Mountain maple and balsam fir early response to partial and clear-cut harvesting under aspen stands of northern Quebec

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Abstract: This study is a component of the Sylviculture et aménagement forestier écosystémique project, which examines ecosystem-based forest management strategies in mixedwood boreal forests. Four harvesting treatments, one no-harvest, one clearcut, and two partial cuts (33% and 61% of basal area removed), were applied to even-aged aspen stands according to a complete block design. Mountain maple (*Acer spicatum* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.) early response was examined to understand how they react to and interact with canopy opening. Only in clearcuts was maple's response (increase in growth and density) sustained and significant. Balsam fir suffered from a very slight "growth shock" 1 year after harvesting in both clear-cut and two-thirds partial-cut treatments, but growth and vigour increased with canopy opening during the next 2 years. The first year following harvesting, balsam fir growth was negatively affected by understorey aspen and mountain maple. Our results show that the two-thirds partial harvesting treatment could speed up the conversion of pure aspen stands toward mixedwood.

Résumé : Cette étude s'insère dans le cadre du projet Sylviculture et aménagement forestier écosystémique qui examine les stratégies d'aménagement forestier écosystémique en forêt boréale mixte. Quatre traitements de coupe, incluant un témoin, la coupe totale et deux coupes partielles (33 % et 61 % de la surface terrière), ont été appliqués à des peuplements de tremble selon un dispositif en blocs complets. La réponse de l'érable à épis (*Acer spicatum* Lamb.) et du sapin baumier (*Abies balsamea* (L.) Mill.) a été étudiée afin de comprendre comment ces deux espèces réagissent et interagissent suite à l'ouverture du couvert. L'érable à épis n'a répondu de manière soutenue et significative (augmentation en croissance et densité) qu'à la coupe totale. Le sapin a subi un très léger « choc de croissance » l'année suivant la coupe totale et la coupe partielle deux-tiers, mais les deux années suivantes, la croissance et la vigueur de la régénération de sapin ont augmenté avec l'ouverture de la canopée. La croissance du sapin n'a été négativement affectée par la densité des rejets de tremble et d'érable à épis que la première année après la coupe. Nos résultats indiquent que la coupe partielle deux-tiers accélérerait la succession des peuplements de tremble vers une composition plus mélangée.

Introduction

Maintaining mixedwood boreal stands as an integral part of the forested landscape is now a priority across the boreal forest. Increasing public pressure for forestry practices that also protect biodiversity and visual aesthetics has promoted the use of alternative silvicultural interventions, such as those that create smaller openings and take advantage of advance regeneration. Partial cutting is considered a strategy that both improves growth of understorey conifers and mimics the natural processes of gap dynamics as observed in boreal hardwood stands (Lieffers et al. 1996; Bergeron and Harvey 1997; Kneeshaw and Bergeron 1999). An ecosystem-based management approach has been proposed for the mixedwood area of northwestern Quebec (Harvey et al. 2002; Bergeron et al. 2002) with the objective of maintaining and promoting mixedwood stands within the forest landscape. Disturbance-based approaches require an understanding of the relationships between disturbances or silvicultural interventions, resource availability, and the autecology of the main species (MacDonald 1996; Scarrat et al. 1996). Recently, a silvicultural systems experiment, the SAFE project (Sylviculture et aménagement forestier écosystémique), was initiated in the Lake Duparquet Research and Teaching Forest in Abitibi, Quebec (Brais et al. 2004) to test the application of different harvesting intensities as a mean of attaining forest-level objectives. Though the SAFE project comprises three phases, our study focuses on the first phase. Forests in this phase are even-aged aspen stands, which originated from a large fire in 1923. Both mountain maple (*Acer spicatum* Lamb.) and

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balsam fir (*Abies balsamea* (L.) Mill.) represent dominant species in the shrub layer of these stands.

Mountain maple is a highly competitive and important shrub component of boreal mixedwood understorey on fertile mesic sites in northeastern Canada (Archambault et al. 1998). Mountain maple quickly reinvades the understory following fire and can persist in the understorey until very late in the succession (De Grandpré and Bergeron 1993). Harvesting in forests with mountain maple generally contributes to its proliferation (Vallée et al. 1976). With its strong capacity to reproduce via layering from sprouts and basal stems and seed dispersal (Post 1965, 1969; Sarvaala 1999), mountain maple vigorously occupies open areas such as gaps created by spruce budworm outbreaks (Batzer and Popp 1985) and other disturbances such as clear-cutting (Vincent 1965; Perala 1974). Higher resource availability (particularly light) combined with low competition and high reproductive rates of mountain maple may explain the abundance of this species in gaps (Sarvaala 1999; Laflèche et al. 2000). Mountain maple typically grows in dense multi-layered and multi-stemmed thickets (Lei and Lechowicz 1990), and often produces a dense crown coverage, which intercepts considerable incoming light radiation (Aubin et al. 2000; Jobidon 1995). Management of mountain maple is considered critical during the early stages of conifer seedling establishment and growth, because once established mountain maple can persist for over 40 years (Sarvaala 1999). The influence of mountain maple as a competitor to conifer regeneration following clear-cutting has been well studied (Vincent 1965; Post 1965, 1969, 1970; MacLean and Morgan 1983; Jobidon 1997), but its response to partial cutting requires further investigation. Specifically, the influence of a partial canopy tree removal on the growth, demography, recruitment, and mortality of mountain maple needs to be examined.

In mixedwood forests of the study region, forest canopy light transmission is generally low in closed deciduous stands (2%–11% full sunlight; Messier et al. 1999). These light levels are too low for optimal growth of balsam fir, which can be achieved at 25% full sunlight (Parent and Messier 1995; Claveau et al. 2002). The low light availability found between 0 and 1 m in the forest understorey (Messier et al. 1998; Bartemucci et al. submitted2004) likely explains the suppression of smaller stems of balsam fir and white spruce (Larivière 1998). Partial harvesting can be a way of managing light levels and environmental conditions in the understorey, thereby modifying growing conditions for understorey seedlings. Harvesting exposes seedlings to increased light availability, higher temperatures, and greater transpiration demands. Changes in understorey conditions are correlated with the level of harvesting (Dalton and Messina 1995; Carlson and Groot 1997). Furthermore, recent studies suggest that the increased light intensity following harvesting is more important for plant growth than the increased temperature (Carlson and Groot 1997; MacDonald 2000).

The primary objective of this study was to examine short-term response of mountain maple to a gradient of harvesting (clear-cut, two-thirds and one-third partial harvesting, and no harvesting (control)) in aspen-dominated stands. Because partial cutting may limit proliferation of mountain maple over clear-cutting, while improving the growing conditions of advance conifer regeneration, our secondary objective was to determine which harvesting treatment better favoured the growth of balsam fir while limiting mountain maple growth and recruitment. A better understanding of how mountain maple responds to harvesting could lead to effective silvicultural strategies in mixedwood boreal forests, where vegetation management is often required for successful stand regeneration (Harvey and Bergeron 1989).

Material and methods

Study area

The study area, typical of a large area of Quebec, is located in the Lake Duparquet Research and Teaching Forest in the southern part of the boreal forest in Abitibi, Quebec, 45 km northwest of Rouyn-Noranda (48°86′–48°32′N, 79°19′–79°30′W). Forests in the study region are characterized by a mixture of conifer and deciduous tree species, including balsam fir, white spruce (*Picea glauca* (Moench) Voss), and white birch (*Betula papyrifera* Marsh.) (Bergeron et al. 1983). Succession on mesic clay deposits progresses from even-aged stands dominated by trembling aspen (*Populus tremuloides* Michx.) or white birch, to old-growth stands dominated by balsam fir and eastern white cedar (*Thuja occidentalis* L.) (Bergeron and Dubuc 1989). LaSarre is the closest meteorological station to the study area (42 km to the north). The climate is continental with a mean (1961–1990) annual temperature of 0.8 °C. Annual precipitation is 856.8 mm, of which 639 mm falls as rain from April to November. The mean frost-free period is 64 days (Environment Canada 1993). This region is part of the clay belt characterized by lacustrine deposits left by the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). All study sites are located on mesic clay deposits (Brais and Camiré 1992). Soils are Grey Luvisols (Canada Soil Survey Committee 1987), the texture is that of heavy clay (>75% clay), and the humus form is classified as a thin Mor (2–7 cm thick).

Experimental design and treatments

Our study was undertaken in even-aged aspen-dominated stands originating from a large fire in 1923 (Dansereau and Bergeron 1993). Pretreatment stands had a mean basal area of 42.1 m^2/ha, of which aspen trees comprised 92.6% and conifer species accounted for 3.3%. The tall shrub layer (stem diameter >2 cm DBH (diameter at breast height)) was composed mostly of mountain maple, which had an average density of 1327 stems/ha.

In the winter of 1998–1999, four levels of harvesting, including one no-harvest (control) and one clear-cut treatment, were applied to aspen stands following a complete block experimental design with three replications of each treatment. Two partial harvesting treatments removed, respectively, 33% (one-third partial harvesting; residual basal area of 29.7 m^2/ha) and 61% (two-thirds partial harvesting; residual basal area of 16.3 m^2/ha) of 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. Treatment units ranged from 1 to 2.5 ha.

Table 1. Effects of harvesting treatments on mountain maple recruitment for 3 years following harvesting of aspen stands (univariate repeated measures analyses).

(A) Between-subject effects.

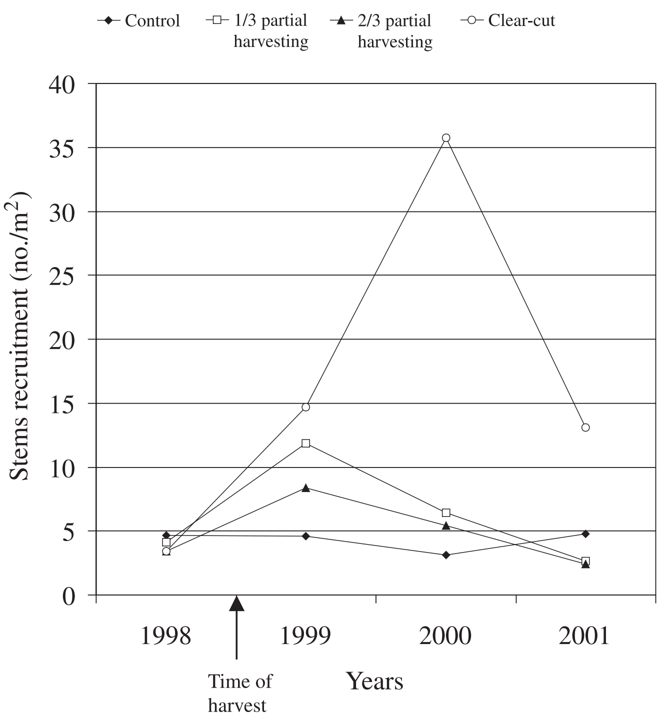
Treatment contrast	MS	*p*
Control vs. partial harvesting	46.6	0.406
Clear-cut vs. partial harvesting	1216.8	0.004*
One-third vs. two-thirds partial harvesting	7.78	0.728
MSE	58.5	

(B) Within-subject effects.

	Mean effect for time		Control vs. partial harvesting		Clear-cut vs. partial harvesting		One-third vs. two-thirds harvesting		
Contrast for time	MS	*p*	MS	*p*	MS	*p*	MS	*p*	MSE
Linear	92.7	0.060	56.2	0.124	41.5	0.175	11.0	0.458	17.6
Quadratic	180.5	0.330	1.4	0.93	514.2	0.126	5.3	0.863	162.8

Note: MS, mean square; MSE, mean square error.
*Probability values of ≤0.05 were considered significant.

Fig. 1. Pre- and post-harvest recruitment of mountain maple stems as measured in 2001 among the various harvesting treatments in aspen stands (ANOVA results and MSE presented in Table 1).



Prior to harvesting, five permanent circular (radius 11.28 m) sampling plots were located in all experimental units. All stems (trees and high shrubs) greater than 5.0 cm 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). Eight 1-m^2 quadrats for vegetation sampling were uniformly distributed within each permanent sampling plot. In partial cuts, trees to be removed were marked prior to harvesting. Brais et al. (2004) underlined that stands in the one-third removal treatment were low thinned with nonvigorous stems removed, while stands in the two-thirds removal 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 clear-cut treatment, whereas in the partial cuts, stems were generally bucked in 2.5-, 5-, or 7.5-m lengths before removal to roadside to avoid damage to residual stems and regeneration. In the partial-cutting 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 clear-cut 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 time of harvesting, so physical soil disturbances (rutting or scarification) were minimal in all treatments.

Canopy openness and temperature measurements

In September of 1999 and 2001, prior to leaf fall, light measurements were taken at 75 cm above the forest floor using a plant canopy analyzer LAI–2000 (LI-COR, Inc., Lincoln, Nebraska). A measurement was taken at each metre along two 50-m transects in each treatment unit, yielding 100 measurements per treatment unit. A second light sensor took simultaneous measurements in a nearby open area. Percentage of canopy openness was calculated from the LAI–2000 measurements.

Mountain maple recruitment, growth, density, and mortality following canopy removal

Mountain maple recruitment was measured as the mean number of mountain maple stems/m^2 that recruited and survived within each treatment unit for each of the last 4 years, as measured in 2001. The recruitment values in 1999, 2000, and 2001 are therefore the number of stems that recruited in those years and survived until 2001. Mountain maple recruitment and growth were sampled in 48 1-m^2 quadrats located adjacent to permanent sampling plots (four harvesting treatments × three replications × four 1-m^2 quadrats). Basal diameter was measured at the root collar for each stem within the quadrat. For each sampled mountain maple stem (1684

Table 2. Effects of harvesting treatments on relative radial growth rates of mountain maple for 3 years following harvesting of aspen stands (univariate repeated measures analyses).

(A) Between-subject effects.

Contrasts between treatments	MS	*p*
Control vs. partial harvesting	<0.1	0.893
Clear-cut vs. partial harvesting	0.2	0.301
One-third vs. two-thirds partial harvesting	<0.1	0.625
MSE	0.9	

(B) Within-subject effects.

	Mean effect for time		Control vs. partial harvesting		Clear-cut vs. partial harvesting		One-third vs. two-thirds harvesting		
Contrast for time	MS	*p*	MS	*p*	MS	*p*	MS	*p*	MSE
Linear	<0.1	0.718	<0.1	0.402	<0.1	0.704	0.1	0.102	0.1
Quadratic	0.1	0.188	<0.1	0.515	0.1	0.098	<0.1	0.657	0.2

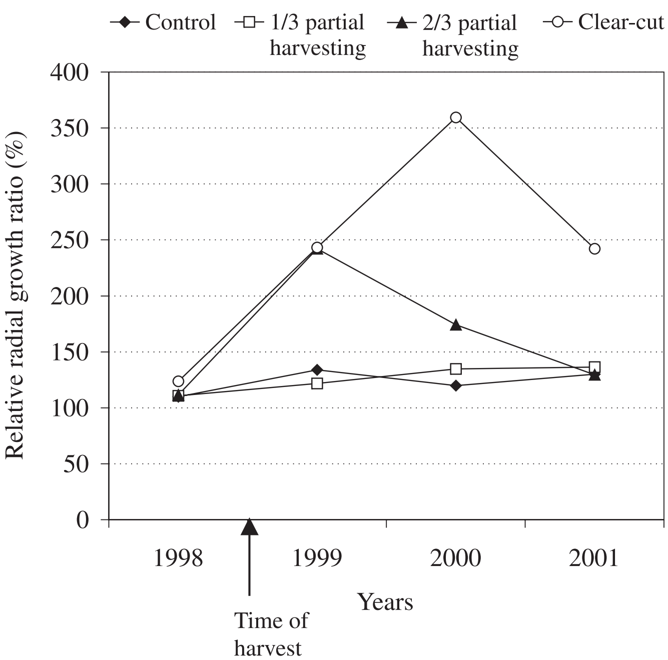


Fig. 2. Pre- and post-harvest relative radial growth of mountain maple stem in aspen stands (ANOVA and MSE results presented in Table 2).

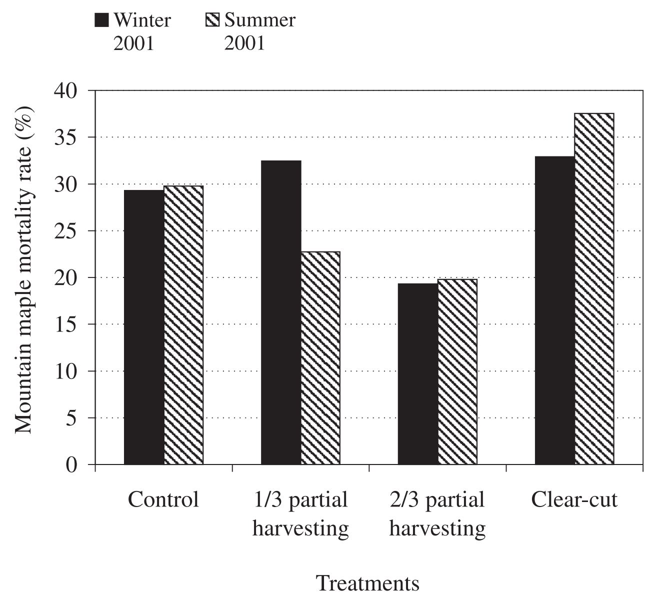


Fig. 3. Mountain maple stem mortality in the winter and summer of 2001, representing second winter and third summer after harvesting of aspen stands (ANOVA and MSE results presented in Table 3).

stems), a disc was removed and numbered at the end of September 2001, when current year's (2001) growth was complete. In the laboratory, each disc was sanded, and its age was determined using a Henson incremental measuring device, which allowed us to determine whether recruitment had occurred before or after forest harvesting. We examined the radial growth response using a subsample of 240 stems. Twenty stems per treatment unit were selected: 10 dominant stems (largest), and 10 subdominant stems (smaller than dominants but at least 6 years old). Most of the mountain maple stems originated from sprouts, and growth rings were fairly easy to see. Growth rings for the past 8 years (5 years before and 3 years after harvesting when possible) were measured to a precision of 0.01 mm along a representative radius. This radius bisected the angle formed by the longest and shortest radii of the stem cross-section (Wright et al. 1998). Relative radial growth rate is defined as the radial growth for each year after harvesting divided by the mean of the preharvest growth rates.

During the first 3 years after harvesting (1999–2001), mountain maple and aspen densities (stems <2 cm DBH) were tallied by height class in eight 1-m^2 quadrats uniformly distributed within each permanent sampling plot for a total of 480 quadrats.

Mountain maple mortality was followed in 120 of the 480 quadrats. At the end of the summer of 2000, two quadrats were systematically selected in each permanent sample plot for a total of 10 quadrats per treatment unit. In each quadrat, all maple stems were tagged, the basal diameter of each stem was measured, and dead stems in each quadrat were tallied. At the end of May and September of 2001, the status

Table 3. Effects of harvesting treatments on mountain maple mortality 3 years after harvesting of aspen stands.

		Mortality rate		
Sampling period	Contrast	df	*F*	*p*
Winter 2001	Control vs. partial harvesting	1	0.1	0.717
	Clear-cut vs. partial harvesting	1	0.7	0.441
	One-third vs. two-thirds partial harvesting	1	1.7	0.232
	MSE	166.9		
Summer 2001	Control vs. partial harvesting	1	0.7	0.447
	Clear-cut vs. partial harvesting	1	3.4	0.114
	One-third vs. two-thirds partial harvesting	1	<0.1	0.903
	MSE	99.6		

Note: Single df (degrees of freedom) contrasts were used to test differences among treatment means. MSE, mean square error.

Fig. 4. Proportion of live and dead mountain maple stems by diameter class after forest harvesting for all treatments combined.

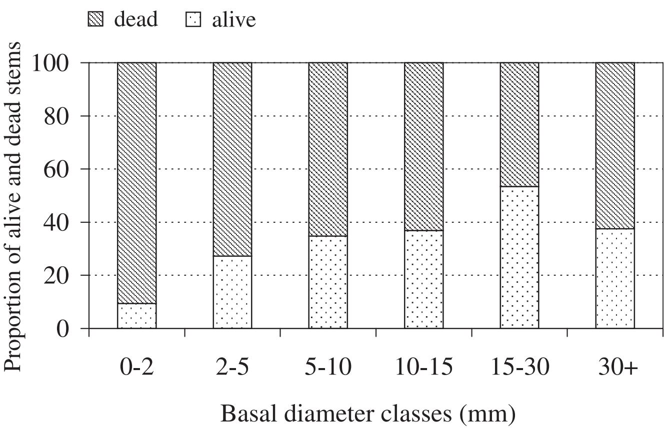
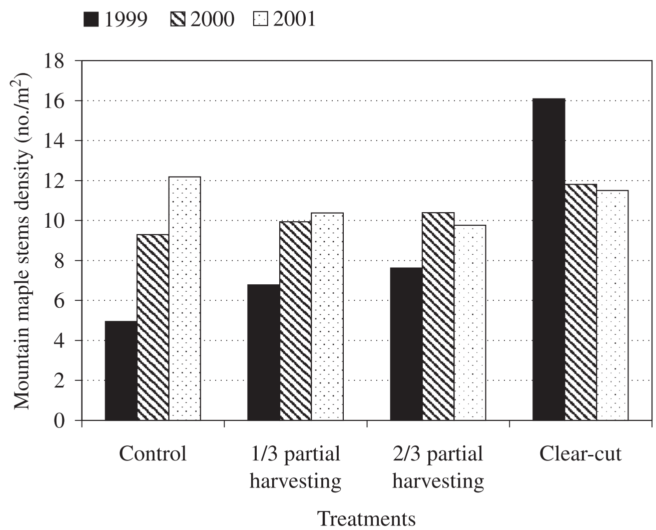


Fig. 5. Mountain maple densities 1–3 years after harvesting aspen stands (ANOVA and MSE results presented in Table 4).



(live or dead) of each mountain maple stem was reassessed. The average mortality rate (%) of mountain maple per m^2 was calculated for each season (winter 2000 or 2001 and summer 2001).

Balsam fir sampling

During the summer of 2001, balsam fir growth response to canopy tree removal was assessed from 226 1-m^2 quadrats (maximum of 4 quadrats per permanent sample plot). For each balsam fir stem in the quadrats, basal diameter, total height, annual height increment (1997–2001), length of the last lateral branch (2001), and live crown length (distance between the lowest living branch and the top height) were measured (Parent and Messier 1995). The relative height growth (%) for any given year was calculated as height increment / total height × 100. The leader to lateral branch ratio, a good indicator of stem vigor, was calculated as leader length / lateral branch length for any given year.

Data analyses

Data analyses were performed using GLM, MEANS, and CORR procedures of the SAS Institute Inc. (1988) version 8.0. Homogeneity of variance between treatments was tested using Bartlett's procedure (Steel and Torrie 1980). Parametric analysis of variance was conducted according to a complete block experimental design with four treatments and three replications per treatment. Contrasts between treatments were designed to answer the following a priori questions (Steel and Torrie1980): (*i*) are the two partially cut treatments different from the control, (*ii*) are the partial-cut treatments different from the clear cut treatments, and (*iii*) is the one-third harvesting treatment different from the two-thirds harvesting treatment? Probability values of ≤0.05 were considered significant. We also used univariate repeated-measures analysis (SAS Institute Inc. 1988) for mountain maple recruitment and growth for the 3 years after harvesting. The Huynh–Feldt estimator was used when the assumption of sphericity of orthogonal components was rejected. The between-subject effects were based on averages over the sampling period (all years combined) of the main effects (harvesting treatments). Comparisons were conducted by means of contrasts as described earlier. Contrasts for time (univariate tests of hypotheses for within-subject effects) were used to describe how the mountain maple mortality rate progresses through the seasons. Linear and quadratic contrasts were used. A correlation analysis was applied to test for linear relationships between balsam fir response and aspen and mountain maple densities for the years 1999, 2000, and 2001.

Table 4. Effects of harvesting treatments on stem densities of mountain maple for 3 years following harvesting of aspen stands (univariate repeated measures analyses).

(A) Between-subject effects.

Contrasts between treatments	MS	*p*
Control vs. partial harvesting	0.68	0.911
Clear-cut vs. partial harvesting	95.52	0.216
One-third vs. two-thirds partial harvesing	0.22	0.949
MSE	50.03	

(B) Within-subject effects.

	Mean effect for time		Control vs. partial harvesting		Clear-cut vs. partial harvesting		One-third vs. two-thirds harvesting		
Contrast for time	MS	*p*	MS	*p*	MS	*p*	MS	*p*	MSE
Linear	26.25	0.073	19.14	0.113	55.58	0.020*	1.59	0.612	5.58
Quadratic	1.60	0.551	0.85	0.551	16.36	0.090	0.12	0.868	4.01

Note: MS, mean square; MSE, mean square error.
*Probability values of ≤0.05 were considered significant.

Results

Effects of harvesting on canopy openness and air temperature

Differences in the level of harvesting resulted in clear differences in canopy openness. The first year after harvesting (1999), light availability at 75 cm above the forest floor was 4.9%, 17.4%, 35.9%, and 86% of full sunlight in the control, one-third, two-thirds, and total harvesting treatments, respectively. The third year after harvesting (2001), light availability at 75 cm above the forest floor was 7.6%, 13.8%, 24.9%, and 58.5% of full sunlight in the control, one-third, two-thirds, and total harvesting treatments, respectively. Air temperature varied slightly among treatments, with a tendency of a slight increase with increasing level of harvesting. The first year after harvesting (1999), the mean air temperature was 16.4, 16.3, 17.6, and 19 °C in the control, one-third, two-thirds, and total harvesting treatments, respectively, and 15.5, 16.7, 17.5, and 17.1 °C the second year after harvesting (2000).

Mountain maple recruitment, growth mortality, and density responses

In the third year after harvesting, mean age of mountain maple stems was 7.9, 6.0, 6.5, and 4.4 years in the control, one-third, two-thirds, and clear-cut treatments, respectively. Average basal diameter was 11.4 mm in control stands, 8.7 mm in one-third harvesting, 10.3 mm in the two-thirds harvesting, and 5.2 mm in clearcuts. The largest and the oldest stems of mountain maple, in terms of basal diameter (mm) and age (years), respectively, were found by decreasing order in the control (29.13 mm; 18.18 years), the two-thirds harvesting (20.49 mm; 12.41 years), the one-third harvesting (19.95 mm; 10.21 years), and the clearcut (12.17 mm; 5.64 years).

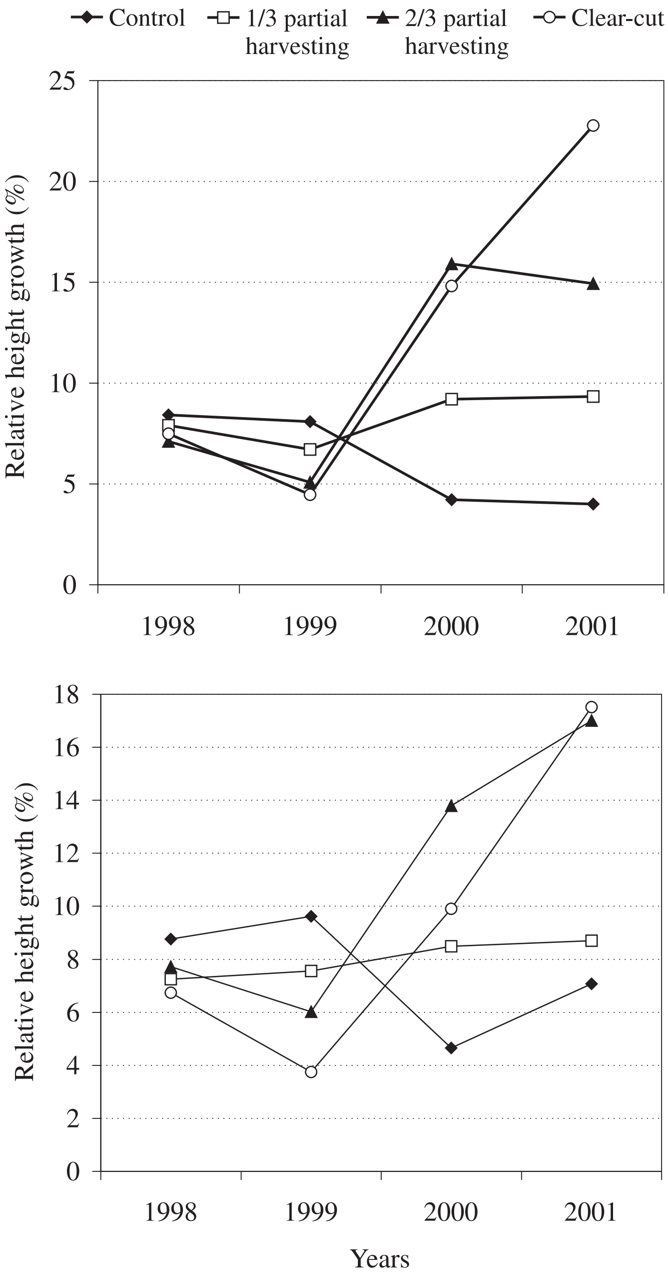
Mountain maple responded with a dramatic increase in stem recruitment because of the clear-cut treatment (Fig. 1; Table 1). Stem recruitment remained significantly higher in the clearcuts than in the partial harvesting treatments over the 3-year period. The largest stem recruitment was in the second year after clear-cutting (2000). At that time (2000), recruitment was higher than in the partial harvesting treatments by a factor of 7 (Fig. 1). The effect of time was significant at the $p = 0.06$ level, and the interaction between time and treatments was not significant. There were no significant differences between the one-third and two-thirds harvesting treatments ($p = 0.728$) and when compared with the control ($p = 0.406$) (Fig. 1; Table 1). Overall, the clear-cut treatment was the most favourable to mountain maple recruitment.

Because we found very few differences among treatments between the dominant (mean of 14.3 years) and subdominant stems (6 years old or more; mean of 9.4 years) of mountain maple, the results are presented with both groups analyzed together (Fig. 2; Table 2). The relative radial growth of mountain maple increased following the two-thirds harvesting and clear-cut treatments with the highest radial growth in the second year after clear-cutting (2000). Despite a large increase in radial growth in partial cuts, there are no significant differences between clearcuts and partial cuts ($p = 0.301$) (Table 2). The comparison between clearcuts and partial cuts was not significant because the two-thirds partial harvesting had growth responses very close to the clearcut, whereas the one-third partial harvesting had growth responses very close to the control (Fig. 2). Postharvest radial growth rates showed no significant differences between the one-third and two-thirds harvestings ($p = 0.625$), and when compared with the control ($p = 0.893$) (Fig. 2; Table 2).

Stem mortality rates of mountain maple were similar in winter and summer 2001 (Fig. 3), and showed no significant differences between clear-cut versus partial harvesting treatments, between the two levels of partial cut, and between partial cuts and the control (Table 3). Although the mean was lower in the two-thirds treatment, percentage of stem mortality tended to decrease with increasing stem size (Fig. 4).

Mountain maple stem densities were highest in the first year after harvesting (16 stems/m^2) in clear-cutting (Fig. 5). From 1999 to 2001, two opposite trends were observed concerning stem density; there was a significant linear decrease in stem density with time in the clearcuts, while stem densities increased in the partial cuts. No significant differences were found between clearcuts and partial cuts and between the two partial cuts (Fig. 5; Table 4), but we found a signifi-

Fig. 6. Relative growth rates of balsam fir, before and 1–3 years after harvesting aspen stands: (*a*) stems <1 m, (*b*) stems 1–3 m (ANOVA and MSE results presented in Table 5).



cant linear effect. At the end of the sampling period, stem densities appeared to be similar in all treatments between 10 and 12 stems/m^2.

Response of balsam fir seedlings of different size

We sampled 338 fir seedlings of which 158 ranged from 16 to 99 cm in height, and 180 seedlings had heights between 100.5 and 270 cm. Three years after harvesting, average basal diameters of saplings less than 1 m tall were 12.2, 14, 15.9, and 17.5 mm in the control stands, one-third, two-thirds, and clear-cut harvesting treatments, respectively. For saplings greater than 1 m tall, average basal diameters were 26.9, 27.5, 28.7, and 31.3 mm in the control, one-third, two-thirds, and clear-cut harvesting treatments, respectively.

Balsam fir relative height and radial (data not shown) growth increased linearly with canopy opening and time following harvesting (Figs. 6*a* and 6*b*) for all treatments, except for the control where it decreased. For stems <1 m as well as stems between 1 and 3 m, the linear increase with time was steeper in the clearcuts than in the partial cuts, and steeper in the two-thirds than in the one-third harvesting treatments, as shown by significant interactions between linear contrasts for time and treatment comparisons (Table 5). Three years after partial harvesting, increases in relative height and radial growth appeared to be stabilizing for the <1-m stems and were still increasing for the 1- to 3-m stems (Figs. 6*a, b*). Stems between 1 and 3 m in the clear-cut and two-thirds harvesting treatments suffered a slight decrease in growth rate following harvesting. The leader to lateral branch ratio (Fig. 7) and the live crown length (data not shown) responded positively with increasing canopy opening. The leader to lateral branch ratio response was significantly higher in the clearcut than in partial cuts for both sizes (Table 6).

Correlations between balsam fir height growth and stem densities of mountain maple and aspen were negative and significant only during the first year after harvesting (Table 7). Balsam fir growth decreased when mountain maple and aspen densities increased for both height classes. Two years after harvesting, the correlation between balsam fir height growth (stems <1 m) and aspen density (Table 7) was still significant, but positive this time.

Discussion

Mountain maple dynamics

Recruitment of mountain maple in partial and total harvesting treatments was facilitated by its strong capacity to reproduce principally by layering from sprouts and stems and some seedling establishment (Jobidon 1995; Sarvaala 1999). Despite the known capacity of mountain maple to take advantage of small canopy gaps (Ghent 1958; Lei and Lechowicz 1990), the conditions created by the dispersed pattern of harvesting used in the partial cuts did not seem to have created conditions that have allowed mountain maple to increase significantly its understorey dominance for more than a couple of years. In effect, recruitment, densities, and growth in partial harvesting treatments were similar to those of the control 2 years after harvesting.

Mortality was relatively high over the 3-year period, and both winter and summer mortality rates were similar. Mortality rates were higher for smaller mountain maple stems (lowest basal diameter classes). Sarvaala (1999) examined early survival of mountain maple stems and showed that most (approximately 90%) germinated seeds die during the first 3–5 years in aspen and mixedwood forests. In fact, rarely do germinated seeds result in tall mountain maple stems (Sarvaala 1999). High density of young seedlings, self thinning, browsing, pathogens, unfavourable climatic conditions, low light levels, poor seedbeds, and high litterfall are some of the reasons for high early mortality rates (Hibbs 1979; Hibbs and Fischer 1979; Oliver 1981; Tappeiner and Zasada 1993). Based on its high mortality rate in shade,

Table 5. Effects of harvesting treatments on balsam fir relative height growth, 1–3 years after harvesting of aspen stands (1999–2001).

(A) Between-subject effects.

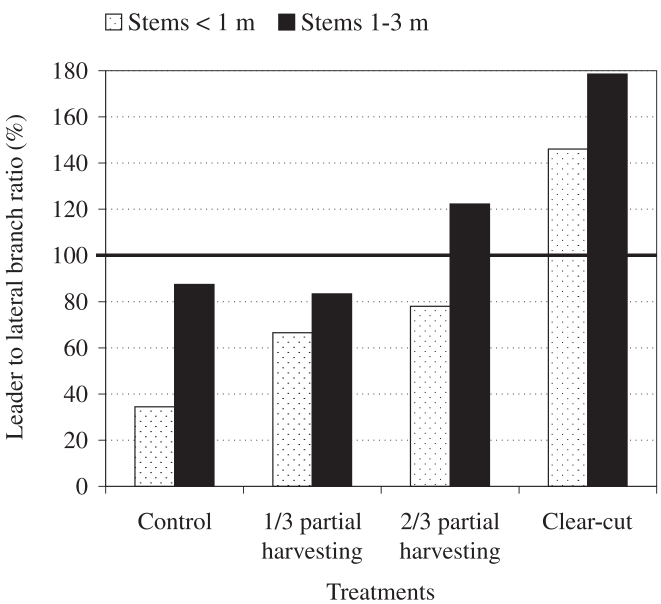
	Stems <1 m		Stems 1–3 m	
Contrasts between treatments	MS	*p*	MS	*p*
Control vs. partial harvesting	<0.1	0.002*	<0.1	0.161
Clear-cut vs. partial harvesting	<0.1	0.003*	<0.1	0.352
One-third vs. two-thirds partial harvesting	<0.1	0.020*	<0.1	0.076
MSE	<0.1		<0.1	

(B) Within-subject effects.

Mean effect for time		Control vs. partial harvesting		Clear-cut vs. partial harvesting		One-third vs. two-thirds harvesting		
MS	*p*	MS	*p*	MS	*P*	MS	*p*	MSE
Stems <1 m								
<0.1	<0.001*	<0.1	<0.001*	<0.1	<0.001*	<0.1	0.006*	<0.1
<0.1	0.090	<0.1	0.047*	<0.1	0.673	<0.1	0.096	<0.1
Stems 1–3 m								
<0.1	0.001*	<0.1	0.008*	<0.1	0.009*	<0.1	0.005*	<0.1
<0.1	0.616	<0.1	0.020*	<0.1	0.380	<0.1	0.340	<0.1

Note: One univariate repeated measures ANOVA was performed per height class. MS, mean square; MSE, mean square error.
*Probability values of ≤0.05 were considered significant.

Fig. 7. Balsam fir leader to lateral branch ratio for seedlings and saplings three growing seasons after aspen harvesting (ANOVA and MSE results presented in Table 6).



mountain maple should be considered a fairly shade-intolerant species (sensu Kobe et al. 1997).

Response of balsam fir seedlings of different size

Similarly, balsam fir responded positively to the partial-cutting systems, especially the two-thirds treatment, which somewhat mimic small-scale gap disturbance. It has been shown that balsam fir has an advantage in gaps originating from slow mortality of overstory trees (Kneeshaw and Bergeron 1999). Our results also support those of Ruel et al. (2000), Kneeshaw et al. (2002), and Parent and Ruel (2002) who showed that balsam fir saplings undergo a "growth shock" the first year after harvesting. Several studies have shown that height growth of balsam fir may not respond immediately to canopy harvesting, or that height growth can even decrease after harvesting (Gordon 1973; Johnstone 1978; Seidel 1980; McCaughey and Schmidt 1982; Nikinmaa 1993; Williams et al. 1999). Part of this delay could be attributed to the fact that height growth is often predetermined in the previous growing season (Kneeshaw et al. 1998), but this does not explain growth reductions or delays exceeding 1 year. Response of advance regeneration to release is dependent on tree characteristics and site conditions, which interact with the degree of physiological shock caused by the sudden change in environmental conditions such as increases in light levels and evapotranspiration, potential radiation, and frost injury (Ferguson and Adams 1980). Despite the first year decrease in relative growth rate, balsam fir regeneration responded well to the two-thirds and complete harvesting treatments. It remains to be seen if this rate increase will persist as canopy closure proceeds in the partial cuts. Finally, the negative correlation between balsam fir growth and mountain maple and aspen density found only the first year after partial harvesting (Table 7) could be related to the strong recruitment the first year followed by a heavy mortality of both mountain maple and aspen thereafter.

Conclusions and ecological and silvicultural implications

Mountain maple obviously plays an important role as an understory light filter (Keedy 1992; Messier et al. 1998; Aubin et al. 2000), which limits the recruitment of shade-intolerant tree species such as aspen and birch in natural conditions (Kneeshaw and Bergeron 1999). In that sense, it may favour succession toward shade-tolerant conifer- dominated forests. The silvicultural strategy of the SAFE project is to use clear-cutting or other even-aged systems as a surrogate for stand reinitiation by fire, and partial (natural mortality) or selection cutting (outbreaks) to accelerate the natural suc-

Table 6. Effects of harvesting on leader to lateral branch ratio of balsam fir saplings the third year after harvesting (2001).

	Stems <1 m tall			Stems 1–3 m tall		
Treatment contrasts	df	MS	*p*	df	MS	*p*
Control vs. partial harvesting	1	0.3	0.009*	1	<0.1	0.646
Clear-cut vs. partial harvesting	1	1.1	<0.001*	1	1.1	0.055*
One-third vs. two-thirds partial harvesting	1	<0.1	0.356	1	0.2	0.331
MSE	<0.1			0.2		

Note: Single df (degrees of freedom) contrasts were performed to test differences among treatment means. MS, mean square; MSE, mean square error.

*Probability values of ≤0.05 were considered significant.

Table 7. Correlation analysis between relative height growth of balsam fir and densities of mountain maple and aspen for the 3 years after logging (1999–2001).

Height class	Variable	Year	*r*	*p*
Stems <1 m	Mountain maple density	1999	–0.7	0.022*
		2000	0.2	0.515
		2001	0.1	0.685
	Aspen density	1999	–0.7	0.007*
		2000	0.7	0.012*
		2001	–0.1	0.844
Stems 1–3 m	Mountain maple density	1999	–0.6	0.040*
		2000	0.3	0.322
		2001	0.1	0.715
	Aspen density	1999	–0.6	0.040*
		2000	0.5	0.060
		2001	–0.1	0.846

Note: One correlation analysis was performed per year and per balsam fir height class (n = 12).

*Probability values of ≤0.05 were considered significant.

cession from intolerant hardwood to mixedwood and conifer-dominated stands (Bergeron and Harvey 1997). Finding the optimal partial harvesting prescription that will both promote the growth of shade-tolerant trees while controlling the expansion of aggressive understory shrubs such as mountain maple is an important objective if one wants to put in place such new forestry practices. In practical terms, the two-thirds harvesting of merchantable basal area seems to successfully release the understorey balsam fir while limiting the growth of the dense mountain maple understorey. It also increased the understory sprouting of aspen (Brais et al. 2004), but we do not know their long-term survival. Obviously, longer-term monitoring of the response of both mountain maple and balsam fir as well as aspen is required to ascertain our sylvicultural prescription. In addition to finding the optimal partial cut, one needs to find a means to increase balsam fir and white spruce stem density and distribution in many of these aspen-dominated stands, if uneven-aged silviculture of aspen-mixedwood stands is to be realized and demonstrated to the forest practitioners (Calogeropoulos et al. 2004).

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