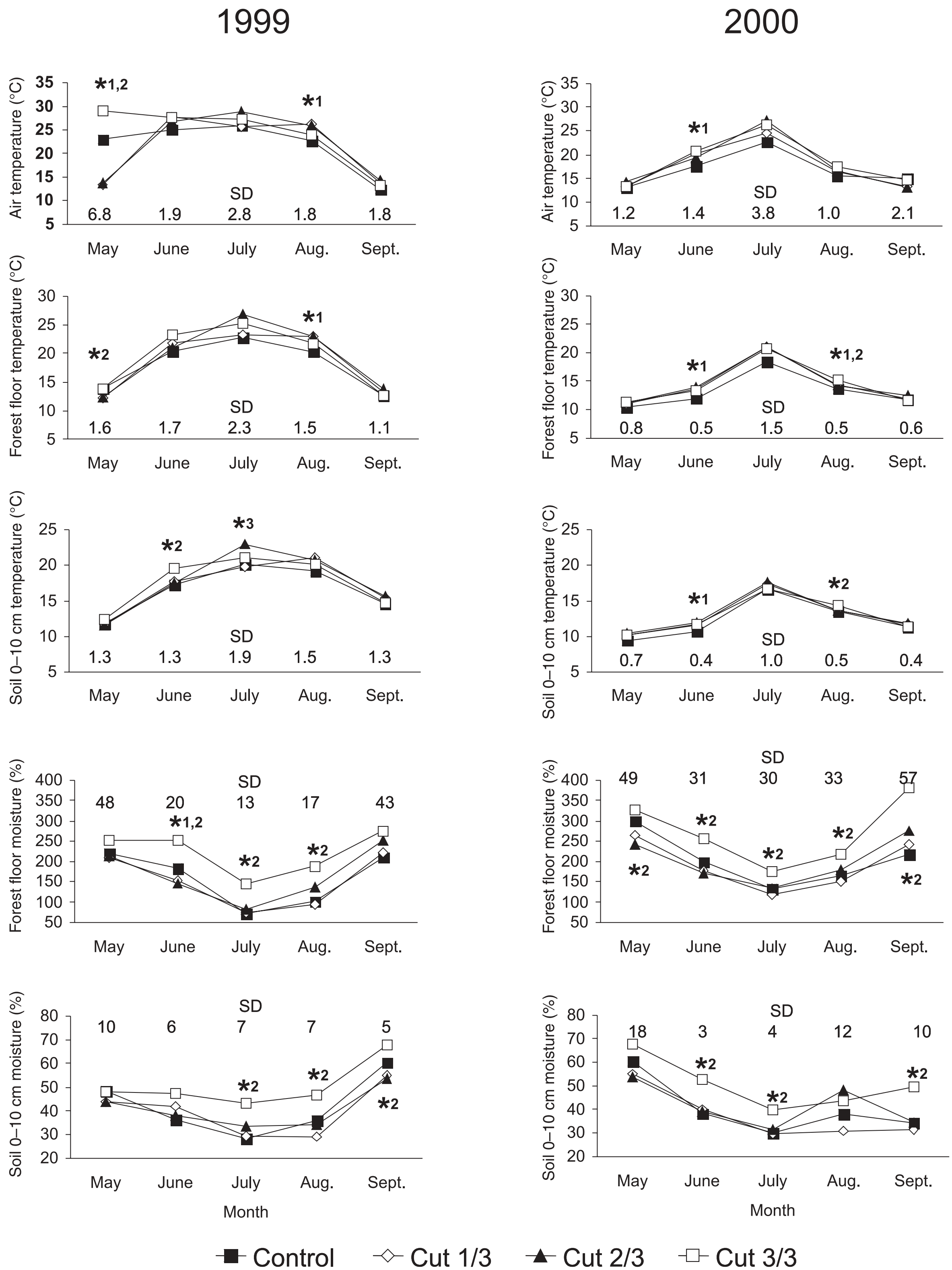
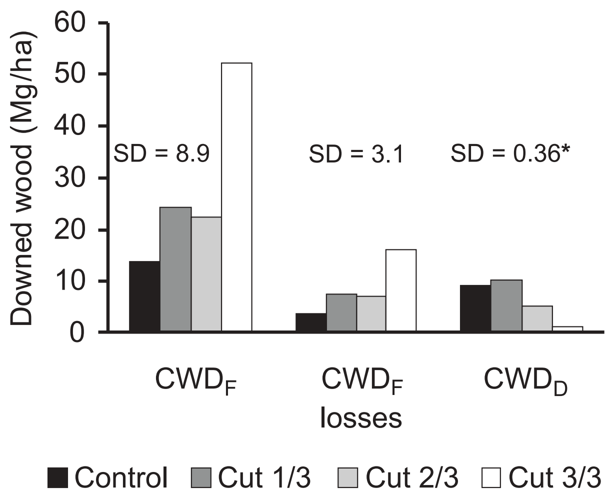


Table 3. Selected forest floor and mineral soil (0–10 cm) properties (dry mass (ash free)) under control trembling aspen stands.

	Forest floor	Mineral soil
pH	5.39	4.60
Organic C (g/kg)	421.1	20.9
Kjeldahl N (g/kg)	14.68	1.34
P (Bray II, mg/kg)	59.91	15.87
Exchangeable Ca ($cmol_c$/kg)	62.91	5.88
Exchangeable Mg ($cmol_c$/kg)	8.55	1.37
Exchangeable K ($cmol_c$/kg)	3.10	0.46
Effective cation-exchange capacity ($cmol_c$/kg)	74.87	8.94
Microbial N (μg N/g soil)	1260	56
Microbial C (μg C/g soil)	9600	430
Microbial C/N ratio	8.0	7.6
Soil basal respiration (μg CO_2-C·(g soil)$^{-1}$·h^{-1})	20.7	1.2

Fig. 4. Dry mass of fresh CWD (CWD_F) and well-decomposed CWD (CWD_D) and fresh wood losses to decomposition following partial and total harvesting of trembling aspen stands. SD is the standard deviation of the population mean. *SD of the log-transformed mean. (Mean comparisons are presented in Table 2.)



cant differences were found for exchangeable Mg between clearcuts and partial cuts ($p = 0.050$) and between the one-third and two-thirds removal treatments ($p = 0.073$). Forest floor exchangeable acidity and pH reflected those trends (Fig. 6), as acidity was lower and pH higher in the clearcuts compared with the partial cuts ($p = 0.030$ and $p = 0.057$, respectively). During the course of the second season, Kjeldahl N significantly increased ($p = 0.061$) in the clearcuts compared with the partial cuts (Fig. 6). Finally, partial and clearcut harvesting had no significant effect on the 0–10 cm mineral soil properties in the first 2 years following harvesting.

Understorey vegetation response to harvesting

Herbaceous biomass

The most abundant herbaceous species in control stands were *Aster macrophyllus* L., *Aralia nudicaulis* L., and *Clintonia borealis* (Ait.) Raf. The herb layer responded quickly to harvesting treatments. One and two years after harvesting, significant differences were found between partial harvesting and control treatments as well as between partial harvesting and clearcut harvesting treatments (Table 4; Fig. 7). The second-year response was more subdued in partial cuts than that in clearcuts: herbaceous biomass in the one-third harvesting treatment was 193% of control biomass in the first year and 191% of control biomass in the second year, while the corresponding values were 293% and 618% for the clearcut harvesting treatment.

Shrub biomass increment

During the course of the first year following harvesting, shrubs (Table 1) responded by an increase in leaf biomass (Fig. 7). All comparisons were significant (Table 4). Despite important increases in stem biomass increment in the two-thirds partial harvesting treatment (138% over the control value) and in the clearcut harvesting treatment (182% over the control value), no significant difference was found. During the second year, control stands produced significantly less leaf and stem biomass than partial harvesting treatments and the clearcut treatment produced significantly more stem biomass than partial cuts. First- and second-year stem biomass increments were similar in the clearcut treatment.

Aspen regeneration

During the first growing season following harvesting, total density of aspen suckers reached 4916, 28 751, 63 333, and 102 916 stems/ha in the control, one-third, two-thirds, and clearcut harvesting treatments, respectively (see Fig. 8 and Table 5 for individual height class values and comparisons). In the control and one-third partial cutting treatments, suckers <25 cm high represented over 60% of total density, while in the two-thirds and clearcut harvesting treatments, suckers <25 cm high represented only 39% and 31%, respectively, of total density. In the second year after harvesting, total sucker density increased in the control and one-third treatment to 16 584 and 41 083 stems/ha, respectively, remained stable in the two-thirds treatment (64 249 stems/ha), and decreased in the clearcut harvesting treatment (94 917 stems/ha). Distribution of suckers between height classes during the second year was similar to that observed in the first year with the

Fig. 5. Forest floor organic C and available P 1 and 2 years following partial and total harvesting of trembling aspen stands. SD is the standard deviation of the population mean. (Mean comparison results are given in the text.)

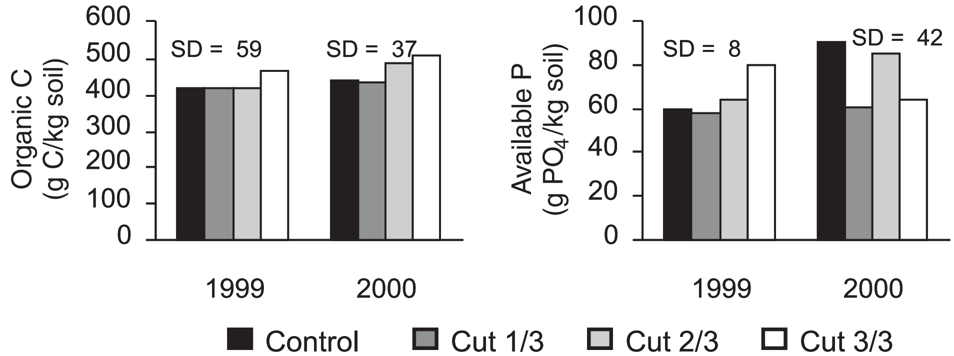
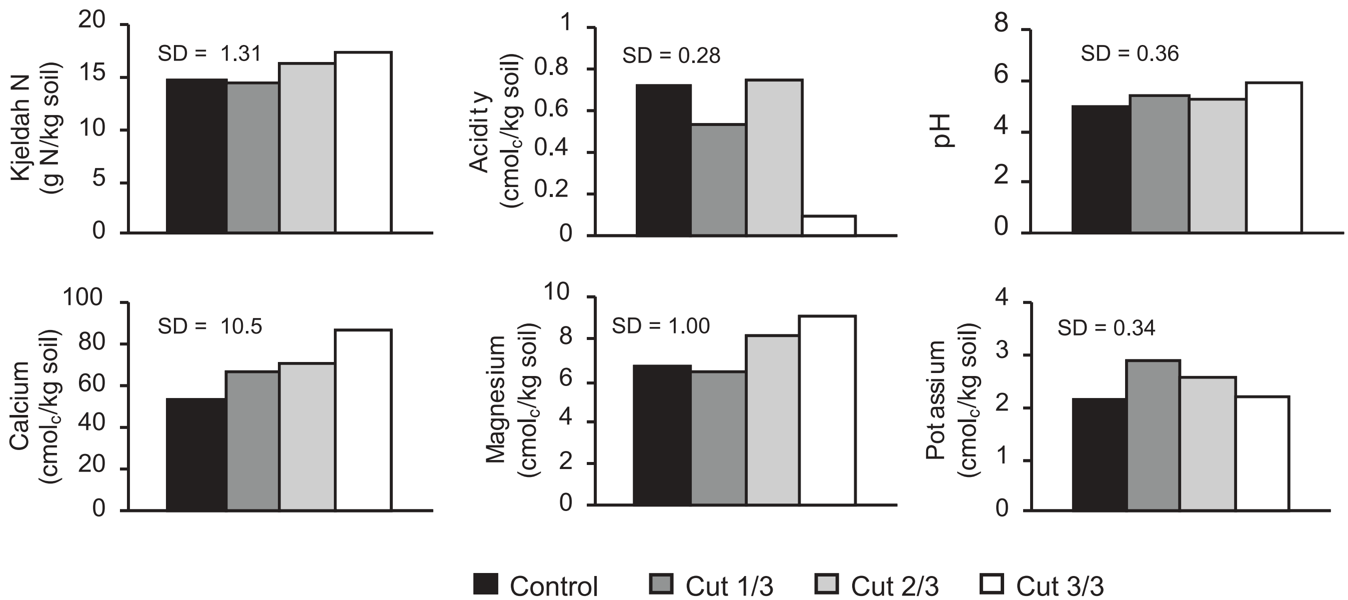


Fig. 6. Selected forest floor properties 2 years following partial and total harvesting of trembling aspen stands. SD is the standard deviation of the population mean. (Mean comparison results are given in the text.)



most notable exception of control stands where suckers <25 cm high represented 84% of the total.

Relationships between ecosystem residual structures, resource availability, soil processes, and vegetation response

Path analyses for both years following harvesting (Figs. 9 and 10) were developed for variables found to be significantly affected by treatments and for soil processes occurring in the forest floor, as the 0–10 cm soil layer was little affected by treatments. The individual models developed for each year were presented together to eliminate redundancy. No criterion was explained by more than three direct predictors and the number of observations was 12 for all models.

Correlations (Table 6) between residual basal area, i.e., the stand structure controlled by the experiment, and other stand structures (CWD) or predictor variables (moisture, temperature, and sky openness factors) showed some degree of colinearity (Legendre and Legendre 1998) but not as much as expected. Hence, correlations between basal area and forest floor moisture were not significant. Colinearity was also present between other predictor variables such as the open sky factor and air temperature. Interpretation of the results must take into account this colinearity. The open sky factor was thus interpreted as a measure of the radiation environment that reflected photosynthetically active radiation but may also include some confounded effects of other wave lengths and, indirectly, temperature. As well, correlations between basal area and CWD masses were noncausal but may have induced some confounding effect.

During the first growing season (Fig. 9), residual living tree basal area conditioned stand response. Vegetation responded to changes in radiation. Aspen biomass increment was rapid and very sensitive to the radiation environment above the high shrub layer (path coefficient = 0.97 and 0.98 for leaf and stem biomass increments, respectively). The gap fraction or open sky factor at 3 m height explained 94% and 96% of aspen leaf and aspen stem biomass increment, respectively. Aspen density was not included in the model for the sake of consistency and simplicity, but contrary to aspen biomass increment, aspen sucker density was more highly correlated with residual basal area ($r = -0.94$, $p < 0.001$, $n = 12$) than with the open sky factor ($r = -0.87$, $p < 0.001$, $n = 12$).

Table 4. A priori comparisons ($p > F$) of harvesting treatments on understorey vegetation aerial biomass increment 1 and 2 years following harvesting.

Height class	Control vs. partial cuts	Clearcut vs. partial cuts	One-third vs. two-thirds partial cuts
First-year response			
Herbs	0.002	0.051	0.317
Shrub leaves	0.014	0.023	0.041
Shrub stems	0.358	0.246	0.164
Second-year response			
Herbs	0.011	0.003	0.333
Shrub leaves	0.088	0.562	0.967
Shrub stems	0.034	0.034	0.455

Fig. 7. Aboveground annual biomass increment in understorey herbs and shrubs 1 and 2 years following partial and total harvesting of trembling aspen stands. SD is the standard deviation of the log-transformed population mean. (Mean comparisons are presented in Table 4.)

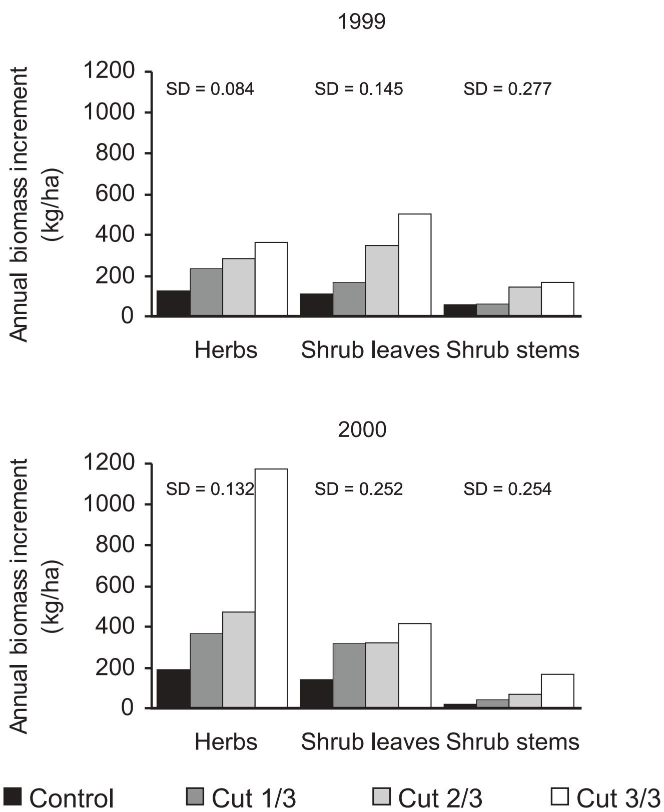
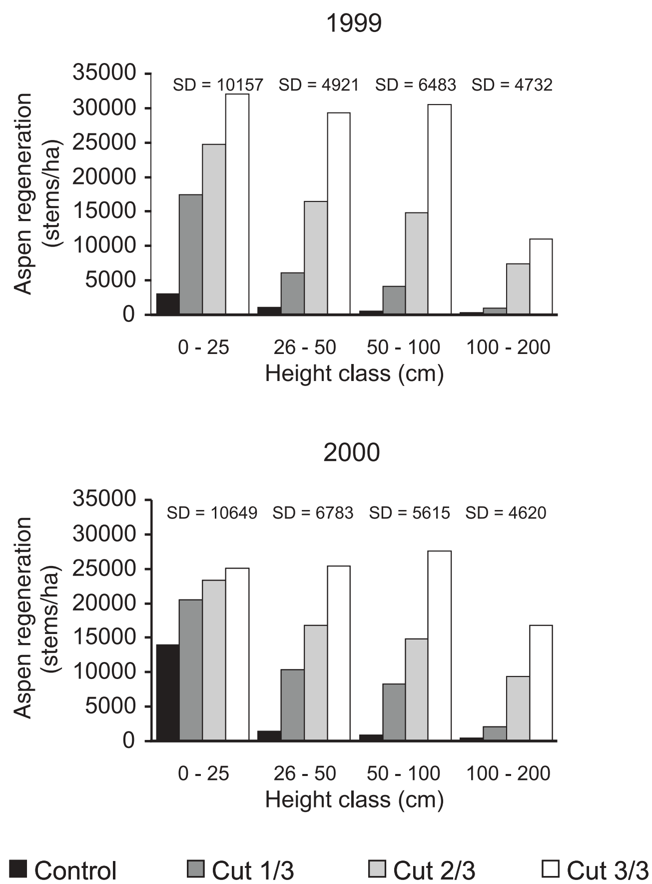


Fig. 8. Trembling aspen regeneration by height class 1 and 2 years following partial and total harvesting of aspen stands. SD is the standard deviation of the population mean. (Mean comparisons are presented in Table 5.)



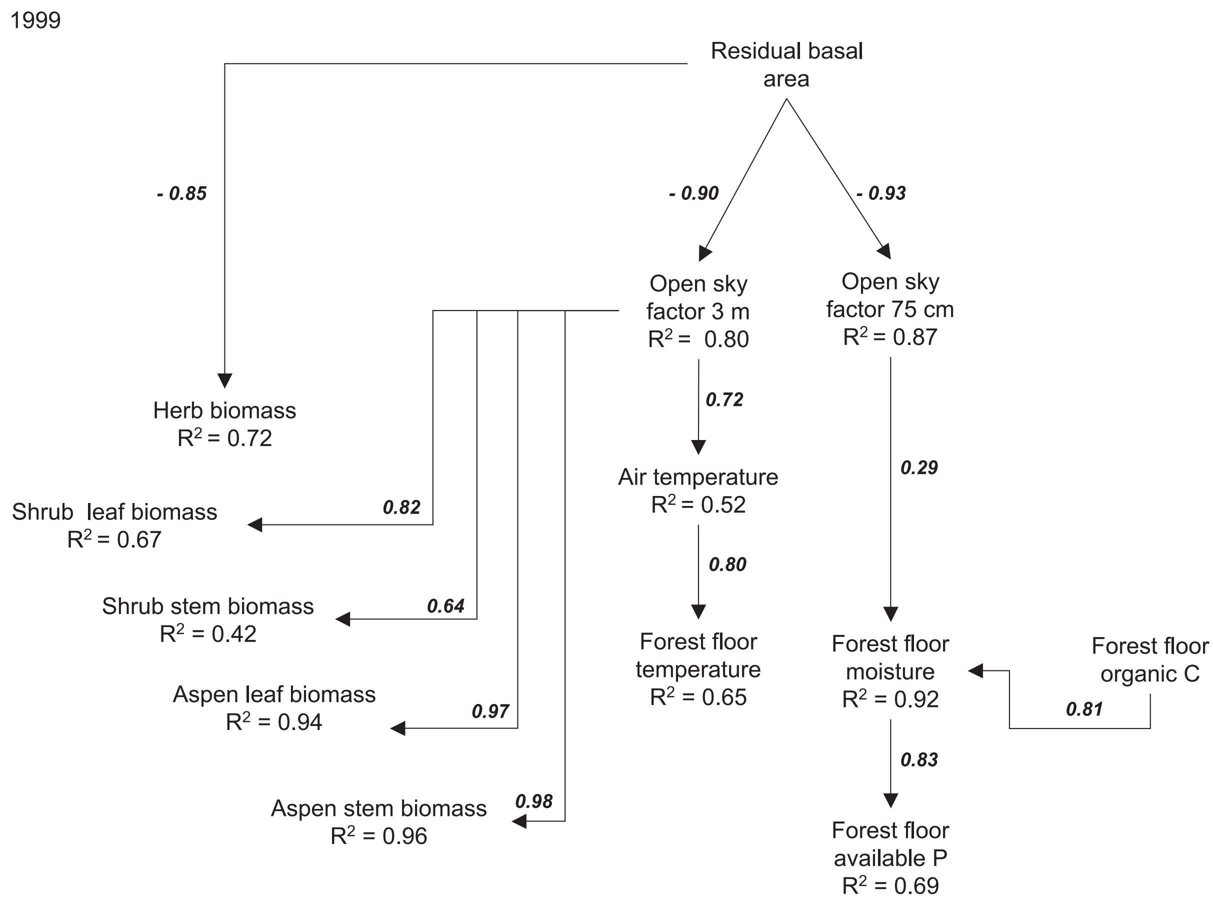
Herbaceous response tracked the residual basal area, while high shrubs responded to the increase in canopy opening by a relatively larger increase in leaf biomass than in stem biomass (path coefficient and R^2 higher for leaves than for stems). Canopy opening caused air and soil temperatures to increase but the open sky factor explained only 52% of air temperature. Increases in soil moisture following harvesting were primarily linked to the increase in soil organic C (path coefficient = 0.81) and secondly to canopy opening (path coefficient = 0.29). Increase in soil moisture led to an increase in P availability. No interaction between vegetation response and nutrient availability was detected.

During the second growing season following harvesting, vegetation response became more complex and relationships between soil processes and residual structure became apparent (Fig. 10). Vegetation dynamics were still mostly controlled by the initial canopy opening after harvesting, but comparison between Figs. 9 and 10 indicates that during the second growing, season herbaceous biomass response was more closely linked to the initial canopy opening (higher R^2 for the second year), while aspen biomass increments were less so. Shrub stem biomass was equally influenced by forest floor Ca concentrations and canopy opening, while shrub

Table 5. A priori comparisons ($p > F$) of harvesting treatments on trembling aspen regeneration (density per height class) 1 and 2 years following harvesting.

Height class (cm)	Control vs. partial cuts	Clearcut vs. partial cuts	One-third vs. two-thirds partial cuts
First year response			
0–25	0.046	0.175	0.416
26–50	0.026	0.002	0.042
51–100	0.097	0.004	0.090
100–200	0.286	0.087	0.152
Second year response			
0–25	0.329	0.681	0.756
26–50	0.045	0.049	0.291
51–100	0.036	0.007	0.196
100–200	0.156	0.015	0.103

Fig. 9. Path analyses of relationships between residual ecosystem structures (stand basal area and soil organic matter), resource availability, and vegetation response during the course of the first growing season following trembling aspen harvesting.



leaf biomass was only conditioned by Ca concentrations, canopy opening having an indirect effect through its effect on Ca concentrations.

The concentration of forest floor organic C was linked to the remaining quantity of well-decomposed CWD observed after harvesting (path coefficient = –0.44). Forest floor organic C affected soil moisture content, while no effect of the initial canopy opening on forest floor moisture was detected during the second growing season. Higher soil moisture contents were associated with lower forest floor temperature (path coefficient = –0.84), while the opposite relationship was noted between forest floor temperature and CWD_F and canopy opening. Higher forest floor microbial C/N was partly linked (R^2 = 0.68) to lower forest floor organic C content (path coefficient = –0.54) and higher exchangeable acidity (path coefficient = 0.46). Canopy opening also had an indirect effect on soil microbial biomass C/N ratio through its direct effect on forest floor exchangeable acidity. Forest floor Kjeldahl N content was linked to decomposition of CWD_F (path coefficient = 0.26) and inversely proportional

Fig. 10. Path analyses of relationships between residual ecosystem structures (stand basal area, CWD, and soil organic matter), resource availability, and vegetation response during the course of the second growing season following trembling aspen harvesting.

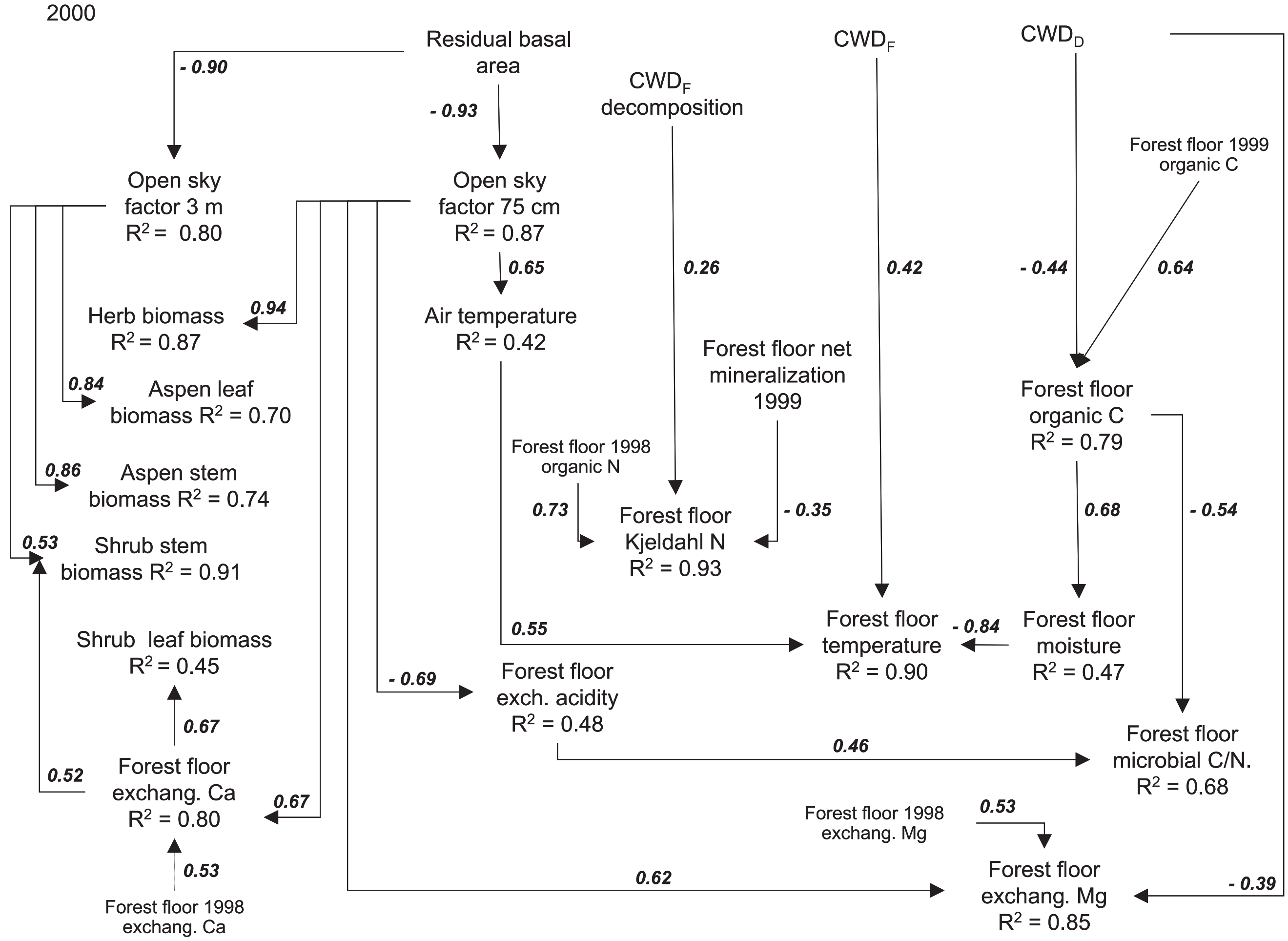


Table 6. Correlations between residual basal area following different levels of harvesting and other predictor variables used in path analyses.

Variable	Pearson correlation	Probability
1999 air temperature	–0.69	0.013
1999 forest floor temperature	–0.64	0.026
1999 forest floor moisture	–0.47	0.127
2000 air temperature	–0.62	0.032
2000 forest floor temperature	–0.44	0.155
2000 forest floor moisture	–0.34	0.278
Fresh CWD mass	–0.80	0.002
Well-decomposed CWD mass	0.60	0.039
Mass loss of fresh CWD	–0.81	0.002

to the rate of net N mineralization (path coefficient = –0.35). Forest floor base cation status (exchangeable Mg^{2+}, Ca^{2+}, and acidity) was affected by canopy opening but not by decomposition of fresh woody debris. Canopy opening increased Ca and Mg concentrations and reduced acidity. Lower CWD_D masses were associated with lower Mg concentrations.

Discussion

Residual structures

Harvesting treatments created an almost linear gradient of residual basal area. Particularly in the clearcut treatment, harvesting induced an increase in fresh CWD_F and caused the CWD_D to be reduced, presumably by crushing, increasing the C concentration of the forest floor. Little other soil physical disturbance was observed following harvesting.

Abiotic conditions

The radiation environment, as characterized by LAI-2000 measurements and hemispherical canopy photographs, did not strictly follow this linear pattern, as solar radiation was proportionally higher in clearcuts. Aspen height in harvested stands was between 25 and 30 m. The regular pattern of harvesting in partial cuts, i.e., small trails and large residual strips, created numerous and regularly spaced small gaps that limited penetration of direct solar radiation for long periods, even in the two-thirds partial harvesting treatment. Residual trees also offered protection against wind and might have attenuated differences in the energy balance (soil and air temperature) of partial cuts relative to unharvested control stands. Carlson and Groot (1997), also working in mixed aspen stands and at a similar latitude (47°43′N), found differences in seasonal average air and soil temperatures between unharvested stands and 18 m wide strips to be 1.2 °C. In the case of the SAFE project, the small size of the clearcuts (average open sky factor <100) may have contributed to reduce differences observed between partial and clearcuts.

Both levels of partial cutting had little impact on soil moisture regime, and the observed consistent increase in forest floor moisture after clearcut harvesting was more the result of an increase in organic matter than of canopy removal, as could be expected. As moist soils need more energy to warm up, the effect of increased radiation on soil temperatures was partly attenuated by higher moisture content in clearcuts.

Nutrient dynamics

Microbial community characteristics were similar to those reported by Bauhus et al. (1998) for aspen stands of the region. Changes in forest floor microbial community in-response to partial and clearcut harvesting were few but consistent with those reported by Siira-Pietikäinen et al. (2001) i.e., a gradual response of the forest floor microbial community characteristics mostly limited to changes in the community structure in response to clearcut treatments and in conjunction with changes in forest floor acidity and organic content. The decrease in microbial C/N ratio that we observed in the clearcut treatment in response to changes in the nature of soil C sources and to lower soil acidity could reflect a change toward a community where the ratio of bacteria to fungi is higher (Marumoto et al. 1982).

The ability of the decomposing community to function was assessed from decomposition and mineralization rates and was not affected by harvesting treatments in the first 2 years. First-year mass losses for fresh leaf litter were consistent with those of Taylor et al. (1989) and rapid initial mass losses in aspen leaves are believed to be caused by physical leaching of soluble components (Huang and Schoenau 1997; Taylor et al. 1989), which is a passive process. Although aspen leaf litter decomposition rates are sensitive to increases in temperature, they are not considered to be sensitive to moisture in the range of temperatures recorded in this experiment (Taylor and Parkinson 1987). Differences in forest floor temperatures between partial cuts and control or clearcut treatments were not high enough to induce significant changes in decomposition rates.

Forest floor nutrient dynamics were characterized by three very different patterns of response to treatments: that of N, base cations, and P. Contrary to what would be expected following disturbance (Mann et al. 1988), N immobilization rather then net release was observed. Forest floor net N immobilization and leaching from fresh logging slash induced an increase in forest floor total organic (Kjeldahl) N. The latter process is plausible, as aspen branches release N during the first years of decomposition (Miller 1983). Leaching of water-soluble organic C, an easily accessible source of energy for soil microorganisms (Huang and Schoenau 1996), could have induced N immobilization, but leaching and immobilization were, according to the results of path analysis, acting independently. Despite net N immobilization, base cation (Ca^{2+} and Mg^{2+}) availability increased in response to change in canopy opening. As these increases were not linked to soil temperature, moisture content, or increased rates of decomposition, it is possible that reduced intake by vegetation was the dominant process controlling cation availability. Greater Ca availability should be of short duration, as it favoured shrub growth and, as a consequence, nutrient sequestration by vegetation.

No mechanism can be provided for the short-term increase in extractable P. In forest ecosystems, P is not very soluble or mobile (Binkley 1986), but following controlled burns, large increases in extractable P have been reported (Macadam 1987; Belleau 2002). In our case, the first-year increase was linked directly to higher forest floor moisture content. Input from fresh or well-decomposed organic matter as a result of harvesting was not retained as a probable cause, as no differences in forest floor total P were found after harvesting (results not shown).

Vegetation response

The immediate vegetation response was conditioned by the radiation environment resulting from treatments, as characterized by the open sky factors. However, the first-year response of the herbaceous component to treatments was directly proportional to residual basal area, which might integrate incident radiation as well as other correlated factors. During the second year, herbaceous response to harvesting was more closely correlated with canopy opening at 75 cm, indicating that the increase in shrub leaf biomass observed in the first year in turn affected the lower vegetation layer.

The shrub layer on these sites exhibited a complex response that was in part caused by species growth patterns, shade tolerance, and nutrient needs. Shrub response to harvesting was characterized first by an initial increase in leaf biomass followed by, in the second year, an increase in stem growth. This pattern indicates that some shrub species exhibited a fixed growth pattern, which is, however, not known to be the case for *A. spicatum* (Kramer and Kozlowski 1979), the dominant shrub species in these stands. Shrubs were also the only vegetation component affected by the soil nutrient status, and more specifically by forest floor Ca concentrations. *Acer spicatum* is a nutrient-demanding species and most of its roots are located in the forest floor (Finér et al. 1997). Although Ca could hardly be a limiting factor on these soils, in conditions of higher light availability, higher forest floor Ca concentrations could promote *A. spicatum* growth.

Aspen recruitment following clearcut harvesting was in the upper range of those reported in other studies (Lavertu et al. 1994; Huffman et al. 1999; Greene and Johnson 1999; Peltzer et al. 2000). Aspen sucker density was strongly dependant on removed basal area (inverse of residual basal area), while aspen leaf and biomass increment were better explained by the radiation environment. The density of aspen suckers is conditioned by mortality of parent trees, i.e., loss of apical dominance (Peterson and Peterson 1992), but sucker growth or height is more closely related to light conditions (Huffman et al. 1999). Compaction and associated soil physical disturbances can stimulate suckering (Corns and Maynard 1998), but compaction has been shown to be limited to the wheel track area of cutovers (Brais and Camiré 1998) and would have affected only 5% of the total area under partial harvesting treatments. The decrease in correlation between sky openness and live aspen biomass observed during the second growing season after harvesting indicated that other factors were affecting sucker growth or survival; among these factors, the most noticeable was the presence of leaf and twig blight (*Venturia populina* (Vuill.)) that reduced sucker growth. Although aspen is a component of the moose's (*Alces alces americana*) diet (Peterson and Peterson 1992), browsing was not apparent.

Silvicultural implications

Two years after harvesting, over 2000, 9000, and 16 000 aspen stems/ha had reached the 1–2 m height class in the one-third, two-thirds, and complete removal treatments. Keeping in mind the interest in testing Bergeron and Harvey's (1997) conceptual model of moving even-aged, structurally simple first-cohort stands into more structurally complex mixedwood compositions through partial cutting, we can venture some early speculation concerning the appropriateness of the two partial cutting treatments for this and other purposes. Aspen suckers recruit and develop well when light is at least 30% of full sunlight, which is approximately the light conditions that we found in the two-thirds partial cut. Thus, aspen suckers appear to be more likely to form a cohort of vigorous stems in the two-thirds partial cut. The higher density of total aspen suckers and greater recruitment of stems into the 1–2 m height class as well as the positive response of residual softwood stems to increased light levels in the two-thirds partial cuts (L. Bourgeois, C. Messier, and S. Brais, submitted[3]) suggest that this treatment may produce a species mix and stand structure more closely resembling older stand types than either the clearcut or the one-third partial treatments. Of course, stand structure over the long term will be affected by the rate of breakup of residual mature aspen stems in controls and partial cutting treatments, and monitoring will provide insight into the effect of stem selection during harvesting on mortality of residual stems.

In contrast with the two-thirds treatment, lower aspen stem density in the 1–2 m height class reflects the less favourable light conditions and slower growth and higher mortality of suckers in the one-third treatment. While initial aspen recruitment and growth following this treatment may not be strong enough to generate a cohort of stems that will attain the tree layer, the residual tree layer in the one-third treatment clearly retains much of the closed, relatively intact structure of the control stands. The moment of final harvest in the one-third partial cuts will be determined by stand health. Low thinning may be used to prolong final harvest in stands of nonclonal species by reducing interstem competition, and removing the most suppressed trees. The same advantage is not clear for clonal species, particularly a species such as aspen that is so susceptible to fungal infection. Some of the speculation concerning longer-term stand responses to partial cutting treatments is being addressed through modelling using the spatially explicit SORTIE model, which has been largely parameterized for the eastern boreal mixedwood (Coates et al. 2003).

Conclusion

Harvesting through removal of aspen stems and increase in photosynthetically active radiation induced an immediate response in vegetation dynamics characterized by large increases in indigenous vegetation biomass and a large amount of aspen suckering. The first-year vegetation response paralleled that of canopy opening. Changes in soil moisture or temperature following partial harvesting were too weak to influence vegetation and nutrient dynamics.

Short-term changes in nutrient dynamics took place mostly in the second year and in response to reduced vegetation uptake and CWD abundance. Interactions between vegetation dynamics and nutrient availability were observed in the second year, and feedback between vegetation uptake and nutrient availability will contribute to attenuate the short-term effect of harvesting on nutrient availability. Harvesting changed the actual abundance and distribution of CWD in these stands and also reduced future inputs of CWD by removing living trees. The long-term implications of these modifications on soil organic matter and nutrient dynamics remain to be assessed.

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