Group and single-tree selection cutting in mixed tolerant hardwood–white pine stands: Early establishment dynamics of white pine and associated species

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In mixed tolerant hardwood – white pine stands of Southwestern Quebec, the effects of group selection cutting on eastern white pine (*Pinus strobus* L.), red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britton) and paper birch (*Betula papyrifera* Marsh.) regeneration are compared to the currently used single-tree selection cutting. The experimental design, initiated in 1998, comprised three cover reduction treatments (circular gap (45 m, 1590 m²)), 25% and 35% single-tree selection cutting), two scarification treatments (scarified and non-scarified) and two seeding treatments for white pine (seeded and non-seeded). The effect of white pine seed predation was studied in the gaps and the adjacent understory, with exclosures for small mammals. After three years, scarification had a positive effect on white pine, yellow birch and paper birch regeneration but also on aspen (*Populus* spp.) and pin cherry (*Prunus pensylvanica* L.f.) in the three cover reduction treatments. Red oak regeneration was negatively affected by scarification. Shade-tolerant species (sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.)) tended to be less present in the regeneration gaps than in the single-tree selection cutting. Considering that white pine seed predation can be critical in mixed tolerant hardwood – white pine stands, a greater rate of seeding is recommended for direct seeding.

Key words: group selection cutting, regeneration gap, single-tree selection cutting, tolerant hardwoods, eastern white pine, yellow birch, paper birch, red oak, scarification, direct seeding, regeneration, seed predation

Dans les peuplements de feuillus tolérants et de pin blanc du sud-ouest du Québec, les effets du jardinage avec trouées sur la régénération du pin blanc de l'est (*Pinus strobus* L.), du chêne rouge (*Quercus rubra* L.), du bouleau jaune (*Betula alleghaniensis* Britton) et du bouleau à papier (*Betula papyrifera* Marsh.) sont comparés au jardinage par pied arbre conventionnel. Le dispositif expérimental, implanté en 1998, comprend trois traitements de réduction du couvert (trouée (45 m diamètre, 1590 m²), jardinage par pied d'arbre 25% et 35%), deux traitements de scarifiage (scarifié et non scarifié) et deux traitements d'ensemencement artificiel pour le pin blanc (ensemencé et non ensemencé). Les effets de la prédation des semences de pin blanc ont été étudiés dans les trouées et leur sous-bois adjacent, à l'aide d'exclos pour petits mammifères. Après trois ans, le scarifiage avait un effet positif sur la régénération de pin blanc, de bouleau jaune et de bouleau à papier mais aussi sur la régénération du peuplier et du cerisier de Pennsylvanie et ce, dans les trois traitements de réduction du couvert. La régénération du chêne rouge a été affectée négativement par le scarifiage. Les espèces tolérantes à l'ombre (érable à sucre (*Acer saccharum* Marsh.) et hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.)) tendaient à être moins présentes dans les trouées de régénération que dans le jardinage par pied d'arbre. Considérant que la prédation des semences de pin blanc peut être critique dans les peuplements de feuillus tolérants et de pin blanc, un plus grand taux d'ensemencement est recommandé pour l'ensemencement artificiel.

Mots-clés : jardinage avec trouées, trouées de régénération, jardinage par pied d'arbre, feuillus tolérants, pin blanc de l'est, bouleau jaune, bouleau à papier, chêne rouge, scarifiage, ensemencement artificiel, régénération, prédation des semences

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Introduction

In Quebec, the greatest concentrations of white pine (*Pinus strobus* L.) are located in the Ottawa River valley watershed, in the southwestern part of the province (Ducruc and Lafond 1977). Pure stands as well as associations with shade-tolerant or intolerant species can be found (Brown 1992). Mixed tol-

erant hardwood – white pine stands are often managed under single-tree selection cutting but this method is not necessarily suitable for white pine regeneration, a mid-tolerant species (Lessard *et al.* 1999). In mixedwood forests of Canada and north-eastern United States, white pine advance regeneration is often present in very small gaps or under partial canopies, but this species is often suppressed by other vegetation and does not reach later developmental stages (saplings and poles) (Leak *et al.* 1995, Carleton *et al.* 1996). In natural tolerant hardwood stands, it was hypothesized that white pine could regenerate in large canopy openings or in low-density stands. Mid-tolerant species have the capacity to respond to openings more rapidly than tolerant species (Marks 1975) and therefore fill a greater part of the free space in the gaps (Barden 1981).

Studies have demonstrated that group selection cutting can be used to maintain a mixture of intermediate and intolerant species in hardwood stands (Leak and Filip 1977, Murphy *et al.* 1993). Regeneration gaps created by this method can emulate the northern hardwood disturbance regime, which is characterized by small fires, windthrow and natural senescence (Borman and Likens 1979, Runkle 1981, Canham and Loucks 1984, Whitney 1986, Frelich and Lorimer 1991). The effects of group selection on regeneration have been documented in Eastern Canada (Hatcher 1966), northeastern (Marquis 1965, Leak and Filip 1977, McClure and Lee 1993, Smith and Ashton 1993) and central United States (Phillips and Shure 1990, Dale *et al.* 1995, Weigel and Parker 1997). Among these studies, only Smith and Ashton (1993) mentioned the effects of regeneration gaps (45 m) on white pine regeneration. The latter study was conducted at a lower latitude, in a hemlock (*Tsuga canadensis* (L.) Carr.) – white pine-dominated stand and, thus, results cannot be transferred to Quebec's tolerant hardwood – white pine stands. The pre-existing overstory and understory composition greatly influence vegetation dynamics after gap creation and therefore white pine response to treatments. Also, the latitude can influence vegetation dynamics since the maximum light location gets more offset to gap centre as latitude increases (Canham 1988a, Canham *et al.* 1990). Moreover, the effects of substrate condition on regeneration inside the gaps were not documented in the literature (Coates and Burton 1997). Scarification usually improves mid-tolerant species establishment (Godman 1957, Godman and Krefting 1960, Horton 1962, Marquis 1965, Hatcher 1966). Since 1998, a combination of group and single-tree selection (see Leak and Filip 1977) is applied on Quebec's public land (500–1500-m² gaps, MRNQ 1998). The present study was initiated to document the effects of this method in the tolerant hardwood – white pine stands of Quebec.

We anticipated that differences between the selection cutting methods should be more evident in seedling growth than in early establishment, as germination is generally independent of light conditions (Farmer 1997). Thus, in this initial phase of the study, attention was paid to seedbed and seeding, as these are preliminary conditions of regeneration success (Marquis 1965, Godman and Krefting 1960). White pine seed predation was also examined, as seeds are an important food source for small mammals (Abbott 1961, Abbott and Quink 1970, Corneet *et al.* 1998, Duchesne *et al.* 2000). Local populations of mice and voles can consume the entire yearly eastern white pine seed crop and thus hinder regeneration efforts by direct seeding (Abbott 1961). Furthermore, white pine seed availability

and predation may be more critical in mixed tolerant hardwood stands than in pure white pine stands, especially knowing that mice and voles select white pine seeds over other species (e.g., balsam fir, black spruce, jack pine) (Abbott 1961, Martell 1979, Duchesne *et al.* 2000).

The following hypotheses were tested: (i) scarification increases seedling density and stocking of intolerant and mid-tolerant species but not of tolerant species; (ii) direct seeding increases white pine seedling density and stocking; (iii) predation is a cause of a lower white pine establishment in large gaps created by group selection cutting. We also examined trends in effects of scarification and seeding across different intensities of harvest.

Materials and Methods

Study area

The study was conducted in the Forêt de l'Aigle (46°16'N, 76°17'W), near Maniwaki, Québec, Canada. The forest is located in the Lac Dumont landscape unit (Robitaille and Saucier 1998) of the western Sugar maple – Yellow birch bioclimatic domain (Saucier *et al.* 1998). Mean annual temperature of the Lac Dumont unit ranges 2.5–5°C, mean annual precipitation from 800–1000 mm, with 25% as snow and 170–180 days growing season (Robitaille and Saucier 1998). The experimental design was installed in 1998, in a mixed northern hardwood – white pine uneven-aged stand (260 m³ha⁻¹) on moderately well drained to imperfectly drained sites. The main species were white pine (38% of volume), sugar maple (*Acer saccharum* Marsh.) (17%), paper birch (*Betula papyrifera* Marsh.) (10%), red oak (*Quercus rubra* L.) (9%) and yellow birch (*Betula alleghaniensis* Britton) (6%). The soil was a Dystric Brunisol (Soil Classification Working Group 1998) developed on a thin glacial till with a sandy loam to loamy sand texture.

Design and data collection

Since the main objective of the experiment was to test group selection cutting under operational conditions, the treatment was executed in areas > 10 ha. The experimental design therefore comprised two contiguous areas of equivalent harvesting intensity (35% basal area). The first area (14.1 ha) was harvested by 35% single-tree selection cutting (30% marking and 5% for losses) and the second (13.4 ha) by group selection cutting (fall, 1998). Marking guidelines for group selection were: (i) respect species proportions when marking; (ii) circular gaps of 45 m diameter (1590 m²); (iii) ≥40 m between gaps; (iv) at least one white pine within 10 m from the canopy gap; (v) 25% single-tree selection cutting between the gaps (20% marking and 5% for losses); (vi) avoid placing gaps in humid depressions. Marking was made in order to obtain 40 m wide gaps but canopy gap size extended to 45 m after harvesting. Felling was manual and trees were hauled by cable skidder. Spot scarification was carried out after harvesting (fall, 1998), in order to expose the mineral soil, with the skidder blade or manually when required. All trees were cut in the gaps, and tree tops were piled on the southern border.

The experimental design comprised 10 main plots (45 m diameter) of each cover reduction treatment: 25% single-tree selection cutting (S25), 35% single-tree selection cutting (S35) and 10 selected gaps. Each main plot had 20 scarified and 20 non-scarified subplots (1 m²). Half of the subplots (10 scarified and 10 non-scarified) were seeded (white pine, 50% seed ger-

minability) in October 1998, 1999 and 2000, with 9.65 kg ha⁻¹ (564 000 seeds ha⁻¹, 28 viable seeds/subplot). Seeding rate was calculated to obtain 10 000 seedlings ha⁻¹ with the equation of Duchesne *et al.* (1998). White pine natural seed rain was recorded during fall 1998 and 1999 with four seedtraps, of the type described in Hughes *et al.* (1987), in each main plot. Overall, mean white pine seed rain was 466 660 seeds ha⁻¹ during fall of 1998 (S25: 438 000; S35: 514 000; Gap: 448 000) and 330 seeds ha⁻¹ during the fall of 1999. Regeneration of all commercial species was tallied at the end of three growing seasons (1999–2001), with distinction of germinant seedlings from non-germinants.

Soil temperature, soil moisture (upper first 5 cm) and air temperature were recorded continuously (CR10X, Campbell Scientific) from June 2, 2000 to October 15, 2001. Soil moisture was not measured during the winter (October 16, 2000 to May 14, 2001). Dataloggers were installed in the centre of two representative gaps and two 35% single-tree selection plots, with two temperature probes (thermistor 107BAM) and one moisture probe (CS615) extending 10 m in three different directions (North, South and East or West). Soil temperature and moisture were recorded hourly and mean was calculated on a daily basis. Depth of organic horizon averaged 3 cm in the gaps and 5 cm in the 35% single-tree selection plots. These small differences can possibly be attributed to soil disturbance during harvesting operations.

White pine seed predation experiment

The predation experiment was carried out in the ten selected gaps and their surrounding understory (25% single-tree selection cutting). The split-plot design comprised 10 transects in the north-south axis (blocks) with distance from gap centre (0 m, 10 m, 20 m, 30 m, 40 m) as main plot and enclosure as subplot (excluded, non-excluded). Enclosures (20 × 20 × 20 cm), built with galvanised wire-mesh (6-mm openings), were installed 10 cm deep in the soil in October 1999. Non-excluded subplots (20 × 20 cm) were located 1.5 m from the enclosures. Both subplots were seeded with 20 white pine seeds (50% germination rate) in October 1999 and 2000. The number of white pine germinants was recorded monthly in 2000 (June–October) and 2001 (May–August, October).

Statistical analysis

Effects of scarification and direct seeding on white pine regeneration (density and stocking) within each cover reduction treatment were tested in a factorial model of ANOVA (SAS 8.1), where each main plot was computed as a block (degrees of freedom: block 9; scarification 1; direct seeding 1; scarification × seeding 1; error 27; total 39). There were four experimental units per main plot (combinations of two scarification and two direct seeding treatments). Scarification was the only effect tested for the associated species (degrees of freedom: block 9; scarification 1; error 9; total 19). Geometrical means were used to decrease the effect of extreme values of regeneration densities. Stocking was calculated as a percent of subplots regenerated in each main plot. When required, logarithmic or square root transformations were performed on the data, in order to correct for heterogeneity of variance among treatments. The ANOVA did not test the cover reduction treatment effects since a site effect was confounded and could not be extracted by statistical analysis. Initial white pine basal area was higher ($p =$

0.0534) in the 35% single-tree selection cutting area (14.9 m² ha⁻¹) than in the group-selection area (6.0 m² ha⁻¹), which could cause important differences in white pine recruitment. Results therefore include only trends among cover reduction treatments. Recruitment of most species was very poor in 2000 (except for three species) and 2001 and densities were not of silvicultural interest (< 200 stems ha⁻¹). For this reason, only the results of 1999 germinants are presented and the 2000 germinants of aspen, paper birch and red maple (*Acer rubrum* L.). Trembling aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.) were grouped for statistical analysis. ANOVA was also performed on 2001 total number of seedlings and stocking per species, three years after treatment. Descriptive statistics were used for datalogger soil temperature and moisture. A split-plot factorial model with repeated measurements (SAS 8.1) was used in the predation experiment.

Results

Soil temperature and moisture

Greater soil temperature fluctuations were observed in the gaps compared to the 35% single-tree selection cutting (Fig. 1). During the spring, soil temperatures increased more rapidly in the gaps than under the 35% single-tree selection and therefore reached optimum conditions for seed germination more rapidly (e.g., white pine 18–24°C, Fraser 1970). The 2001 growing season tended to be drier than 2000, especially during June to August (Fig. 2). In 2000, soil moisture was similar in the gaps and in the 35% single-tree selection cutting but in 2001, soil moisture tended to be lower in the gaps than in the 35% single-tree selection cutting.

First-year germinants

White pine

Scarification had a positive effect on density and stocking across all canopy reduction treatments in 1999 (Fig. 3). Scarification dramatically increased germinant density and increased the stocking by about two-fold in the three cover reduction treatments. In absence of scarification, white pine germinant density remained below 1000 stems ha⁻¹. Direct seeding had a significant positive effect on germinant density and stocking in the 25% and 35% (density only) single-tree selection and a positive trend was observed in the gaps. No significant interaction was observed between scarification and direct seeding treatments.

Associated species

In 1999, scarification had a significant effect on germinant density and stocking of most species (Fig. 4). The effect was positive on yellow birch, paper birch, aspen, balsam fir (*Abies balsamea* (L.) Mill.), northern white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss) and pin cherry (*Prunus pensylvanica* L.f.) density and stocking in all cover reduction treatments (Fig. 4). In most cases, both density and stocking responded in a similar manner to treatments, but the differences between treatments appeared smaller with the stocking. Despite a higher stocking on scarified subplots, an important stocking ($> 60\%$) of the most intolerant species (paper birch, aspen and pin cherry) was also recorded on non-scarified subplots of the gaps. Scarification increased American beech (*Fagus grandifolia* Ehrh.) density and stocking under the 25% and 35% single-tree selection cutting. Recruitment of American beech and sugar

Fig. 1. Daily maximum and minimum soil temperature (5 cm) (June 2, 2000 to October 16, 2001) in (a) 35% single-tree selection cutting (S35) and (b) the gaps.

maple was negligible (< 10 germinants ha^{-1}) in the gaps (and red oak under all covers) and were not submitted to ANOVA. Sugar maple density and stocking were increased by scarification under the 35% selection. Red maple density was decreased by scarification in the gaps and in the 35% selection, but was not significantly affected in the 25% selection, probably because of high variability. However, scarification did not influence red maple stocking under any of the cover reduction treatments. In 2000, scarification had a highly positive effect ($p < 0.0001$) on paper birch and aspen density and stocking in both 25% and 35% single-tree selection cutting but had no effect in the gaps. There was no effect of scarification on red maple germinants in 2000.

Three-year regeneration

White pine

After three years, scarification had a positive effect on total number of white pine seedlings in all canopy treatments (Fig. 3).

Stocking of scarified subplots was still more than two-fold that of non-scarified in 2001. White pine had a good stocking (70–83%) on scarified subplots, but the total number of seedlings was not very high in the gaps (4906 seedlings ha^{-1}). With time, the density (stem ha^{-1}) gradually decreased from 16 758 (1999) to 13 889 (2000) and 4906 (2001) in the gaps, while it decreased during the same years from 29 771 to 27 957 and 15 000 in the 25% selection and from 54 995 to 45 654 and 37 404 in the 35% selection. After three years, only the 35% selection showed significant differences in density and stocking between the seeded and non-seeded treatments.

Associated species

After three years, scarification had a significant effect on total regeneration density and stocking of most species (Fig. 4). Density and stocking of red maple and American beech were not influenced by scarification treatments while only trends of pos-

Fig. 2. Daily mean soil moisture (5 cm) in the gaps and the 35% single-tree selection cutting (S35) (a) June 2 to October 15, 2000 and (b) May 15 to October 16, 2001.

itive effects were observed for the stocking of northern white cedar. Scarification improved density and stocking of yellow birch, paper birch, aspen, balsam fir, white spruce and northern white cedar (trend, stocking only) under all tested cover reduction treatments. Pin cherry density and stocking were also significantly higher on scarified subplots, but only in the 25% and 35% selection cutting. Stocking of red oak total regeneration was affected negatively by scarification under all cover reduction treatments, but results need to be interpreted with caution because the number of seedlings was quite low. Scarification reduced sugar maple total regeneration density and stocking in all cover reduction treatments. After three years, paper birch, yellow birch and aspen were the most abundant species in the gaps while regeneration of beech, sugar maple, red oak and white spruce was poor.

Effects of predation on white pine early establishment

The single effects of exclosure and month were highly sig-

nificant on early establishment of white pine in both 2000 and 2001 (Table 1). Results also indicate strong interactions (exclosure $\times$ distance 2000, 2001; exclosure $\times$ month 2000, 2001; and distance $\times$ month 2001) for white pine germinants. Higher numbers of germinants were found in the exclosure subplots than in the control subplots but the exclosure $\times$ distance interaction indicated that the effect was less pronounced at 30 m from the centre for both years (Fig. 5). Furthermore, the exclosure $\times$ month interaction shows that the germinant number increases throughout the growing season in the exclosure subplots, while it remains stable and low in the control subplots. No evident trends emerge from the distance $\times$ month interaction.

Discussion

Effects of scarification on shade tolerance groups

Scarification was expected to have no effect on shade-tolerant species germination because they have a large seed size

Fig. 3. Mean white pine density and stocking in all canopy reduction treatments (S25 = 25% single-selection cutting, S35 = 35% single-tree selection cutting) by (a) scarification (NS = non-scarified, SC = scarified, 99 = 1999 germinant density, 01 = 2001 total seedling density) and (b) direct seeding treatments (SEED = seeded, NSEED = non-seeded). The p value indicates the probability of difference ($\alpha = 0.05$) between treatments (scarification or direct seeding) within each canopy reduction and year.

and a strong radicle that can penetrate the leaf litter (Godman *et al.* 1990, Walters and Yawney 1990). Surprisingly, the treatment increased density of almost all species, except for red oak and red maple. In the case of beech, root injury following scarification probably stimulated suckering and increased seedling density (Jones and Raynal 1986). When considering advanced regeneration, total regeneration of sugar maple was decreased by scarification.

It is known that scarification can improve regeneration establishment of the smaller seed size mid-tolerant species (God-

man 1957, Godman and Krefting 1960, Horton 1962, Marquis 1965, Hatcher 1966). In this experiment, regeneration of mid-tolerant species (white pine, yellow birch and white spruce) and intolerant species (paper birch, aspen and pin cherry) was favoured by scarification. Mineral soil exposure is considered necessary to provide ideal conditions for white pine germination and seedling development (Lancaster and Leak 1978). However, scarification effects can differ depending on site moisture regime. In Horton (1962), scarification increased white pine stocking on fresh and moist sites but had no effect on drier sites.

Fig. 4. Mean companion species density and stocking in all canopy reduction treatments (S25 = 25% single-selection cutting, S35 = 35% single-tree selection cutting) by scarification treatment (NS = non-scarified, SC = scarified) and year (99 = 1999 germinant density, 01 = 2001 total seedling density). The p value indicates the probability of difference ($\alpha = 0.05$) between scarification treatments within each canopy reduction and year.

Fig. 4. Continued.

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Intolerant species have regeneration strategies adapted to site perturbation: small wind-dispersed seeds for paper birch (Marquis 1969), suckering for aspens (Perala 1990) or buried seeds for pin cherry (Marks 1974). In the present study, important regeneration of these species was also found in the gaps on non-scarified plots (> 40% stocking, 668 to 1491 stems ha⁻¹). Marquis (1965) also observed important paper birch and pin cherry regeneration on undisturbed sites, especially in large gaps (2700 m²).

Relative success of regeneration gaps

Regeneration gaps will be considered successful if management objectives are achieved. The main objective of this study was to increase the target species (white pine, yellow birch, paper birch and red oak) stocking and density in the regeneration, while decreasing or controlling less desired species (shade-tolerant and intolerant species). Three years after gap creation, white pine, yellow birch and paper birch stocking were satisfactory

in scarified subplots, with mean values of 70%, 70% and 96%, respectively. However, these results must be considered as minima because stocking was calculated with 1-m² subplots, which is smaller than usual and can therefore underestimate the stocking. In Smith and Ashton (1993), white pine established in 1590 m² gaps following site preparation (scarification and advanced regeneration removal) and direct seeding, but after 18 years, it was restricted to the lower stratum, under the cover of pioneer species. In similar experiments, birches established successfully in 405–1013-m² gaps (Hatcher 1966) and 405–2700-m² gaps (Marquis 1965).

With regard to white pine, one could question if the number of seedlings (4906 ha⁻¹) is sufficient to eventually fill in the gaps. This could be possible since a density of 370 stems ha⁻¹ is recommended for the selection of final crop trees (Stiell 1985). Still, such values from pure stands are not necessary applicable to mixed species stands and we hypothesize that sufficient numbers of white pine and birch seedlings

Table 1. ANOVA of distance, month and enclosure effects on white pine germinants in the predation study

Effect	2000			2001		
	df	MS	p > F	df	MS	p > F
Block	9	37.115	0.1071	9	9.759	0.0007**
Distance	4	8.356	0.8072	4	7.496	0.0202*
Error (B × D)	36	20.882		36	2.248	
Month	4	23.240	< 0.0001**	4	12.398	< 0.0001**
Error (B × M)	36	1.488		36	1.354	
Dist. × Month	16	1.457	0.3815	16	1.723	0.0269*
Error (B × D × M)	144	1.352		144	0.917	
Enclosure	1	622.784	< 0.0001**	1	113.342	0.0036**
Error (B × E)	9	12.721		9	7.411	
Excl. × Dist.	4	42.936	< 0.0001**	4	8.662	< 0.0001**
Excl. × Month	4	7.860	0.0019**	4	9.453	< 0.0001**
Error	100	1.716		128	1.031	
Total	446			483		

could survive to fill in the gaps. In the present study, white pine seedlings experienced an important mortality rate (65%) after only one year in the gaps (from 2000 to 2001). This could be partly explained by drier soil conditions during July and August 2001. White pine mortality rate was only 18% in the 35% single-tree selection cutting and where soil moisture tended to be higher than in the gaps in 2001. Red oak regeneration failure in gaps (and on scarified subplots) can be due to the timing of application. There was already red oak advanced regeneration present before the experiment was established and seedlings were killed or removed during the harvesting and scarification operations. Understory disturbance was especially severe in the gaps, as the operators were asked to destroy the advanced regeneration in order to change the regeneration composition. Best red oak germination usually occurs when acorns are in contact with or buried in mineral soil and covered by a thin layer of leaf litter (Sander 1990) but soil disturbance can be favourable to red oak regeneration (Crow 1988, Runkle 1990). The limited dispersion capacity of red oak (Sander 1990) can also explain its poor subsequent regeneration recruitment in the gaps.

Shade-tolerant species tended to be less present in the regeneration gaps than in the 25% and 35% single-tree selection cutting. The most important result is that American beech and sugar maple failed to regenerate in the gaps. This result confirms that these species are more successful in smaller canopy gap environments (e.g., 15–75 m², Canham 1988b). The lower soil moisture measured in the gaps may have hindered survival of the shallow-rooted seedlings (Godman *et al.* 1990, Tubbs and Houston 1990). Also, faster warming up of gap soil surface during the spring may have been unfavourable to sugar maple since the seeds germinate under low temperatures (1–10°C, Godman *et al.* 1990).

Significant competition was rather due to intolerant species, especially aspen, which generally outgrew the target species. This aspen invasion is not currently critical, but release operations may be required later. Similarly, Marquis (1965) observed, after three years, high yellow birch and paper birch stocking on disturbed sites, but a very low proportion of free-to-grow seedlings (3% in 2700-m² gaps and 12% in 405–1215-m² gaps). In tolerant hardwoods of eastern Quebec, Hatcher (1966) noted that yellow birch outgrew its principal competitor sugar maple and underbrush competition and, thus, birch development was not compromised. After 18 years, Smith and Ashton (1993) found no tolerant hardwoods (black cherry (*Prunus serotina* Ehrh.) and red maple) in 45-m gaps,

and the more tolerant softwood species (hemlock, white pine) were suppressed under a birch cover. Pin cherry and grey birch were initially prominent but had died or become moribund. Since there is significant competition by the intolerant species in the present study, one could speculate that a smaller gap size could reduce such competition as intolerant species are more abundant in large gaps and tolerant species in small gaps (Marquis 1965, Canham 1988b, McClure and Lee 1993, Dale *et al.* 1995, Hannah 1999).

Direct seeding and seed predation

We expected direct seeding to have a greater impact on white pine density and stocking. The treatment increased white pine recruitment during the first year but after three years, the differences were still significant only in the 35% single-tree selection. In the present experiment, 564 000 seeds ha⁻¹ were broadcast in order to obtain 10 000 seedlings ha⁻¹, using the Duchesne *et al.* (1998) equation. In this situation, the number of seeds might not have been sufficient or the chosen target seedlings number could be too low. Cornett *et al.* (1998) used 4 millions seeds ha⁻¹ in a caging experiment, based on natural seed input in pure stands, which can be 3.1–4.4 million seeds ha⁻¹ during a good seed year (Graber 1970). Horton and Wang (1969) used 37 000 repellent-coated seeds ha⁻¹ in order to get 2500 seedlings ha⁻¹.

Since regeneration efforts can be negatively affected by predation, repellent-coated seeds or a greater amount of seeds should have been used in the present experiment. In this study, better survival in excluded plots could have been influenced by changes in microclimate and insect density (Suominen *et al.* 1999a, b). White pine seeds are preferred food for small mammals, especially mice and voles (Abbott 1961, Martell 1979). Using the olfactory stimuli, deer mice (*Peromyscus maniculatus* Wagner) and red-backed voles (*Clethrionomys gapperi* Vigors) select white pine seeds over balsam fir seeds (Abbott 1961, Duchesne *et al.* 2000), black spruce and jack pine seeds (Martell 1979). However, the effect of seed removal can be ambiguous as seeds removed from experimental plots could potentially be cached in another part of the forest, resulting in a redistribution rather than a net loss of seeds (Abbott and Quink 1970, Vander Wall 1994). Cornett *et al.* (1998) recommend seeding at higher densities than would occur naturally, in order to compensate for seed predation. Such problems with direct seeding remind us of the need to synchronize scarification with good seed crops (Horton 1962, Morneau 1997).

Fig. 5. Significant interactions in the white pine predation study ($n = 10$): (a) enclosure $\times$ distance and (b) enclosure $\times$ month (NE = non-excluded; E = excluded). The number of white pine germinants was recorded monthly in 2000 (June–October) and 2001 (May–August, October).

Conclusion and Recommendations

After three years, regeneration gaps with scarification have succeeded in increasing white pine, yellow birch and paper birch regeneration while decreasing maple and beech regeneration. Scarification had a positive effect on white pine, yellow birch and paper birch but a negative effect on red oak regeneration. The short term results presented in this paper suggest that the regeneration gap, newly proposed as a management tool in Quebec's management guide (MRNQ 1998) can successfully establish natural regeneration, if combined with soil disturbance by scarification. The scarification used in this case was scalping (spot) but it is also possible that other soil disturbance methods could promote successful natural regeneration establishment. For instance, organic layer disturbance by the skidder in the gaps when logging during the fall could be an economical solution. In this study, direct seeding effects were poor and since predation was found to have critical effects on white pine regeneration, a greater rate of seeding combined with the use of repellent-coated seeds is recommended for direct seeding. White pine seed predation may have been more important in our study, since it was located in mixedwood stands. Both gap creation and scarification increased regeneration of intolerant species. As a result, competition can potentially hinder survival and growth of target species. Release operations might be required at a future date. Monitoring over time will be important to evaluate seedling response to competition (see Raymond 2004) but also potential white pine weevil (*Pissodes strobi* Peck.) or white pine blister rust (*Cronartium ribicola* J.C. Fish) damage. A smaller gap size should also be tested, with the objective to reduce intolerant species abundance. The manager will be faced to the following options: i) creating larger gaps (e.g., 2H, H = stand height) and planning release treatments during the first years after gap creation; or ii) creating smaller gaps, which require more initial resources to carry out in the field but potentially less need for release afterwards. We must also keep in mind that it can be advantageous to grow eastern white pine under par-

tial cover during the period of its life where the species is most susceptible to the white pine weevil (Lavallée *et al.* 2001).

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