Effect of cutting intensity on microenvironmental conditions and regeneration dynamics in yellow birch – conifer stands

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Abstract: This paper presents the 5 year results of different cutting intensities (removal of 0%, 40%, 50%, 60%, and 100% of the basal area) applied in two mixed yellow birch (*Betula alleghaniensis* Britt.) – conifer stands of eastern Quebec, Canada. Two sites 90 km apart were used: Armagh and Duchesnay. Each site had four replicates of the treatments in a randomized block design. The effect on light availability was similar in the two sites: the 0%, 40%, 50%, 60%, and 100% cuts transmitting a mean of 5%, 21%, 26%, 30%, and 94% of full light, respectively, during the first summer. Soil temperature increased only in the 100% cut (4–5 °C, maximum daily temperature). Soil disturbance during harvest was higher at Duchesnay than at Armagh, which clearly improved seedbed receptivity, particularly to yellow birch. After 5 years, treated areas contained 21 000 to 48 300 seedlings/ha at Duchesnay compared with 5500 – 10 500 seedlings/ha at Armagh. Significant losses of coniferous advance growth were observed at both sites, but a subsequent seedling recruitment occurred only at Duchesnay. Red spruce (*Picea rubens* Sarg.) showed superior establishment in the 60% cut (4400 seedlings/ha) than under other cutting intensities (1600–2100 seedlings/ha), whereas balsam fir (*Abies balsamea* (L.) Mill.) responded well to all partial cutting treatments. At both sites, pin cherry (*Prunus pensylvanica* L.f.) was the main competing species in the 100% cut, whereas densities of the preestablished mountain maple (*Acer spicatum* Lamb.) and striped maple (*Acer pensylvanicum* L.) either remained the same or increased in the partial cuts.

Résumé : Cet article présente les résultats de 5 ans de différentes intensités de coupe (prélèvements de 0 %, 40 %, 50 %, 60 % et 100 % de la surface terrière) appliquées dans deux peuplements mixtes de bouleau jaune (*Betula alleghaniensis* Britt.) et conifères de l'est du Québec, Canada. Deux sites distants de 90 km ont été utilisés, Armagh et Duchesnay, et chaque site avait quatre répétitions des traitements dans un dispositif en blocs aléatoires. L'effet sur la lumière disponible a été le même dans les deux sites, les coupes à 0 %, 40 %, 50 %, 60 % et 100 % transmettant en moyenne 5 %, 21 %, 26 %, 30 % et 94 % de la pleine lumière, respectivement, durant le premier été. La température du sol n'a été augmentée que dans la coupe à 100 % (4–5 °C du maximum journalier). La perturbation du sol durant la récolte a été plus forte à Duchesnay qu'à Armagh, ce qui a nettement amélioré la réceptivité des lits de germination, particulièrement pour le bouleau jaune. Après 5 ans, les aires traitées contenaient 21 000 à 48 300 semis/ha à Duchesnay, comparativement à 5 500 à 10 500 semis/ha à Armagh. Des pertes significatives de conifères préétablis ont été observées dans les deux sites, mais un recrutement de semis ne s'est par la suite produit qu'à Duchesnay. L'épinette rouge (*Picea rubens* Sarg.) s'est mieux établie dans la coupe à 60 % (4 400 semis/ha) que dans les autres intensités de coupe (1 600 – 2 100 semis/ha), alors que le sapin baumier (*Abies balsamea* (L.) Mill.) a bien réagi à toutes les coupes partielles. Dans les deux sites, le cerisier de Pennsylvanie (*Prunus pensylvanica* L.f.) a été la principale espèce compétitrice dans la coupe à 100 %, alors que la densité de l'érable à épis (*Acer spicatum* Lamb.) et de l'érable de Pennsylvanie (*Acer pensylvanicum* L.) préétablis a été maintenue ou augmentée dans les coupes partielles.

Introduction

Mixedwood stands dominated by yellow birch (*Betula alleghaniensis* Britt.) are among the most productive stands in Quebec, Canada. They are most common in the balsam fir (*Abies balsamea* (L.) Mill.) – yellow birch bioclimatic domain (Saucier et al. 1998) occurring between the 47th and 48th parallels, in the transition zone between the broadleaved forest to the south and the coniferous (boreal) forest to the north. This late-successional forest (hereafter referred to as the mixedwood forest) is a species-rich forest, marking the northern limit of yellow birch, an important tree species in eastern North America (Erdmann 1990) and of other southern species such as sugar maple (*Acer saccharum* Marsh.), white elm (*Ulmus americana* L.), red maple (*Acer rubrum* L.), eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), and red spruce (*Picea rubens* Sarg.). This forest supplies varied and high-quality products to the forest industry. Close to urban centres, it also offers a great recreational potential largely based on its species richness that gives aesthetic, wildlife habitat, and biodiversity values.

Although maintaining mixed-species stands has become an objective in Quebec's forest management policy (MRNQ 1992), foresters' expertise regarding their management and regeneration is still very limited. The mixedwood forest presents the challenge of controlling the competing vegeta-

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tion while regenerating the desired species. Competing species such as mountain maple (*Acer spicatum* Lamb.), beaked hazelnut (*Corylus cornuta* Marsh.), and mooseberry (*Viburnum alnifolium* Marsh.) are generally well established in the understory, whereas other species, such as pin cherry (*Prunus pensylvanica* L.f.) and raspberry (*Rubus idaeus* L.), are likely stored in the soil seed bank. Past clearcuts have generally resulted in widespread site invasion by these competing species (Archambault et al. 1998; Laflèche et al. 2000) to the detriment of yellow birch and other valuable species, such as white spruce (*Picea glauca* (Moench) Voss) and red spruce, which are becoming in short supply in this forest zone (Fortin 2003).

Sustaining the composition and structure of the mixedwood forest also presents the challenge of taking into consideration the desired species' varying ecological characteristics. For example, yellow birch and red spruce are resistant to natural disturbing agents and can live up to 400 years, whereas balsam fir is prone to windthrow. Trees >70 years old are subject to decay and are highly susceptible to spruce budworm (*Choristoneura fumiferana* Clem.) attack (Doucet et al. 1996). In terms of light requirement, balsam fir (Frank 1990) and red spruce (Blum 1990) are very shade tolerant and often present abundant advance growth that represents a potential for the future stand. Red spruce is known to respond well to release even after a long period of suppression (Blum 1990), but its sensitivity to full light (Alexander et al. 1995), frost (DeHayes et al. 2001), and high temperatures (Vann et al. 1994) must be considered. Midtolerant yellow birch (Forcier 1973, 1975) and white spruce (Nienstaedt and Zasada 1990) rarely establish under a full canopy. They require an opening to regenerate, which can also favour noncommercial species as well as less desired commercial species, such as red maple, a shade-tolerant species that is commonly found in the mixedwood forest, and white birch (*Betula papyrifera* Marsh.), which has autecology similar to yellow birch (Perala and Alm 1990). Both red maple and white birch exhibit rapid early growth and can invade a clearcut site by natural seeding and sprouting.

In Quebec, there is increasing interest in management methods that emulate natural stand dynamics (e.g., Lieffers and Beck 1994; Bergeron and Harvey 1997). In the mixedwood forest, the natural disturbance regime is dominated by the death of overmature trees, windthrow, and insect epidemics (Grondin et al. 1996), which create small openings in the canopy, usually of less than 300 m^2 (Kneeshaw and Prévost 2007). These openings can often be as small as the area of a single tree crown (Hébert 2003). Although an irregular to uneven-aged forest structure can be naturally maintained, the classical selection cutting method is not well adapted to multispecies stands, which present a wide range of longevities and light requirements. For example, removal of 25%–35% of the basal area (BA), as has long been the rule, while retaining trees across a full range of size classes, implies that a large proportion of mature balsam fir is not harvested and may be lost by windthrow or natural mortality. Nevertheless, most yellow birch – conifer stands contain a good number of small merchantable yellow birch and spruce stems (10–30 cm diameter at breast height (DBH)) with a high growth potential. A large proportion of these stands have abundant advance growth of fir and red spruce. Therefore, a sound silvicultural system for the mixedwood forest should include treatments that preserve small merchantable stems and advance growth.

In this study, we made the hypotheses that a partial canopy opening aimed at harvesting mature balsam fir and other species to improve overall stand quality and growth would (*i*) promote the establishment of yellow birch and red spruce seedlings by improving light availability in the understory, (*ii*) favour the development of red spruce advance growth, and (*iii*) limit the development of competing species. The main objective of the study was to define an optimal threshold for opening the canopy that would maintain both red spruce and yellow birch in the future stand. The study also aimed at relating the dynamics of light availability in the understory to regeneration establishment, growth, and survival. This paper presents the 5 year results of this study.

Materials and methods

Experimental sites

The study was carried out in the Québec City region at two sites that were 90 km apart. Both sites support high-quality yellow birch – conifer stands. The Armagh site (46°50′N, 70°32′W) is located in Bellechasse County, in land region 3d (Basses-Appalaches) of the sugar maple – yellow birch bio-climatic domain (Saucier et al. 1998). The site location corresponds to the northern edge of the foothills of the Appalachians massif. The Duchesnay site (46°54′N, 71°41′W) is in Portneuf County, in land region 4d (Contreforts de Charlevoix et du Saguenay) of the balsam fir – yellow birch bioclimatic domain. This site corresponds to the southern edge of the foothills of the Laurentian massif. At both locations, the landscape is characterized by an undulating topography and podzolic soils developed from deep glacial till. The bedrock sources are slaty schists from the Armagh group at Armagh and granitic gneiss from the Grenville province at Duchesnay. The climate of the two locations is classified as subpolar, subhumid, continental (Robitaille and Saucier 1998), with 112 and 114 frost-free days (Canadian Climate Program 1982) and mean annual precipitations of 1073 and 1320 mm (27% and 26% of which fall as snow) at Armagh and Duchesnay, respectively. Mean daily maximum temperatures are recorded in July (Armagh, 23.2 °C; Duchesnay, 24.2 °C) and minimum temperatures are recorded in January (Armagh, –16.5 °C; Duchesnay, –18.9 °C) (Canadian Climate Program 1993).

Before the cut, the merchantable BA at Armagh (32.1 m^2/ha) was composed of 38% yellow birch, 24% red maple, 23% balsam fir, and 13% red spruce (Table 1), with white birch and striped maple (*Acer pensylvanicum* L.) as main companion species. The understory was composed of a mixture of species totalling 40 900 stems/ha, of which 64% and 90% were <0.3 m and <1.0 m in height, respectively. This short regeneration (<1 m high) was comprised of red maple (10 400 stems/ha), balsam fir (8900 stems/ha), mountain maple (7300 stems/ha), striped maple (5600 stems/ha), yellow birch (3700 stems/ha), and relatively few red spruce (800 stems/ha). Advance growth taller than 1.0 m was mainly composed of mountain maple (1400 stems/ha) and red spruce (1100 stems/ha), whereas other species were less abundant in this strata (400–600 stems/ha).

Table 1. Cutting intensity (CI; planned removal of 0%, 40%, 50%, 60%, and 100% of the basal area; actual percent cut = 100 × (precut BA – postcut BA)/precut BA) related to density of merchantable stems (*N*, stems/ha), basal area (BA, m^2/ha), and percentage of the total basal area (%) at the Armagh and Duchesnay sites.

	Armagh precut (1997)			Armagh postcut (1998)		Duchesnay precut (1998)			Duchesnay postcut (1999)	
CI (%)	*N*	BA	%	BA	% cut	*N*	BA	%	BA	% cut
Spruce and fir										
0	461	11.5 (2.0)	36	10.8	—	311	12.6 (3.8)	38	12.8	—
40	453	11.3 (1.6)	34	5.7	50	297	13.2 (2.8)	39	8.2	38
50	461	12.7 (1.2)	39	4.6	64	231	12.6 (3.5)	38	5.7	55
60	494	11.3 (0.6)	37	4.5	67	355	14.4 (4.3)	37	6.0	49
100	386	10.0 (1.4)	32	0.0	100	289	12.4 (4.3)	40	0.0	100
Yellow birch										
0	189	11.8 (0.7)	37	12.1	—	231	16.1 (1.7)	52	16.5	—
40	175	15.0 (2.7)	44	9.4	37	147	13.6 (2.4)	41	9.7	29
50	139	11.6 (2.1)	37	8.9	23	194	12.6 (1.1)	40	9.0	29
60	169	12.0 (1.5)	40	5.2	57	252	12.2 (0.5)	44	6.5	47
100	158	9.8 (1.6)	31	0.0	100	206	11.8 (0.9)	41	0.0	100
Red maple										
0	122	7.5 (1.7)	23	7.4	—	36	2.2 (1.2)	7	2.3	—
40	125	6.7 (2.4)	20	5.1	24	108	5.2 (1.7)	16	2.5	52
50	114	7.3 (3.3)	22	3.6	51	81	6.2 (1.0)	20	2.6	58
60	114	6.1 (1.9)	20	3.2	48	74	4.9 (2.1)	16	1.5	69
100	233	11.8 (3.2)	36	0.0	100	86	4.1 (1.5)	15	0.0	100
All species										
0	839	32.1 (2.1)	—	31.6	—	634	31.8 (1.6)	—	32.5	—
40	795	33.6 (1.6)	—	20.7	38	578	33.0 (1.2)	—	20.5	38
50	748	32.4 (2.2)	—	17.1	47	569	31.8 (1.7)	—	17.6	45
60	853	30.3 (1.1)	—	13.0	57	733	32.1 (4.1)	—	14.0	56
100	806	32.2 (2.2)	—	0.0	100	623	29.2 (2.7)	—	0.0	1000

Note: Values for precut BA are means with SEs given in parentheses.

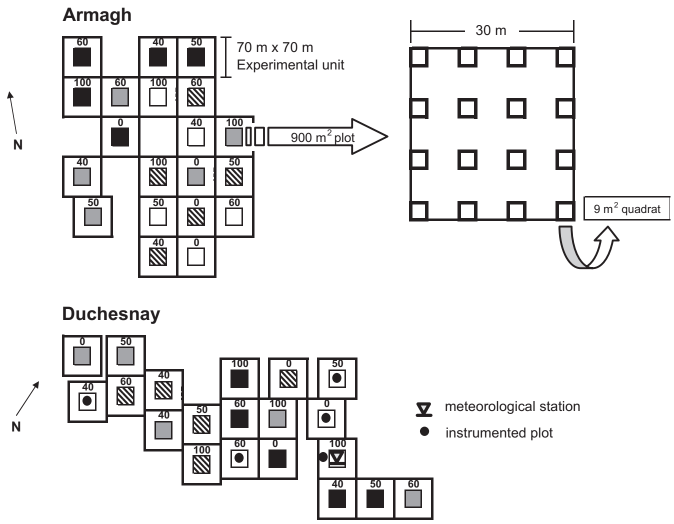
At Duchesnay (31.6 m^2/ha) (Table 1), there was a higher percentage of red spruce (26%), a similar amount of yellow birch (42%), and less balsam fir (15%) and red maple (14%) in the main canopy than at Armagh. Sugar maple and American beech (*Fagus grandifolia* Ehrh.) were the principal companion species; white birch and striped maple were also found in places. The understory was less dense (28 500 stems/ha) than that at Armagh (p = 0.047), with less short regeneration of balsam fir (2800 stems/ha), yellow birch (1300 stems/ha), and striped maple (2100 stems/ha); similar amounts of red maple (10 900 stems/ha); a little more red spruce (1600 stems/ha); and a significant proportion of sugar maple (1600 stems/ha). Advance growth >1.0 m was comparable with that of Armagh, except for a lower mountain maple density (800 stems/ha).

Experimental design

At each location, the experiment was comprised of four completely randomized blocks, each one containing five treatments: three partial cutting intensities (removal of 40%, 50%, and 60% of merchantable BA), which are hereafter referred as light (L), moderate (M) and severe (S); a careful logging around advance growth (CLAAG) total overstory removal (T; 100% of BA); and an uncut control (C, 0%). Based on the inventory of merchantable stems before the cut, experimental units were first classified into forest types according to their proportion of softwood, yellow birch, and red maple. The five treatments were randomly assigned within each of these forest types, which are actually blocks in statistical terms (e.g., Prévost and Pothier 2003). This layout was designed to reduce the experimental error associated with the initial proportions of softwood (balsam fir was harvested in priority) and of the two other major species (yellow birch and red maple), which differ greatly in their reproductive strategies (seeding versus sprouting ability).

Each experimental unit measured 70 m × 70 m (≅ 0.50 ha in area) and contained a 30 m × 30 m central plot (900 m^2), from which precise mensurational measurements were taken (Fig. 1). Before cutting, the DBH of all stems ≥1.3 m in height was measured in the 900 m^2 plots. This initial inventory was used to mark the stems to be removed in the partial cutting to control the desired BA removal. For each experimental unit, the equivalent marking was then done in the 20 m wide buffer strip. The aim of the marking was the harvest of mature fir because of the species propensity to windthrow. At the same time, we wanted to improve the general quality of the stand by prioritizing the removal of trees with low vigour and defective stems. For adjacent trees of equal vigour and quality, the priorities for marking were (*i*) noncommercial species, (*ii*) balsam fir, (*iii*) black ash (*Fraxinus nigra* Marsh.), (*iv*) American beech, (*v*) white birch, (*vi*) white spruce, (*vii*) red spruce, (*viii*) red maple, (*ix*) sugar maple, and (*x*) yellow birch. Marking was designed to create a uniform canopy and avoid openings that were too

Fig. 1. Layout of the experimental design at the Armagh and Duchesnay sites. For each 70 m × 70 m experimental unit, the values indicate the cutting intensities (% of basal area) and the fill pattern indicates the block.



large, although harvesting small groups of mature firs was allowed. In the total cut, all stems ≥9.1 cm DBH were systematically marked in a single operation in the 70 m × 70 m unit. Cutting was done from 17 November to 21 December 1997 at Armagh and from 19 October to 18 November 1998 at Duchesnay. It was expected that logging during the leafless period would provide passive site preparation by creating enough disturbance in the fresh leaf litter to improve seedbed receptivity to spruce and yellow birch (Nyland 2002). At each site, softwood was harvested before the hardwood. Felling was done using a chainsaw, and trees were debranched on site and skidded tree length to the landings (Tree Farmer model C4 at Armagh and Timberjack model 550 at Duchesnay). The treatments in an individual block were completed before moving to another replicate.

Vegetation monitoring

Within each 900 m^2 plot, sixteen 3 m × 3 m quadrats (9 m^2) were established for precut regeneration surveys. Commercial species and the principal noncommercial species were tallied by height class (1–5, 6–30, 31–60, 61–100, 101–200, 201–300, and >300 cm), and percent coverage of the principal seedbeds (leaf litter, fresh humus, other soil horizons (H, Ae, B), feathermoss, wood debris, and rocks) was noted. After the cut, all residual stems of commercial species >1.3 m in height were numbered in each of the 900 m^2 plots. Species and DBH were also noted. Annual regeneration surveys were conducted at both locations.

Environmental followup

The photosynthetic photon flux density (PPFD, Sunfleck 80, Decagon Devices, Pullman, Wash.) was measured above each 9 m^2 quadrat before cutting at the Armagh site and for 5 years after cutting at both Armagh and Duchesnay. In each quadrat, eight measurements were made 1.3 m above the soil by systematically displacing the apparatus to cover the whole surface, the mean PPFD was registered. These measurements were repeated one to five times per year between June and August from 10:00 to 14:00 solar time on sunny days only.

Beginning in June 1999, one block at Duchesnay was equipped with an automatic data-acquisition system (CR10X, Campbell Scientific Canada, Edmonton, Alta.). This block had a mixed composition that is representative of the overall yellow birch – conifer stand. In each experimental unit, soil temperature was monitored with thermistors (107B-AM) in two undisturbed soil profiles. In each profile, two thermistors were inserted at the junction of the organic (H) and mineral (Ae) horizons. Air temperature and relative humidity (CS500), wind speed (MET ONE cup anemometer; Campbell Scientific Canada, Edmonton, Alta.), incident light (LI-COR quantum sensor, LI190SB; LI-COR Inc., Lincoln, Nebr.) and precipitation (tipping bucket rain gauge, TE525M) were also measured in the 100% cut treatment. Soil temperature was measured at 15 min intervals, whereas the other variables were sampled every 5 min, and hourly means were recorded. Standardized data were also available from the Armagh (46°45′N, 70°32′W) and Duchesnay (46°52′N, 71°39′W) meteorological stations.

Data analysis

Data from the two sites were pooled and submitted to a common analysis of variance that treated sites, cutting intensities, and measurement years as fixed effects and blocks as random effects. The MIXED procedure of SAS (version 9.1; SAS Institute Inc. Cary, N.C.) was used in conjunction with restricted maximum likelihood (REML) estimates for the variance components and Satterthwaite's method for approximating the degrees of freedom. For analysis of repeated measurements of light transmission and seedling density, an appropriate covariance structure was first selected using the Akaike's information criterion (AIC). When precut measurements were available (seedbed coverage and seedling density), the significance of their inclusion as covariates in the model was tested afterwards. In all cases where a factor was statistically significant ($p < 0.05$), the significant differences of least squares means (LSMEANS) were obtained using the SIMULATE adjustment for p values and confidence limits (LSMEANS/adjust = simulate option). For significant interactions among main factors, levels of one factor were compared at a fixed level of the other factors using the %SimIntervals SAS Macro to adjust p values for contrasts of interest only (Westfall et al. 1999). One-tailed p values were used to compare seedbed coverage between the sites, because the greater soil disturbance in Duchesnay allowed us to predict that seedbed improvement would be better at this site. When a covariate was included in the model, multiple comparisons were done at its mean value. Homogeneity of variances and normality of data were verified graphically. Because soil temperature was monitored in one replicate only at Duchesnay, it was impossible to statistically test the effect of cutting intensity on this parameter; means and standard errors are then presented as an indication of treatment differences.

Results

Microenvironmental conditions

Photosynthetic photon flux density

Harvesting changed the PPFD taken at 1.3 m above the soil surface (Table 2) and patterns of light transmission were comparable for the two sites under study (Fig. 2). All cutting intensities increased light transmission to the understory, but the effect of the three partial cuts was quite similar, and limited, when compared with complete overstory removal. For example, during the first summer following the treatment, the 0%, 40%, 50%, 60%, and 100% cuts transmitted 6%, 23%, 26%, 31%, and 92% of full light, respectively, at Armagh, and 3%, 20%, 26%, 29%, and 95% of full light, respectively, at Duchesnay. Afterwards, an overall time effect was observed ($p < 0.001$) because of a gradual decrease of available light related to postcut vegetation development. This decrease was inversely related to the residual cover (Fig. 2), but the relationships between treatments evolved differently at the two locations, as indicated by the significant interaction between site, cutting intensity, and time ($p = 0.020$). The effect was particularly pronounced in the 100% cut at Duchesnay, where rapid vegetation development greatly increased light interception above the 1.3 m level. During year 5, the 100% cut transmitted less light at this location (45% of full light) than at Armagh (65%), whereas the partial cuts at both sites allowed similar light transmission to the understory (15 to 21%).

Soil temperature (Duchesnay site)

Harvesting at Duchesnay had an effect on soil temperature in the 100% cut only (Table 3). In that experimental unit, the temperature reached a maximum of 27.4 °C during the first summer after cutting (1 August 1999); this is 7–10 °C higher than the maximum registered in any other treatment (17.8–20.6 °C). During that summer, the daily maximum was consistently higher (mean 4–5 °C) in the 100% cut (19.5 °C) than in all other treatments (14.4–15.0 °C), where temperatures were comparable. The effect of the total cut remained detectable on soil temperature in subsequent years, although this difference with respect to the partial cuts decreased with time, because of the gradual decrease of solar radiation reaching the soil surface. The mean daily maximum temperature in the 100% cut was still higher by 3–4 °C during year 2, 2–3 °C during years 3 and 4, and 1–2 °C during year 5.

Seedbed coverage

Before the treatment, leaf litter was the dominant seedbed at both locations with 84%–91% coverage of the ground surface, whereas feathermoss, rocks, and debris totalled 9%–16% coverage (not shown). Less than 1% of the surface was covered by soil horizons known as receptive seedbeds (mixed or intact H, Ae, and B horizons). Harvesting significantly changed the coverage of all seedbeds (Table 4A). Site effects were detected for percent cover of unreceptive leaf litter and fresh humus ($p = 0.053$), as well as for receptive seedbeds ($p = 0.037$). The amount of receptive seedbed coverage was three times greater at Duchesnay than at Armagh (Table 4B). As expected, the coverage of receptive soil horizons increased with cutting intensity. The 60% and 100% cuts presented significant seeded improvements when compared with the control. Results at the two locations were not different for other seedbeds ($p = 0.171$ and 0.198). Compared with the control, the 100% cut was the only one to show a change in feathermoss coverage (decrease) and rocks and debris coverage (increase), whereas all cutting intensities reduced the coverage of unreceptive leaf litter.

Table 2. Analysis of variance of photosynthetic photon flux density measurements repeated 1, 2, 3, 4 and 5 years after cutting (removal of 0%, 40%, 50%, 60%, and 100% of the basal area) at the Armagh (1998–2002) and Duchesnay (1999–2003) sites.

Source of variation	ndf*	ddf†	$p > F$
Site (S)	1	8.4	0.251
Cutting (C)	4	22.8	<0.001
S × C	4	22.8	0.448
Time (T)	4	21.6	<0.001
S × T	4	21.6	0.089
C × T	16	23.2	<0.001
S × C × T	16	23.2	0.020

*ndf, degrees of freedom for the numerator.
†ddf, degrees of freedom for the denominator.

Regeneration dynamics

Regeneration dynamics differed between the sites and among the species, and strong time effects were found for the main commercial species at both sites (Table 5). Site effects were found for recruitment of yellow birch ($p < 0.001$) and red maple ($p = 0.005$), whereas recruitment of red spruce and balsam fir was not clearly related to the site. Moreover, site × time interactions were found for these four commercial species indicating that their establishment was a dynamic process over the study period. Pin cherry, mountain maple, and striped maple reacted similarly to the treatments at both sites ($p = 0.380$ to 0.665, statistics not presented). For the most part, harvesting had a significant effect on all species.

Yellow birch

Recruitment of yellow birch was initially proportional to cutting intensity at both sites, but it was much more successful at Duchesnay than at Armagh (Fig. 3). For example, in year 2, when most of the first-year germinants had reached 5 cm in height, the density of seedlings varied from 40 000 to 70 000 seedlings/ha at Duchesnay, compared with values of 3000 – 11 000 seedlings/ha at Armagh. Afterwards, the relationship between the treatments evolved differently over the years at each location, as indicated by the interaction between site, cutting intensity, and time ($p = 0.051$). The number of yellow birch seedlings remained proportional to cutting intensity at Duchesnay, where the 5 year recruitment was better in the 100% cut (48 300 seedlings/ha) than in the 40% cut (21 000 seedlings/ha) and the control (500 seedlings/ha). At this time, nearly 14 000 seedlings/ha were taller than 1 m in the 100% cut, compared with 2500–6000 seedlings/ha in the partial cuts (not presented). At Armagh, the density of seedlings remained low and no treatment appeared to be better than the others for this species after 5 years. Because a peak in seedling establishment occurred at year 3 at this site, the majority of the seedlings were in the 5–100 cm classes (7400 – 10 000 seedlings/ha).

Red spruce

Red spruce establishment was limited compared with that of yellow birch (Fig. 4). All cutting intensities initially removed a good part of the preestablished red spruce regener-

Fig. 2. Percent transmission of photosynthetic photon flux density (PPFD) through the canopy for selected days, 1–5 years after the cuts at the Armagh (1998–2002) and Duchesnay (1999–2003) sites. Values in parentheses are the ranges of PPFD (μmol·m^{-2}·s^{-1}) recorded for each day during the sampling procedure. The letters on the *x* axis are the five cutting intensities: C, uncut control (0%) and L, light (40%); M, moderate (50%); S, severe (60%); T, total overstory removal (100%). For cutting intensity within a year, means associated with the same letter are not different, according to simulation-based adjusted *p* values for pairwise comparisons.

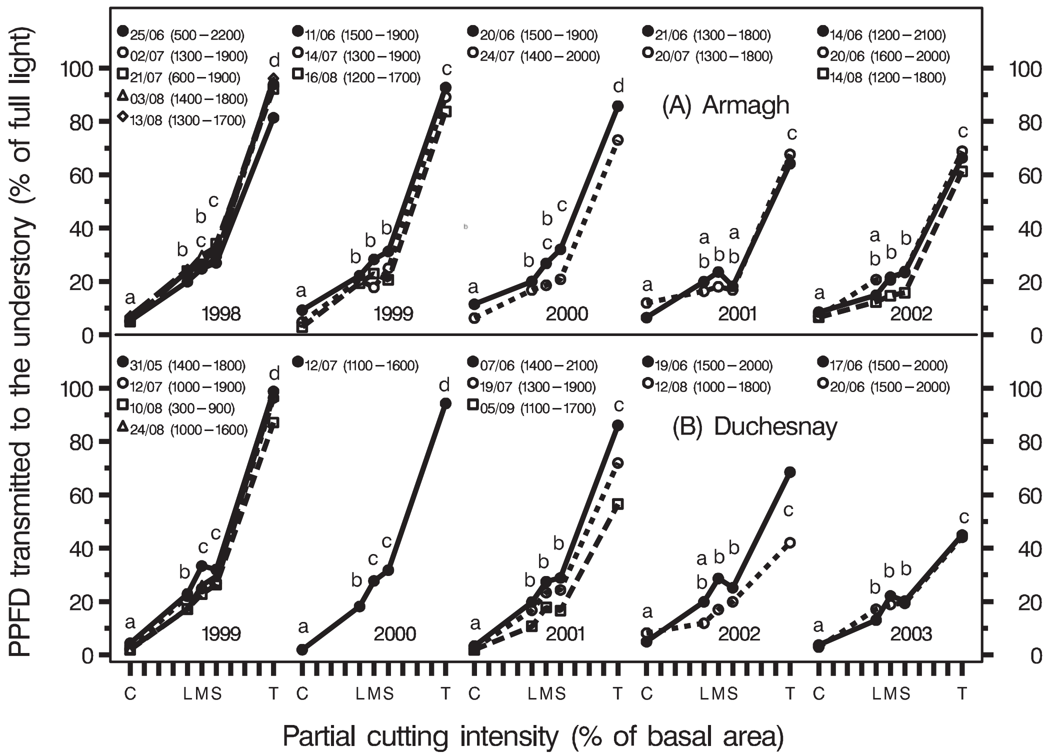


Table 3. Soil temperature (°C) related to cutting intensity and air temperature in the control (uncut; 0%), 1–5 years (1999–2003) after treatment at the Duchesnay site.

			Cutting intensity (% of basal area)				
Period*	Temperature	Air	0	40	50	60	100
1999	Mean summer	14.4	13.9	14.0	14.0	14.4	17.0
(10/07 to 15/10)	Mean daily maximum	19.1	14.8	14.9	14.4	15.0	19.5
N = 98	Summer maximum	28.5	19.8	20.6	17.8	19.1	27.4
2000	Mean summer	12.0	10.8	11.6	11.6	10.6	13.3
(03/05 to 31/10)	Mean daily maximum	16.8	11.8	12.6	12.7	11.5	15.4
N = 182	Summer maximum	26.1	17.4	18.0	19.5	17.0	23.3
2001†	Mean summer	12.5	11.4	10.9	12.2	11.8	13.4
(11/05 to 31/10)	Mean daily maximum	17.1	12.3	11.6	13.3	12.6	15.1
N = 137	Summer maximum	30.4	17.4	16.2	19.5	17.5	20.9
2002	Mean summer	12.9	11.7	11.1	12.3	12.1	13.6
(18/05 to 31/10)	Mean daily maximum	17.9	12.6	11.8	13.4	12.9	15.3
N = 167	Summer maximum	31.3	18.8	17.2	20.4	18.9	22.5
2003	Mean summer	13.3	12.2	11.6	12.6	13.9	13.9
(21/05 to 31/10)	Mean daily maximum	17.9	13.0	12.2	13.5	14.7	15.3
N = 164	Summer maximum	30.7	18.1	17.0	18.7	20.9	21.4
1999–2003	Mean	13.0 (0.4)‡	12.0 (0.5)	11.8 (0.5)	12.6 (0.5)	12.6 (0.7)	14.3 (0.7)
	Mean daily maximum	17.8 (0.4)	12.9 (0.5)	12.6 (0.6)	13.4 (0.3)	13.3 (0.7)	16.1 (0.8)
N = 5	Mean summer maximum	29.4 (0.9)	18.3 (0.5)	17.8 (0.8)	19.2 (0.4)	18.7 (0.7)	23.1 (1.2)

*Values in parentheses are the range of dates over which the means and maxima were calculated.
†The 2001 season includes 37 days of missing data (19/07 to 24/08).
‡Values in parentheses are SEs; for annual means, standard errors vary from 0.2 to 0.6 °C.

Table 4. Relative seedbed coverage (% of the soil surface) related to cutting intensity at the Armagh and Duchesnay sites, before and 1 year after treatment.

(A) Analysis of covariance testing pretreatment (year 0) seedbed coverage as a covariate in the model

		Receptive soil horizons (H, Ae, and B)		Feathermoss		Rocks and debris		Leaf litter and fresh humus	
Source of variation	ndf*	ddf†	$p > F$	ddf	$p > F$	ddf	$p > F$	ddf	$p > F$
Site (S)	1	6.0	0.037	22.5	0.171	6.1	0.198	6.0	0.053
Cutting (C)	4	23.1	0.001	22.5	0.025	23.2	0.009	23.1	<0.001
S × C	4	23.1	0.239	22.5	0.314	23.2	0.806	23.1	0.219
Covariate (Co)	1		—	26.5	<0.001		—		—
Co × S	1		—	26.5	0.010		—		—

(B) Site and treatment means

	Receptive soil horizons (H, Ae, and B)	Feathermoss	Rocks and debris	Leaf litter and fresh humus
Site				
Armagh	2.9	2.2	15.9	78.7
Duchesnay	10.5	1.4	19.0	68.4
Cutting intensity (%)				
0	0.7a	2.5b	11.3a	85.6c
40	4.4ab	1.8ab	19.3ab	73.9b
50	6.0abc	2.4ab	17.6ab	73.9b
60	8.7bcd	2.0ab	15.6ab	72.7b
100	13.6d	0.3a	23.4b	61.9a

Note: For cutting intensity, means followed by a same letter are not different, according to simulation-based adjusted *p* values for pairwise comparisons.
*ndf, degrees of freedom for the numerator
†ddf, degrees of freedom for the denominator.

Table 5. Analysis of covariance of recruit density (no./ha) measurements repeated 1–5 years after cutting (removal of 0%, 40%, 50%, 60%, and 100% of the basal area) at the Armagh (1998–2002) and Duchesnay (1999–2003) sites.

		Yellow birch		Red spruce		Balsam fir		Red maple	
Source of variation	ndf*	ddf†	$p > F$	ddf	$p > F$	ddf	$p > F$	ddf	$p > F$
Site (S)	1	145.0	<0.001	115.0	0.152	144.0	0.113	8.1	0.005
Cutting (C)	4	145.0	<0.001	31.2	0.001	144.0	0.039	11.0	<0.001
S × C	4	145.0	<0.001	31.4	0.218	144.0	0.349	11.0	0.012
Time (T)	4	145.0	<0.001	48.9	<0.001	144.0	<0.001	38.8	<0.001
S × T	4	145.0	<0.001	48.9	<0.001	144.0	<0.001	38.8	0.006
C × T	16	70.4	<0.001	26.5	0.240	16.0	0.149	41.5	<0.001
S × C × T	16	70.4	0.051	26.5	0.179	16.0	0.435	41.5	0.456
Covariate	1		—	30.5	<0.001	8.6	<0.001		—

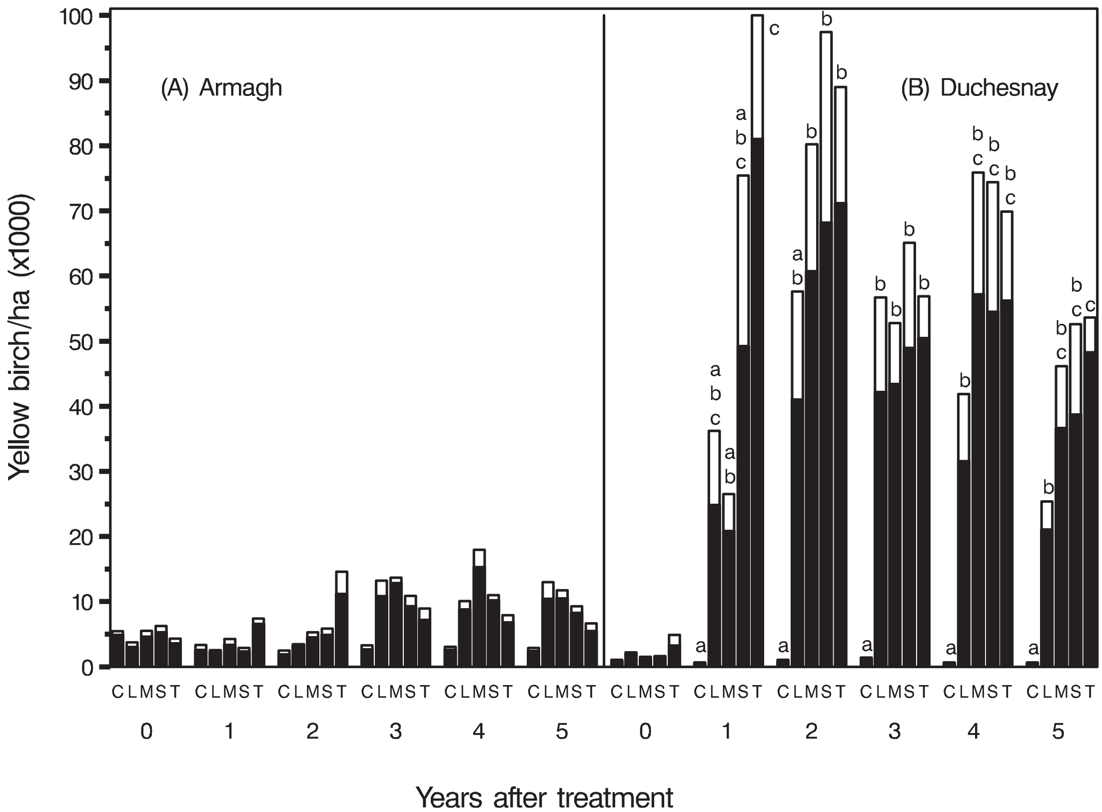
Note: For each species, pretreatment (year 0) density of stems was tested as covariate in the model.
*ndf, degrees of freedom for the numerator.
†ddf, degrees of freedom for the denominator.

ation at both sites. A gradual establishment of new seedlings was observed thereafter at Duchesnay only, as confirmed by the site × time interaction ($p < 0.001$) (Table 5). In general, recruitment of new seedlings was better in the 60% cut than in the 100% cut ($p = 0.007$), whereas other treatments gave comparable results. After 5 years, the 60% cut at the two sites had twice as many seedlings (mean 2900 seedlings/ha) as the three other cutting intensities (1300–1500 seedlings/ha), whereas the control had an intermediate seedling density (2200 seedlings/ha). These red spruce seedlings were mainly present in the <1 m height classes because of the loss of advance growth in taller classes and slow growth of seedlings recruited after the cut.

Balsam fir

Before cutting, the density of balsam fir regeneration was highly variable at both locations (Fig. 5). The major effect of harvesting was the initial loss of the advance growth, which was particularly high in the 100% cuts at the two sites (mean 7300 stems/ha) compared with the 40%, 50%, and 60% cuts (1700, 2200, and 1900 stems/ha, respectively). Like red spruce, balsam fir recruitment was better at Duchesnay. This was confirmed by the site × time interaction ($p < 0.001$). Furthermore, recruitment was more successful in the partial cuts. On average at both sites, the density of fir seedlings in the 60% cut (6800 seedlings/ha) was higher ($p = 0.015$) than in the 100% cut (3700 seed-

Fig. 3. Density of yellow birch seedlings related to cutting intensity (% basal area), 1–5 years after treatment at the Armagh and Duchesnay sites. The letters on the *x* axis are the five cutting intensities: C, uncut control (0%) and L, light (40%); M, moderate (50%); S, severe (60%); and T, total overstory removal (100%). The solid bars show the means, and the open bars show the SEs. For cutting intensity within a year, means associated with the same letter are not different, according to simulation-based adjusted *p* values for pairwise comparisons.



lings/ha) after 5 years. More than 80% of these seedlings were shorter than 0.3 m at the time of measurement.

Red maple

Red maple generally established well following harvest at both locations. Although a peak in recruitment occurred during the first summer at Duchesnay, the process was gradual at Armagh (patterns not presented). Five years after harvest, partial cutting appeared to be more beneficial to red maple than total overstory removal at both locations (Fig. 6). At Armagh, the three partial cuts had between 40 000 and 50 000 more stems/ha than the 100% cut, whereas at Duchesnay the same was true only for the 60% BA removal. However, more red maples taller than 1 m were found in the 100% cut (4900 and 8100 stems/ha) than in the partial cuts (1600 to 3600 stems/ha) at both locations.

Noncommercial species

Pin cherry emergence was abundant and proportional to cutting intensity during the first two summers after cutting at both sites (patterns not shown), reaching means of 4300, 5000, 8400, and 28 200 seedlings/ha in the 40%, 50%, 60%, and 100% cuts, respectively. Thereafter, mortality of this shade-intolerant species was severe in all treatments. After 5 years, the 100% cut still contained 11 000 and 17 000 seedlings/ha at Armagh and Duchesnay, respectively, compared with less than 4000 seedlings/ha in the partial cuts (Fig. 6). In terms of height growth, pin cherry largely dominated the regeneration strata in the 100% cut, with 3400 and 12 300 stems/ha >2 m tall, and more than 8000 (70% of total) and 16 000 stems/ha (90%) >1 m tall (not shown) at Armagh and Duchesnay, respectively.

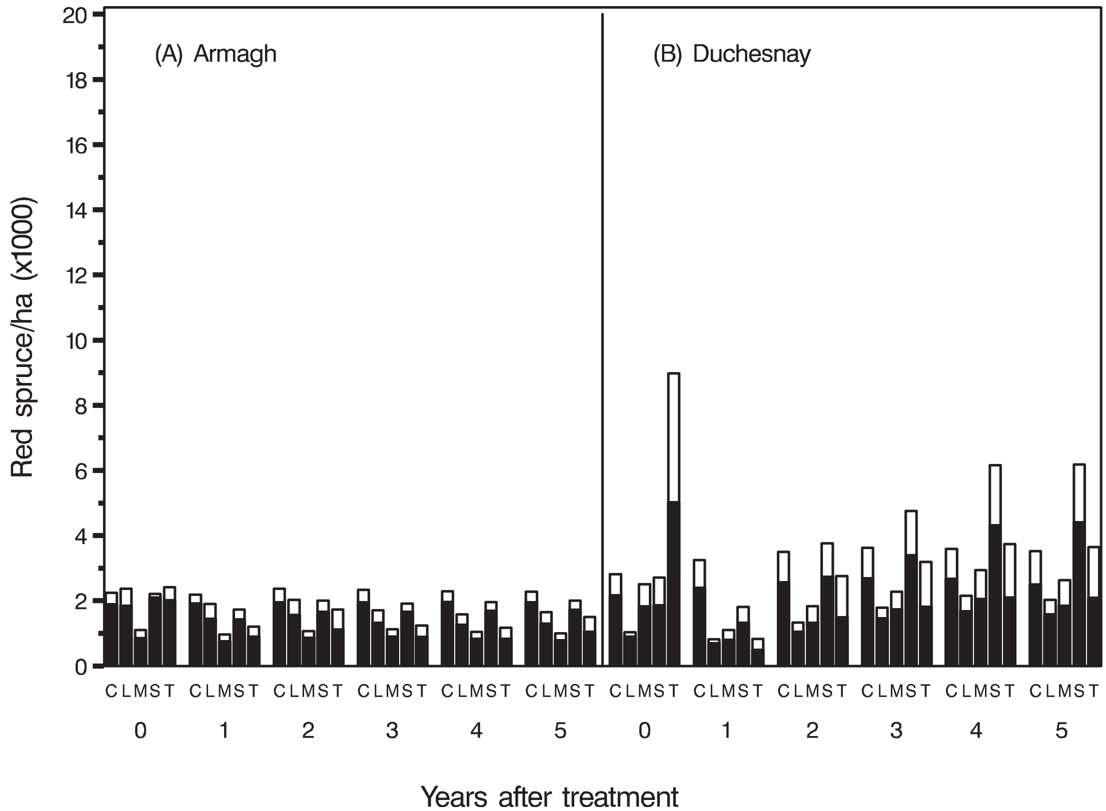
The density of mountain maple was maintained in the 100% cut and increased in the partial cuts at both sites (Fig. 6). At Armagh, the species clearly flourished in the 60% cut which contained more stems (11 600 stems/ha) than the control (7700 stems/ha). At Duchesnay, the density of stems, as well as the number of individuals attaining taller height classes, tended to decrease with increased cutting intensity, likely as a consequence of logging damage to this preestablished species. For example, the 40%, 50%, and 60% cuts, respectively, contained 5000, 3500, and 1500 stems/ha >1 m tall at year 5. Striped maple was reduced in density by the 100% cut (1800 and 2200 seedlings/ha for Armagh and Duchesnay, respectively) compared with the control (12 200 and 6000 stems/ha, respectively), whereas the density of this very shade-tolerant species was not affected by partial cutting (Fig. 6).

Discussion

Light environment

The two yellow birch – conifer stands under study were quite similar in species composition and structure before the cut (Table 1). Except for the short regeneration (<1 m in height) that was more abundant at Armagh, the two stands had the same BA (32 m^2/ha), contained similar proportions

Fig. 4. Density of red spruce seedlings related to cutting intensity (% basal area), 1–5 years after treatment at the Armagh and Duchesnay sites. The letters on the *x* axis are the five cutting intensities: C, uncut control (0%) and L, light (40%); M, moderate (50%); S, severe (60%); and T, total overstory removal (100%). The solid bars show the means, and the open bar show the SEs.



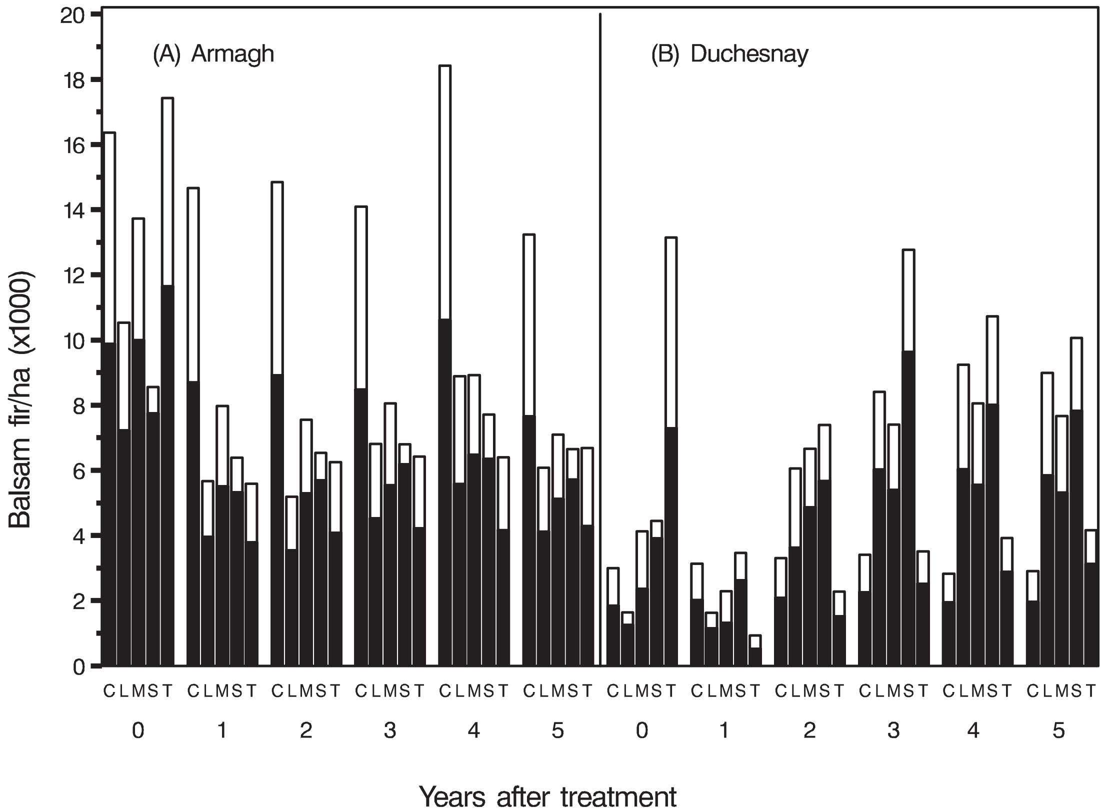
of conifers in the main cover (39% and 41% at Armagh and Duchesnay, respectively) and had comparable densities of preestablished regeneration >1 m tall. Thus, it is not surprising that the immediate effect of treatments on PPFD measured at 1.3 m above the ground was similar in both stands (Fig. 2). The three partial cuts severely limited light transmission to the understory compared with complete overstory removal. Because these cuts did not create large openings and prioritized the removal of low vigour and defective stems, trees with well developed crowns were retained, therefore keeping the understory in the shade of the main canopy (Oliver and Larson 1996). Furthermore, partial cutting was less detrimental to advance growth than total overstory removal. Light interception by the understory (low shade) remained significant after the cut. Although the CLAAG method was used, numerous sapling to pole-stage stems were lost during logging operations, particularly in the 100% cut because of the number of large trees that were removed. Consequently, light interception by the regeneration stratum was minimal during the first summer in the 100% cut, where more than 90% of the incoming light reached the 1.3 m level at each location. The lack of short regeneration may also explain why the 100% cut was the only one that exhibited soil warming when compared with the control.

As was noted in a former study using the same approach in a boreal mixedwood stand (Prévost and Pothier 2003), postcut light transmission decreased with time because of crown expansion of the residual trees and development of the regeneration stratum. In the present study, decreases in the three partial cuts were quite similar at the two locations, and each intensity of cut transmitted nearly equivalent levels of light regardless of site location after 5 years (15% of full light in the 40% cut and 20% of full light in the 50% and 60% cuts). In the 100% cut, the postcut decrease in light transmission differed greatly between the locations. At the end of the study, less light was available at Duchesnay than at Armagh. Data indicate that a strong increase in light interception occurred during years 3–5 in the total cut at Duchesnay (Fig. 2), when numerous stems of yellow birch, red maple, and pin cherry were gradually exceeding the height at which light measurements were made (data not shown). This phenomenon also occurred at Armagh but to a lesser extent and later in the study period because of slower vegetation development at the site.

Seedbed conditions

Hardwood leaf litter is known to be detrimental to small-seeded species such as yellow birch (Erdmann 1990) and red spruce (Blum 1990), whereas mineral soil is an excellent seedbed for both species. Although the CLAAG method was used in this study, it was foreseen that the seedbed could be improved through disturbance of the soil surface during harvest and skidding. Evaluation of the condition of the seedbed following the cut (Table 4B) indicated that the degree of soil disturbance was one of the greatest differences between the two study sites. The exposure of receptive soil horizons was three or four times less successful at Ar-

Fig. 5. Density of balsam fir seedlings related to cutting intensity (% basal area), 1–5 years after treatment at the Armagh and Duchesnay sites. The letters on the *x* axis are the five cutting intensities: C, uncut control (0%) and L, light (40%); M, moderate (50%); S, severe (60%); and T, total overstory removal (100%). The solid bars show the means, and the open bars show the SEs.



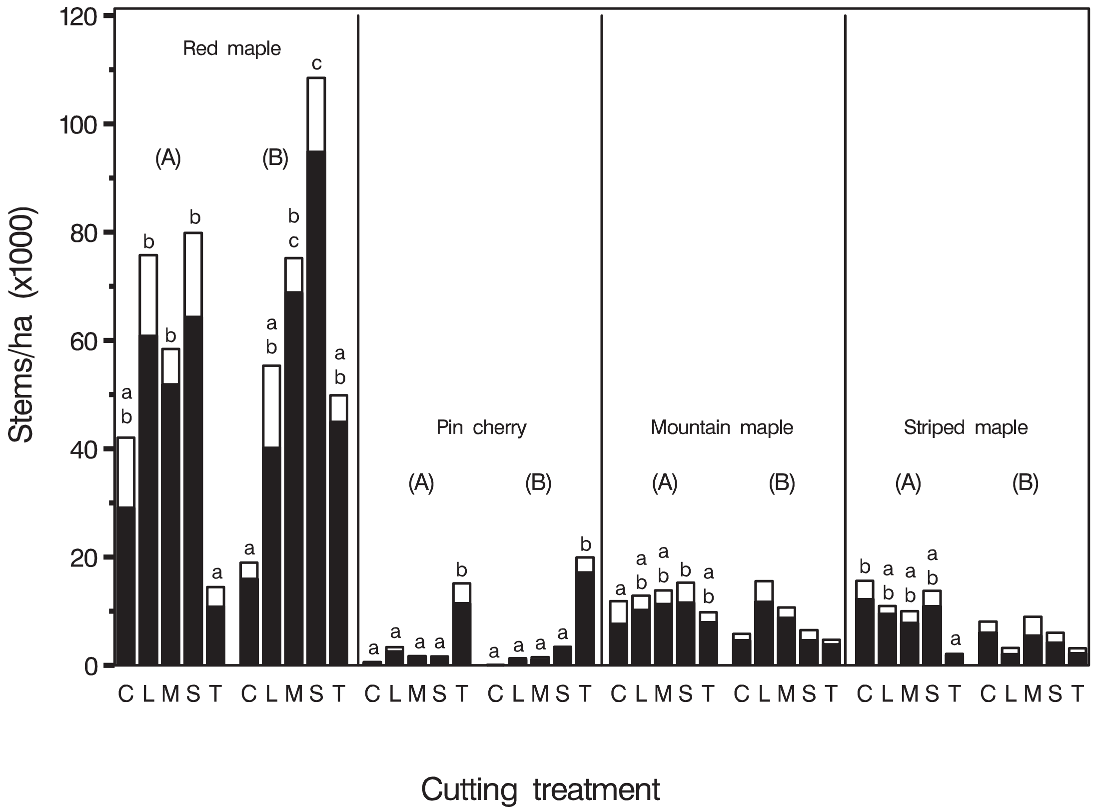
magh than at Duchesnay. Besides a possible site effect related to the soil itself, some other factors may explain this result. Initially, the experiment was planned to set up the two experimental designs in midfall. However, compared with Duchesnay, which was cut in October–November 1998, the treatments were applied 1 month later in the season at Armagh (November–December 1997), when the soil surface was already frozen. Furthermore, autumn 1997 was characterized by sustained snowfalls much earlier in the season than is usual for the region, and harvesting operations were carried out over a continuous snowpack (60–100 cm in depth) for the last 4 weeks at Armagh. Consequently, the soil disturbance was minimal compared with that at Duchesnay, where all operations were completed in the absence of snow cover in 1998. It is also likely that the area disturbed by machinery and skidding was minimized in Armagh because of the high density of advance regeneration to be protected. Moreover, the type of machinery that was available at each location may have amplified the disturbance effect, because the Timberjack-550 skidder used at Duchesnay was much heavier and less maneuverable than the C4 Tree Farmer used at Armagh. Without a doubt, this difference in soil disturbance between the two locations had a strong effect on vegetation dynamics in subsequent years.

Vegetation dynamics

This light-manipulation experiment was planned with the objective of finding an optimal threshold dimension for canopy opening that would conserve and trigger the establishment of yellow birch and red spruce, while avoiding development of competing species. Vegetation dynamics were greatly influenced by the different cuts and their associated microenvironmental conditions. However, the factor that seemed to influence seedling establishment the most was the degree to which logging produced a passive site preparation (Nyland 2002). At Duchesnay, where soil disturbance was more severe in all cuts, two to nine times more yellow birch seedlings (>5 cm high) were found 5 years after treatment than at Armagh. Red spruce, whose advance growth was targeted to become a component of the future stand, also appeared to benefit from this seedbed improvement, judging by the significant establishment of new seedlings. Pin cherry, which regenerates from a seed bank, also initially established in proportion to the degree of soil disturbance. All factors that were previously identified to explain the difference in disturbance between the study sites (snow cover, density of advance growth, type of machinery) can be cited to explain this general trend. Seed rain (not observed) as well as weather conditions during the postcut establishment period may also have contributed to the site-specific response to the treatments.

The intermediate shade tolerance of yellow birch (Forcier 1973) makes it a gap-phase species that needs canopy opening and soil disturbance to regenerate (Erdmann 1990). In the present study, the initial yellow birch recruitment was proportional to BA removal (Fig. 3, year 2) and receptive seedbed coverage (Table 4) at both locations, but the final results were a little contradictory. After 5 years, seedling

Fig. 6. Density of red maple, pin cherry, mountain maple, and striped maple (seedlings/ha) related to cutting intensity (% basal area), 5 years after treatment at the Armagh (A) and Duchesnay (B) sites. The letters on the *x* axis are the five cutting intensities: C, uncut control (0%) and L, light (40%); M, moderate (50%); S, severe (60%); and T, total overstory removal (100%). The solid bars show the means, and the open bars show the SEs. For cutting intensity within a site, means associated with the same letter are not different, according to simulation-based adjusted *p* values for pairwise comparisons.



density tended to increase with cutting intensity at Duchesnay, whereas the opposite trend was observed (at a smaller scale) at Armagh. These results suggest that there was an interaction between the residual cover and seedbed quality. Although the soil moisture regime was not monitored, it is known that moisture-holding capacity is the key factor of a good seedbed (Farmer 1997) especially for yellow birch, which is very sensitive to drought (Perala and Alm 1990). It is possible that, at Armagh, an adequate soil surface moisture regime was maintained only in the partial shade of a residual cover because of the poor seedbed quality. Moreover, better seedling survival under a canopy could explain why significant yellow birch recruitment occurred in the three partial cuts during year 3 at Armagh (Fig. 3), whereas some mortality was observed in the 100% cut under extreme microenvironmental conditions. At Duchesnay, better coverage by good seedbeds in the more severe cuts likely compensated for loss of receptivity during drought periods.

Red spruce has been dramatically declining across its whole range because of inadequate management methods over the past decades (Seymour 1992). In the mixedwood forest, this very shade-tolerant species is naturally associated with yellow birch as a component of the main canopy as well as advance growth (mostly in the Appalachians). Logically, most preestablished red spruce stems would have been protected with an efficient application of the CLAAG method, but this has not been the case. Considering the large size of the trees to be handled with the type of machinery that is available, the CLAAG method has been revealed to be a theoretical concept that is rarely applied in this forest type. Developing harvesting methods that could efficiently protect sapling to pole-stage stems would be necessary to realize the great potential of red spruce advance regeneration in the mixedwood forest.

Establishing new red spruce seedlings was an objective of this experiment. Because physiological studies have shown that red spruce is vulnerable to full light conditions (Alexander et al. 1995) and very sensitive to frost (DeHayes et al. 2001) and high temperatures (Vann et al. 1994), partial cutting was seen as a means of maintaining an understory microclimate that would be optimal for this species. Light measurements (Fig. 2) as well as soil temperature monitoring (Table 3) confirmed that microclimate was much less affected by partial cutting than by complete overstory removal. It was also anticipated that the retention of red spruce seed-trees in the residual canopy of the partial cuts would promote the establishment of new seedlings, especially under conditions of adequate seedbed and microclimate. This was the case in the 60% cut at Duchesnay, where we obtained the best establishment of new red spruce seedlings (Fig. 4). Hence, the very shade-tolerant red spruce benefited from severe canopy opening when combined with high soil disturbance. This is in line with results obtained by Prévost and Pothier (2003) in the boreal mixedwood type, where more severe canopy opening (65% of BA) also produced the best conditions for red spruce establishment. In the yellow birch – conifer stand, the 60% cut only allowed 30% of full light to reach the seedlings during the first year following the cut, which is low compared to more than 90% of full light reaching the seedlings in the 100% cut. Considering red spruce's high sensitivity to light, it is not surprising that complete overstory removal was detrimental to the species, both in terms of losses of advance growth as well as limitation of seedling establishment.

Balsam fir plays an important role in the natural dynamics of the mixedwood forest, as a gap-maker that periodically creates conditions that favour establishment of several species, such as yellow birch, spruce, and fir itself. In the present study, the proportion of balsam fir was initially higher at Armagh than at Duchesnay, both in the main canopy (23% vs. 15% of BA) as well as in the understory (9300 vs. 3300 stems/ha). Despite this situation, a significant post-cut recruitment was observed only at Duchesnay (Fig. 5), presumably because of soil disturbance, although balsam fir is less demanding of seedbed condition than the spruces. Furthermore, this shade-tolerant species established better in the three partial cuts than it did in the 100% cut, likely as a result of more favourable microenvironmental conditions. The seed supply may also have contributed to a better recruitment, because some intermediate-aged seed-trees remained uncut in the partial cuts. At both locations, considerable reductions in advance fir regeneration were observed following complete overstory removal, which is in line with the results of Archambault et al. (1998), for clear-cutting in balsam fir – yellow birch ecosystems of eastern Quebec.

Red maple is not a target species in the regeneration strategy for the mixedwood forest. However, it is a prolific seed producer that can germinate on a variety of seedbeds (Walters and Yawney 1990) or adopt a short-term seed-banking strategy that may increase seedling recruitment (Hille Ris Lambers and Clark 2005). Already well established as advance growth at both sites, red maple recruitment was abundant following the cut (Fig. 6), as a result of both natural seeding and stump sprouting. Clumps of poorly formed red maple sprouts were found in all our cutting treatments, but sprouting was less pronounced in the partial cuts because fewer red maples were harvested. More stems of seedling origin were recruited in the partial cuts than in the 100% cut, because the remaining forest canopy likely provided sustained seed rains and adequate establishment conditions for the shade-tolerant red maple. Although it is clear that red maple will remain a component of the mixedwood forest, it is unknown whether or not it may become a valuable part of the forest capital.

It is well known that pin cherry can occupy a site from the germination of buried seeds following disturbance (Wendel 1990), and its widespread development in the 100% cut (Fig. 6) is in line with past studies in the mixedwood forest (Archambault et al. 1998; Laflèche et al. 2000). However, it is not clear how much the short-lived pin cherry can affect yellow birch in the mixedwood forest. Studies in the northeastern hardwood forest have shown that its competitive effect depends upon its density in relation to the species of interest. For yellow birch, Safford and Filip (1974) and Leak (1988) found a negative effect on survival and growth during the regeneration stage, but neither Heitzman and Nyland (1994) nor Ristau and Horsley (1999) found a negative effect. However, it is generally recognized that yellow birch has the ability to be codominant when pin cherry develops at intermediate densities (Wendel 1990). In the present study, yellow birch had its best height growth in the 100% cut where pin cherry was the main competing species, and it is foreseen that a lateral pressure would improve the self-pruning process because the species is prone to develop epicormic branches. Pin cherry is likely to be more detrimental to conifers that are rapidly overtopped and may be greatly affected in the absence of a release cutting (Jablanczy 1979;; Ruel 1992). Fir and spruce were generally found below the pin cherry cover in the 100% cut; although juvenile red spruce may survive under a full canopy, it is known that its growth will be affected through competition for light, water, and nutrients.

Mountain maple has the ability to invade cutover areas and occupy a site for decades following harvest (Vincent 1965; Vallée et al. 1976; Bédard et al. 1978; Archambault et al. 1998). This aggressive species may form a dense cover with horizontal branching (Lei and Lechowicz 1990) that allows less light penetration than pin cherry (Messier and Bellefleur 1988) and, therefore, may considerably affect underlying species. At our study sites, it was anticipated that mountain maple might increase in density following canopy opening. In fact, its development was lower in the 100% cut than in the partial cuts (Fig. 6), where logging damage to this preestablished species was less severe and light transmission to the understory was sufficiently increased to produce a growth response. This development of mountain maple, coupled with the high shade from the residual cover, may also explain why pin cherry occupied much less space in the partial cuts than in the 100% cut.

Our results are generally consistent with results from former studies in the mixedwood forest (Archambault et al. 1998; Laflèche et al. 2000). Five years after cutting, competing species such as pin cherry, mountain maple, and striped maple (with the exception of the total cut) formed a fairly dense cover in which only the broad-leaved red maple and yellow birch were able to maintain a dominant or codominant crown position. Because of severe failures in advance growth protection during harvest, coniferous species were mainly found below this hardwood cover, and that situation is unlikely to change in the near future. Furthermore, the coniferous component of the mixedwood forest will be mainly comprised of balsam fir, with a possible reduction in the representation of red spruce.

Silvicultural implications

Successful germination and establishment of forest trees depend on a narrow set of environmental factors (seedbed, temperature, moisture, and light) for which a minor shift can be critical (Farmer 1997). Results from this study indicate that this general rule applies well to the species of the mixedwood forest. Although a range of light availability was created in this light-manipulation experiment, the improvement in seedbed condition during harvest was revealed to be the key factor in establishment of the small-seeded yellow birch. A need for seedbed improvement was noted by

Laflèche et al. (2000), who attributed yellow birch regeneration failures to an insufficient soil disturbance with the CLAAG method at 19 sites in eastern Quebec. In the present study, the lack of soil disturbance at the snow-covered site confirms the current knowledge that winter harvesting is not suitable for regenerating this species, if subsequent soil scarification is not planned. Results also suggest that maintaining both yellow birch and red spruce in the mixedwood forest will remain a challenge for foresters. In fact, the concept of a beneficial soil disturbance during harvest is difficult to reconcile to a careful logging approach that would be suitable in stands presenting valuable red spruce advance growth. Although it is clear that abundant yellow birch establishment can be obtained, the loss of red spruce and balsam fir advance growth and the uncertain postcut establishment of these two species are costs that must be considered if maintaining the coniferous proportion of the stand is a management objective. To that effect, it would be necessary to develop harvesting approaches that could efficiently protect coniferous saplings to pole-stage stems.

The varying results that we obtained with the same group of cutting treatments in two comparable sites illustrate why silviculture must be considered as an art as well as a science. Although silvicultural outlines can de drawn, results must be interpreted with care. Yellow birch can be successfully regenerated in uniform partial cuts that remove 40%–60% of the BA. Patch clear-cutting is also suitable for regenerating this species provided sufficient soil disturbance is achieved. The 0.5 ha experimental units in this study must be considered as a maximum clearcut area. The patch clearcuts of 0.04–0.3 ha that are generally recommended for this species in the northeastern hardwood forests (Marquis 1965; Erdmann 1990) appear to be adequate for the mixedwood forest. Our results clearly show that patch clearcuts are much less successful for regenerating red spruce and balsam fir than are partial cuts. The best postcut establishment of red spruce seedlings in the 60% BA removal at Duchesnay confirms that a partial but severe canopy opening, combined with soil disturbance, may successfully regenerate this very shade-tolerant species (Prévost and Pothier 2003). Hence, among the tested treatments, the 60% cut appears to be the most susceptible to trigger establishment of both yellow birch and red spruce seedlings. Therefore, partial cutting can be seen as a means of starting a new cohort of valuable species in yellow birch – conifer stands with a lack of advance growth. Subsequent operations and long-term observations will be necessary to assess whether this treatment can be the first step of a silvicultural system aimed at maintaining a multiple-cohort stand. In the short term, it is foreseen that our selection criteria for partial cuts will permit the concentration of wood production on high-quality trees with good growth potential, while preserving values associated with the maintenance of a continuous forest cover.

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References

Alexander, J.D., Donnelly, J.R., and Shane, J.B. 1995. Photosynthetic and transpirational responses of red spruce understory trees to light and temperature. Tree Physiol. **15**: 393–398. PMID:14965948.

Archambault, L., Morissette, J., and Bernier-Cardou, M. 1998. Forest succession over a 20-year period following clearcutting in balsam fir – yellow birch ecosystems of eastern Québec, Canada. For. Ecol. Manage. **102**: 61–74. doi:10.1016/S0378-1127(97)00109-6.

Bédard, J., Crête, M., and Audy, E. 1978. Short-term influence of moose upon woody plants of an early seral wintering site in Gaspé Peninsula, Quebec. Can. J. For. Res. **8**: 407–415. doi:10.1139/cjfr-8-4-407.

Bergeron, Y., and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92**: 235–242. doi:10.1016/S0378-1127(96)03924-2.

Blum, B.M. 1990. *Picea rubens* Sarg. (red spruce). *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. US Dep. Agric. Agric. Handb. 654. pp. 250–259.

Canadian Climate Program. 1982. Canadian climate normals 1951–1980. Vol. 6. Frost. Atmospheric Environment Service, Downsview, Ont.

Canadian Climate Program. 1993. Canadian climate normals 1961–1990. Québec. Atmospheric Environment Service, Downsview, Ont.

DeHayes, D.H., Schaberg, P.G., and Strimbeck, G.R. 2001. Red spruce (*Picea rubens* Sarg.) cold hardiness and freezing injury susceptibility. *In* Conifer cold hardiness. *Edited by* F.J. Bigras and S.J. Colombo. Kluwer Academic Publishers, Norwell, Mass. pp. 495–529.

Doucet, R., Pineau, M., Ruel, J.C., and Sheedy, G. 1996. Sylviculture appliquée. *In* Manuel de foresterie. *Edited by* L'Ordre des ingénieurs forestiers du Québec. Les Presses de l'Université Laval, Sainte-Foy, Que. pp. 965–1004.

Erdmann, G.G. 1990. *Betula alleghaniensis* Britton (yellow birch). *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. US Dep. Agric. Agric. Handb. 654. pp. 133–147.

Farmer, R.E. 1997. Forest microsites as regeneration niches. *In* Seed ecophysiology of temperate and boreal zone forest trees. St. Lucie Press, Delray Beach, Fla. pp. 219–243.

Forcier, L.K. 1973. Seedling pattern and population dynamics, and the reproductive strategies of sugar maple, beech and yellow birch at Hubbard Brook. Ph.D. thesis, Yale University, New Haven, Conn. Diss. Abstr. Int. B34(5).

Forcier, L.K. 1975. Reproductive strategies and the co-occurrence of climax tree species. Science (Washington, D.C.), **189**: 808–810. doi:10.1126/science.189.4205.808. PMID:17777590.

Fortin, M. 2003. Raréfaction de l'épinette rouge. *In* Les enjeux de biodiversité relatifs à la composition forestière. *Edited by* P. Grondin and A. Cimon. Ministère des Ressources naturelles, de la Faune et des Parcs, Direction de la recherche forestière et Direction de l'environnement forestier, Québec, Que. pp. 45–65.

Frank, R.M. 1990. *Abies balsamea* (L.) Mill. (balsam fir). *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. US Dep. Agric. Agric. Handb. 654. pp. 26–35.

Grondin, P., Ansseau, C., Bélanger, L., Bergeron, J.F., Bergeron, Y., Bouchard, A., Brisson, J., De Grandpré, L., Gagnon, G., Lavoie, C., Lessard, G., Payette, S., Richard, P.J.H., Saucier, J.P., Sirois, L., and Vasseur, L. 1996. Écologie forestière. *In* Manuel de foresterie. *Edited by* L'Ordre des ingénieurs forestiers du Québec. Les Presses de l'Université Laval, Sainte-Foy, Que. pp. 133–279.

Hébert, R. 2003. Are clearcuts appropriate for the mixed forest of Québec. For. Chron. **79**: 664–671.

Heitzman, E., and Nyland, R.D. 1994. Influences of pin cherry (*Prunus pensylvanica* L.f.) on growth and development of young even-aqed northern hardwood. For. Ecol. Manage. **67**: 39–48. doi:10.1016/0378-1127(94)90006-X.

Hille Ris Lambers, J., and Clark, J.S. 2005. The benefits of seed banking for red maple (*Acer rubrum*): maximizing seedling recruitment. Can. J. For. Res. **35**: 806–813. doi:10.1139/x05-017.

Jablanczy, A. 1979. Regeneration on white spruce cutovers in eastern Nova Scotia. Nova Scotia Department. of Lands and Forests, Halifax, N.S.

Kneeshaw, D.D., and Prévost, M. 2007. Natural canopy gap disturbances and their role in maintaining mixed species forests of central Quebec, Canada. Can. J. For. Res. **37**. : 1534–1544. doi:10.1139/x07-112.

Laflèche, V., Ruel, J.C., and Archambault, L. 2000. Évaluation de la coupe avec protection de la régénération et des sols comme méthode de régénération de peuplements mélangés du domaine bioclimatique de la sapinière à bouleau jaune de l'est du Québec, Canada. For. Chron. **76**: 653–663.

Leak, W.B. 1988. Effects of weed species on northern hardwood regeneration in New Hampshire. North. J. Appl. For. **5**: 235–237.

Lei, T.T., and Lechowicz, M.J. 1990. Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. Oecologia, **84**: 224–228.

Lieffers, V.J., and Beck, J.A., Jr. 1994. A semi-natural approach to mixedwood management in the prairie provinces. For. Chron. **70**: 260–264.

Marquis, D.A. 1965. Regeneration of birch and associated hardwoods after patch cuttings. USDA For. Serv. Northeast. For. Range Exp. Stn. Res. Pap. NE.32.

Messier, C., and Bellefleur, P. 1988. Light quantity and quality on the forest floor of pioneer and climax stages in a birch – beech – sugar maple stand. Can. J. For. Res. **18**: 615–622. doi:10.1139/cjfr-18-5-622.

Ministère des Ressources naturelles du Québec (MRNQ). 1992. Manuel d'aménagement forestier. Ministère des Ressources naturelles du Québec, Direction des programmes forestiers, Québec, Que.

Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca* (Moench) Voss (white spruce). *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA For. Serv. Agric. Handb. 654. pp. 204–226.

Nyland, R.D. 2002. Site preparation. *In* Silviculture: concepts and applications. 2nd ed. *Edited by* S. Spoolman. McGraw-Hill, New York. pp. 86–116.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, New York.

Perala, D.A., and Alm, A.A. 1990. Regeneration silviculture of birch: a review. For. Ecol. Manage. **32**: 39–77. doi:10.1016/0378-1127(90)90105-K.

Prévost, M., and Pothier, D. 2003. Partial cuts in a trembling aspen – conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can. J. For. Res. **33**: 1–15. doi:10.1139/x02-147.

Ristau, T.E., and Horsley, S.B. 1999. Pin cherry effects on Allegheny hardwood stand development. Can. J. For. Res. **29**: 73–84. doi:10.1139/cjfr-29-1-73.

Robitaille, A., and Saucier, J.P. 1998. Paysages régionaux du Québec méridional. Ministère des Ressources naturelles du Québec, Direction de la gestion des stocks forestiers et Direction des relations publiques, Québec, Que.

Ruel, J.C. 1992. Impact de la compétition exercée par le framboisier (*Rubus idaeus* L.) et les feuillus de lumière sur la croissance du sapin (*Abies balsamea* (L.) Mill.) en régénération. Can. J. For. Res. **22**: 1408–1416. doi:10.1139/cjfr-22-9-1408.

Safford, L.O., and Filip, S.M. 1974. Biomass and nutrient content of 4-year-old fertilized and unfertilized northern hardwood stands. Can. J. For. Res. **4**: 549–554. doi:10.1139/cjfr-4-4-549.

Saucier, J.-P., Bergeron, J.-F., Grondin, P., and Robitaille, A. 1998. Les régions écologiques du Québec méridional (3e version): un des éléments du système hiérarchique de classification écologique du territoire mis au point par le ministère des Ressources naturelles du Québec. L'Ordre des Ingénieurs forestiers du Québec, Québec, Que. Aubelle 124.

Seymour, R.S. 1992. The red spruce – balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. *In* The ecology and silviculture of mixed-species forests. *Edited by* M.J. Kelty, B.C. Larson, and C.D. Oliver. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 217–244.

Vallée, J., Couture, R., and Joyal, R. 1976. Étude de la régénération après coupe des essences composant la diète alimentaire de l'orignal. Phytoprotection, **57**: 155–164.

Vann, D.R., Johnson, A.H., and Casper, B.B. 1994. Effect of elevated temperatures on carbon dioxide exchange in *Picea rubens.* Tree Physiol. **14**: 1339–1349. PMID:14967608.

Vincent, A.B. 1965. Growth habits of mountain maple in the Ontario Clayb Belt. For. Chron. **41**: 330–344.

Walters, R.S., and Yawney, H.W. 1990. *Acer rubrum* L. (red maple). *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. US DEp. Agric. Agric. Handb. 654. pp. 60–69.

Wendel, G.W. 1990. *Prunus pensylvanica* L. f. (pin cherry). *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. US Dep. Agric. Agric. Handb. 654. pp. 587–593.

Westfall, P.H., Tobias, R.D., Rom, D., Wolfinger, R.D., and Hochberg, Y. 1999. Multiple comparisons and multiple tests using the SAS system. SAS Institute Inc., Cary, N.C.