

Establishment of natural regeneration under severe browsing pressure from white-tailed deer after group seed-tree cutting with scarification on Anticosti Island

Julien Beguin, Marcel Prévost, David Pothier, and Steeve D. Côté

Abstract: The use of large clearcuts with protection of advance regeneration is inappropriate for regeneration of balsam fir (*Abies balsamea* (L.) Mill.) under severe browsing from white-tailed deer (*Odocoileus virginianus* (Zimmermann)). However, little is known about the effects of tree-retention methods along with scarification on the establishment of balsam fir in a context of severe herbivory. Consequently, we hypothesized that seed-tree-group cutting in conjunction with soil scarification creates favourable conditions for balsam fir regeneration. In 1998 and 1999 we set up three circular forest groups of different sizes (40, 60, and 80 m in diameter) surrounded by three different intensities of scarification (no treatment, single pass, double pass) in two balsam fir stands on Anticosti Island, Quebec, Canada. Moreover, we used a network of fenced and unfenced regeneration plots to evaluate the impact of white-tailed deer browsing. The results showed that up to 7 years after harvest, seed-tree-group cutting did not improve the establishment of conifer species. Scarification had a negative impact on the abundance of conifer species, whereas white birch (*Betula papyrifera* Marshall) density was significantly higher in areas scarified twice than in unscarified areas. Overall, the development of palatable tree species appears unlikely at deer densities >20 individuals/km².

Résumé : L'utilisation de grandes coupes à blanc avec protection de la régénération s'est avérée inefficace pour régénérer le sapin baumier (*Abies balsamea* (L.) Mill.) en présence de densités élevées de cerf de Virginie (*Odocoileus virginianus* (Zimmermann)). Cependant, peu d'études ont évalué l'efficacité de coupes avec rétention d'arbres, jumelées avec une préparation de terrain, pour favoriser l'établissement de la régénération soumise à un fort broutement. Nous avons donc testé l'effet d'une coupe avec réserve d'îlots semenciers, jumelée avec différentes intensités de scarifiage, pour améliorer les conditions d'établissement du sapin baumier. En 1998 et 1999, nous avons installé des îlots semenciers de 40, 60 et 80 m de diamètre autour desquels nous avons effectué trois intensités de scarifiage (aucun traitement, un passage et deux passages) dans deux sapinières sur l'île d'Anticosti (Québec, Canada). De plus, nous avons installé un réseau de parcelles clôturées et non clôturées pour évaluer l'effet du broutement. Sept ans après la coupe, les résultats montrent que la réserve d'îlots semenciers et le scarifiage n'ont pas amélioré l'établissement des conifères. Le scarifiage a néanmoins permis d'augmenter significativement la densité de bouleau à papier (*Betula papyrifera* Marshall). Toutefois, le développement des essences consommées par le cerf apparaît compromis à des densités locales >20 individus/km².

[Traduit par la Rédaction]

1. Introduction

Cervids are a key functional component of ecosystems and play a central role in nitrogen cycling (Singer and Schoenecker 2003), energy transfer between trophic levels (Okarma 1995), and plant community dynamics (Risenhoyer and Maass 1987). However, deer populations in various regions have increased during the last few decades (Gill 1990; Rooney 2001), resulting in high local densities that

can affect the maintenance of many ecosystem components. Deer browsing has direct impacts, with significant ecological and economical consequences, when populations are overabundant, as selective browsing can deeply modify forest tree and plant species composition (Côté et al. 2004). Indeed, severe deer browsing effects have been reported to be the main cause of regeneration failure in various forest types (Anderson and Loucks 1979; Danell et al. 2003; Husheer et al. 2003; Rooney and Waller 2003). The impacts of selec-

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tive browsing include the direct killing of seedlings of preferred species, the reduction of seedling growth, and the conferring of an apparent advantage for herbaceous plant or tree species that are tolerant of browsing (Horsley et al. 2003; Tremblay et al. 2007). In turn, these impacts may indirectly change natural succession pathways and ecological processes at different spatial and temporal scales (Côté et al. 2004). In the context of cervid overabundance, testing silvicultural methods to reduce browsing damages on economically valuable species becomes an important challenge for many regions that are facing, or will soon be facing, problems with recruitment of important tree species.

White-tailed deer (*Odocoileus virginianus* (Zimmermann)) were introduced to Anticosti Island about a century ago. During the first four decades following introduction, deer populations had increased to such an extent that they limited the establishment of regeneration of palatable trees, primarily the deciduous species (e.g., white birch (*Betula papyrifera* Marsh.)). Following the reduction of deciduous forage species, deer populations have been intensively foraging on balsam fir (*Abies balsamea* (L.) Mill.), to the benefit of less browsed species such as white spruce (*Picea glauca* (Moench) Voss) (Potvin et al. 2003). Balsam fir is the staple food for white-tailed deer in winter on Anticosti Island, representing 70% of the diet (Lefort et al. 2007). The current conversion of balsam fir stands to spruce stands at a large spatial scale as a result of chronic deer browsing threatens both the integrity of the Anticosti Island ecosystem and deer hunting, the main economic activity on the island. Indeed, the increased presence of unpalatable species could have a negative impact on deer population levels, which could decline in the near future as foraging resources become scarce.

Balsam fir and black spruce (*Picea mariana* (Mill.) BSP) are shade-tolerant species whose regeneration strategy is based mainly on the establishment of seedlings (for both balsam fir and black spruce) or layers (for black spruce) under the dominant canopy (Frank 1990; Viereck and Johnson 1990). On Anticosti Island the use of large clearcuts with protection of balsam fir advance regeneration did not mitigate deer browsing because nearly all palatable-tree regeneration was severely browsed (Casabon and Pothier 2007). Therefore, counting solely on balsam fir advance regeneration is not a promising option for regenerating these stands as long as deer browsing remains so severe. However, it is possible that some forms of tree-retention treatment may create abundant regeneration of several palatable tree species and allow balsam fir seedlings to develop beyond the reach of deer. Up to 8 years after clear-cutting, Hughes and Bechtel (1997) found that balsam fir regeneration originating from natural seeding after cutting was more abundant than the advance regeneration close to the forest edge. Abundant regeneration can be achieved by improving seed supply, the amount and distribution of the receptive seedbed, and the moisture conditions of the seedbed (Jeglum 1987). Natural seed supply can be improved by reducing the distance between seed sources and germination substrate, since the density of wind-dispersed seeds decreases with distance from the seed source (Greene et al. 1999). In addition, scarification may create a large number of receptive seedbeds for germination by improving soil properties such as

moisture level, temperature, bulk density, and hydraulic regime (Plamondon et al. 1980; Prévost 1992; MacKenzie et al. 2005), and by removing the dry layer of feather mosses left after clear-cutting that can prevent seed germination (unpublished results). Balsam fir germinates better on exposed mineral soil than in litter and humus (Bakuzis and Hansen 1965, p. 184), and accordingly, Prévost and Pothier (2003) found higher densities of small seedlings (<30 cm in diameter) in scarified areas than in unscarified areas. Scarification was also found to improve seedling establishment of the shade-intolerant white birch (Perala and Alm 1990; Prévost 1997), which develops well after clear-cutting (Harvey and Bergeron 1989) and is a species preferred by white-tailed deer (Crawford 1982; Dumont et al. 2005). As a result, we hypothesized that white-tailed deer feed on preferred species, thus decreasing pressure on less preferred species such as balsam fir and enabling some individuals to grow beyond the reach of deer.

The main objective of this study was to evaluate the efficiency of seed-tree-group cutting in increasing the amount of dispersed seeds and established seedlings over the adjacent clear-cut areas. Moreover, we tested different scarification intensities around seed-tree groups to evaluate their capacity to improve balsam fir germination and early establishment in a context of a high level of herbivory. Our research hypotheses are that (i) the presence of a residual group of seed trees combined with soil scarification allows abundant balsam fir regeneration, (ii) some balsam fir seedlings escape from deer browsing and are recruited to the sapling stage, and (iii) scarification improves white birch establishment, altering the foraging strategy of white-tailed deer towards the reduced use of balsam fir regeneration.

2. Material and methods

2.1. Study area

The experiment was carried out on Anticosti Island (7943 km²) in the Gulf of St. Lawrence, Quebec, Canada (49.06°–49.95°N, 61.67°–64.52°W). The island is characterized by a cold maritime climate with total annual precipitation of 937 mm, of which 327 mm falls as snow. Mean air temperature is –10.5 °C in January and 15.3 °C in July, with an average of 1005 degree-days above 5 °C (Environment Canada 1982). Elevation ranges from 0 to 313 m and topography is mainly gentle. The forests of Anticosti Island belong to the boreal zone and are part of the eastern balsam fir – white birch bioclimatic region (Saucier et al. 2003), where the main tree species are balsam fir, white spruce, and black spruce. Associated tree species are white birch, trembling aspen (*Populus tremuloides* Michx), balsam poplar (*Populus balsamifera* L.), and tamarack (*Larix laricina* (Du Roi) K. Koch). The current population density of white-tailed deer is estimated at about 20 individuals/km² (Potvin and Breton 2005), but densities can be higher locally. The experiment was conducted in two stands older than 100 years, both dominated by balsam fir (Table 1). Both sites were characterized by mesic conditions, with shallow podzols and efficient drainage. Prior to cutting, the ground vegetation was dominated by feather mosses, predominantly *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt.

Table 1. Stand characteristics by group diameter in the seed-tree-group cutting experiment on Anticosti Island (mean \pm 1 SD).

Diameter of seed-tree group (m)	Stand density (stems/ha)	Stand basal area (m ² /ha)	% Stand basal area (m ² /ha)		Stand mean height (m)
			Balsam fir	White spruce	
40	2296 \pm 690	40.7 \pm 7.9	64 \pm 21	25 \pm 23	13.0 \pm 1.5
60	2500 \pm 696	41.2 \pm 6.7	57 \pm 25	25 \pm 17	13.0 \pm 1.1
80	2364 \pm 938	38.4 \pm 4.8	63 \pm 15	34 \pm 28	13.1 \pm 1.5
Mean	2387 \pm 748	41.0 \pm 6.3	61 \pm 20	28 \pm 22	13.1 \pm 1.1

2.2. Experimental design

Two sites 10 km apart were harvested using the tree-length method in the fall of 1998 (site 1) and 1999 (site 2). In an effort to provide a seed supply for natural regeneration of balsam fir, circular groups of trees were left unharvested. Each site contained seed-tree groups of three diameters (40, 60, and 80 m) in a completely randomized design with three and four replications in sites 1 and 2, respectively (Fig. 1). The remaining seed-tree groups were at least 200 m from each other. In addition, white birch seed-trees were not harvested (density \approx 20–50 stems/ha). In October 1998 (site 1) and September 1999 (site 2), a Wadell disk-trencher was used to apply a scarification treatment around the 21 groups of trees. Three scarification levels were randomly applied around each group: a control (C), which was left undisturbed, a single-pass scarification, and a double-pass scarification with the second pass perpendicular to the first. Each treatment was applied to a pie-shaped subplot covering a 60° angle from the centre of the seed-tree group and 100 m from the edge of the group (Fig. 1). Within each subplot, 10 circular regeneration sub-subplots (4 m²) were established in two transects, 20 m apart, at 10, 30, 50, 70, and 90 m from the edge. In addition, one of the two regeneration sub-subplots located at 30 m was enclosed within a 1.5 m high fence to evaluate the effects of deer browsing on the establishment and height growth of natural regeneration.

2.3. Data collection

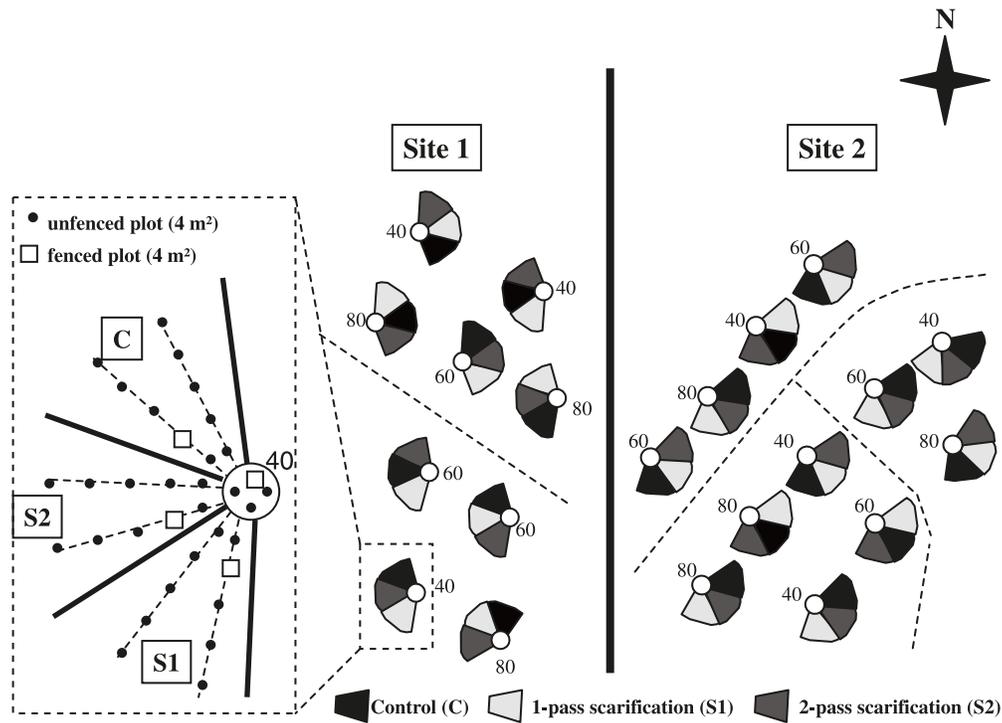
Regeneration surveys were conducted from July to August of 1999 (site 1 only), 2000, 2001, and 2006 during which we recorded the number of all stems (including advance regeneration and immediate or delayed regeneration) and seedling height (in six classes: <5, 5–30, 31–60, 61–100, 101–200, and 201–300 cm) for each tree species. In 2006 we also recorded herbaceous vegetation cover to evaluate the effects of competitive plant species on tree species establishment and height growth. We retained five species or taxon groups that could compete directly with seedlings for light and soil nutrients, based on their percent cover: graminoids, ferns, Canada thistle (*Cirsium arvense* (L.) Scop.), fireweed (*Epilobium angustifolium* L.), and American red raspberry (*Rubus idaeus* L.). We compared surveys conducted 1, 2, and 7 years after cutting, using the density and height of all stems. In the following paragraphs, year 7 after cutting refers to year 7 for site 1 and year 8 for site 2.

2.4. Statistical analyses

Seedling density and dominant height for main tree species were analysed according to a split-split-plot and a split-plot design, respectively, using repeated measures (Cochran

and Cox 1992). Variation in plant cover was analysed as a split plot but with a single measurement 7 years after cutting. Seedling density, including advance regeneration and seedlings established after clear-cutting, was estimated according to seed-tree-group dimension, scarification level, presence or absence of a fence, and year after cutting, whereas the model for dominant height and plant cover did not take into account seed-tree-group dimension because it was irrelevant ecologically. Seed-tree-group dimension, scarification intensity, distance to edge, presence or absence of a fence, and year after cutting were designated as fixed factors. Sites, seed-tree-group repetitions, and their interaction with fixed factors were designated as random factors. All data were analysed with mixed models using the MIXED procedure in SAS (SAS Institute Inc. 2003; Littell et al. 2006). The small number of black spruce and white spruce seedlings did not permit separate statistical analyses to be applied, so we pooled them. Seedling density was evaluated from regeneration sub-subplots (fenced vs. unfenced) located 30 m from the edge to avoid any a priori distance effect on seedling establishment. Dominant height was assessed for each species (or genus for spruce) by calculating the mean for all unfenced sampling plots within each pie-shaped area. We also estimated the dominant tree height in each fenced plot. To test whether natural seedling improved the establishment of regeneration as a function of the distance to edge, we subtracted the seedling density measured during the first survey after cutting from densities measured in subsequent years because we assumed that most of the regeneration measured 1 year after cutting was advance regeneration (see Figs. 2 and 3). Moreover, we retained only unfenced plots in this analysis, since fenced plots were restricted to 30 m from edge. For all tests we checked the assumptions of normality of residuals and homogeneity of variance and applied square-root transformation when needed. To take into account the temporal correlation between surveys, we selected the best structure of variance-covariance matrix in our models among nine different structures (variance components, compound symmetry, heterogeneous compound symmetry, spatial power, toeplitz, heterogeneous toeplitz, autoregressive (1), heterogeneous autoregressive (1), and unstructured). We retained the matrix that minimized Akaike's Information Criterion (Littell et al. 2006). We removed seven exclosures (11%) from the analyses because they were damaged and browsing of vegetation inside them was apparent. Means between treatments were compared using protected least square means, and when the number of comparisons exceeded the number of degrees of freedom, we adjusted the significance level (α value) with the Bonferroni correction. Since retransfor-

Fig. 1. Experimental design showing the disposition of seed-tree groups 40, 60, and 80 m in diameter and the locations of scarified areas within the two sites on Anticosti Island. The diagram on the left-hand side shows the organization of sampling plots in two transects, by scarification level, from the edge of each seed-tree group.



mation did not give reliable estimates of standard error using smearing estimate methods (Duan 1983) or alternative methods (Manning 1998; Ai and Norton 2000; Doshi et al. 2005), we present arithmetic means by treatment combination and standard errors from models on untransformed data as the best approximation. All statistical tests on mean comparisons were performed on transformed variables.

3. Results

3.1. Effects of seed-tree-group size, scarification, and deer browsing on seedling density

The size of residual seed-tree groups had no effect on the density of balsam fir seedlings, irrespective of year after cutting (Table 2). However, the effect of deer browsing on balsam fir seedling density varied as a function of scarification intensity and year after cutting ($p = 0.018$; Table 2). Seven years after cutting, balsam fir density was roughly four times higher in fenced than in unfenced plots within unscarified areas (Fig. 2A) and areas scarified only once, whereas no difference was detected in areas scarified twice. Conversely, 1 year after cutting, balsam fir density was significantly lower after soil scarification (Fig. 2A) and tended to decrease with increasing scarification intensity, as these treatments likely damaged a high proportion of the advance regeneration. Moreover, the negative impact of soil scarification persisted throughout the study (Fig. 2A).

As with balsam fir, the effect of deer browsing on spruce seedling density varied as a function of scarification intensity and year after cutting (Table 2). One year after cutting, spruce density in fenced plots was negatively affected by soil preparation (Fig. 2B), which, as with balsam fir, dam-

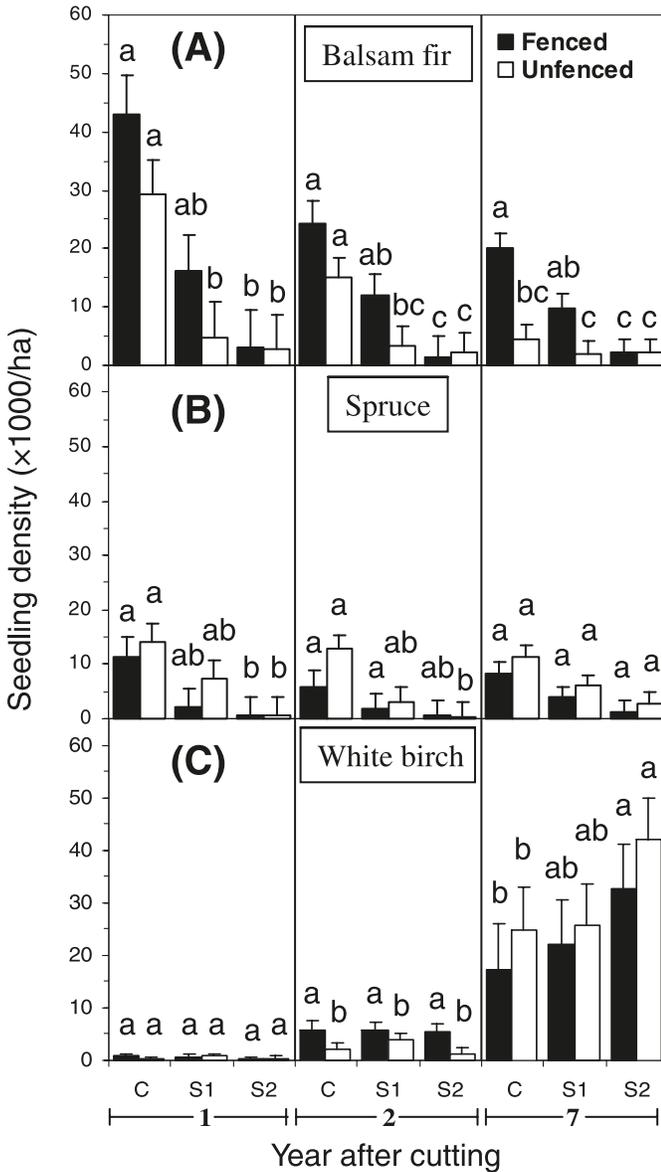
aged a high portion of the advance regeneration. At each measurement period, spruce density did not change significantly between areas scarified once and twice (Fig. 2B). Moreover, 7 years after cutting, we did not detect any effect of deer browsing on spruce density within any level of scarification (Fig. 2B). Instead, spruce seedling density tended to be slightly higher in unfenced than in fenced plots throughout the study (Fig. 2B). Seven years after cutting, spruce seedling density was higher around the smallest seed-tree groups (40 m in diameter) than around larger groups.

The impact of deer browsing on white birch seedlings, unlike coniferous species, was independent of scarification intensity throughout the study (Table 2). Two years after cutting, white birch density was relatively low, but was significantly higher in fenced than in unfenced plots (Fig. 2C), whereas by the end of the study there was no significant difference between fenced and unfenced plots. However, white birch density varied as a function of time after cutting and scarification intensity (Table 2). Two years after cutting, there was no difference between scarification levels, but 7 years after cutting, white birch density was higher in areas scarified twice than in unscarified areas (Fig. 2C). Also, birch density tended to be higher, though not significantly so, in areas scarified twice than in areas scarified once (Fig. 2C).

3.2. Effects of scarification and deer browsing on height of dominant seedlings

The effect of deer browsing on the height of dominant balsam fir seedlings varied as a function of time after cutting (Table 3). Two years after cutting, the height of dominant fir seedlings was less than 20 cm in both fenced and

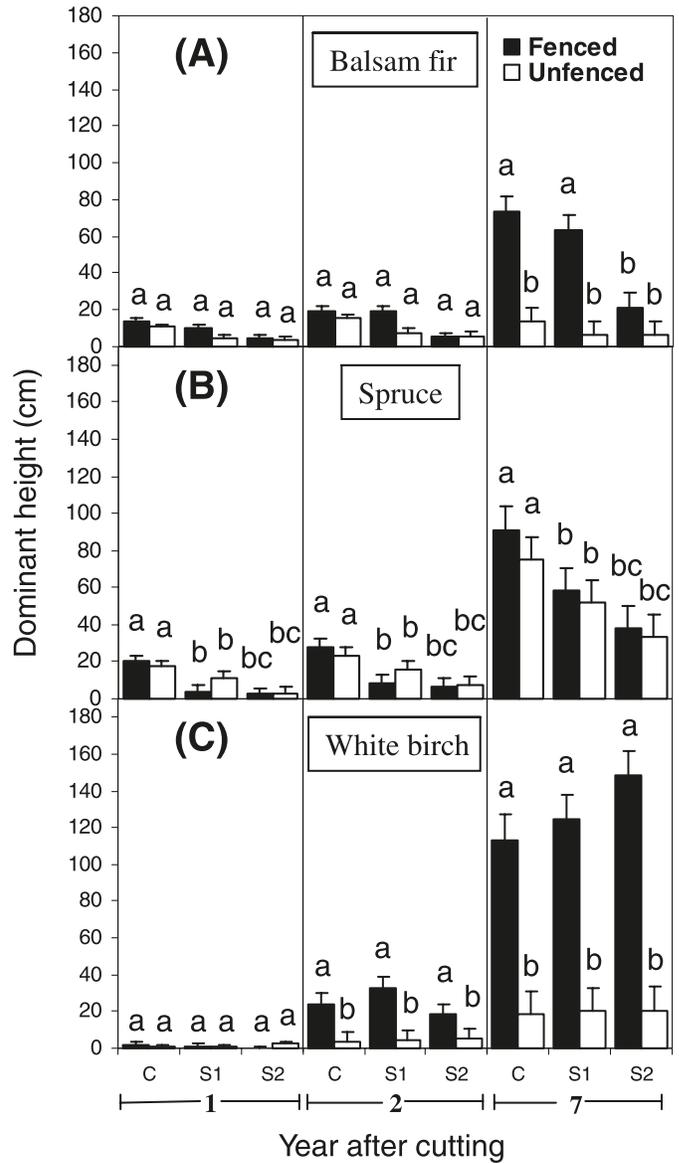
Fig. 2. Densities (mean ± SE) of balsam fir (A), black and white spruce (B), and white birch (C) seedlings as a function of scarification intensity (C, control; S1, single-pass scarification; S2, double-pass scarification), the presence or absence of a fence preventing deer browsing, and year after cutting in plots 30 m from edge on Anticosti Island. For each species and within each year after cutting, a different letter indicates a significant difference according to comparisons of least square means corrected with the Bonferroni method.



unfenced plots (Fig. 3A). Seven years after cutting, however, dominant fir seedlings were significantly taller in fenced than in unfenced plots (Fig. 3A), but this effect also varied as a function of scarification intensity (Table 3). Indeed, dominant fir seedlings were significantly taller in fenced than in unfenced plots in unscarified areas and areas scarified once, whereas no difference was detected between fenced and unfenced plots in areas scarified twice (Fig. 3A).

The height of dominant spruce seedlings was not statistically influenced by deer browsing (Table 3; Fig. 3B). How-

Fig. 3. Dominant heights (mean ± SE) of balsam fir (A), black and white spruce (B), and white birch (C) seedlings as a function of intensity of scarification (C, control; S1, single-pass scarification; S2, double-pass scarification), presence or absence of a fence preventing deer browsing, and year after cutting in plots located 30 m from edge on Anticosti Island. For each species and within each year after cutting, a different letter indicates a significant difference according to comparisons of least square means corrected with the Bonferroni method.



ever, spruce seedlings were taller in unscarified than in scarified areas and tended to be higher in areas scarified once rather than twice (Fig. 3B).

The height of dominant white birch seedlings was influenced by deer browsing in interaction with time after cutting (Table 3). Deer browsing began to affect the dominant height of white birch seedlings in the second year after cutting, and this increased 7 years after cutting (Fig. 3C). We detected no effect of scarification intensity on the dominant height of white birch seedlings during the years after cutting.

Table 2. Analyses of variance with repeated measures (*p* values, MIXED procedure) for seedling density (all height classes) of balsam fir, spruce (black and white), and white birch as a function of diameter of seed-tree group, scarification intensity, presence or absence of a fence preventing deer browsing, and year after cutting in plots 30 m from edge on Anticosti Island.

Source of variation	df/denominator df	Balsam fir	Spruce	White birch
Diameter of group (D)	2/18	0.20	0.14	0.80
Scarification intensity (S)	2/36	<0.001	<0.001	0.11
D × S	4/36	0.12	0.82	0.57
Fence (F)	1/46	0.004	0.21	0.18
D × F	2/46	0.13	0.08	0.15
S × F	2/46	0.11	0.70	0.76
D × S × F	4/46	0.77	0.45	0.42
Year after cutting (Y)	2/200	<0.001	<0.001	<0.001
D × Y	4/200	0.14	0.042	0.89
S × Y	4/200	<0.001	0.23	0.019
D × S × Y	8/200	0.17	0.40	0.79
F × Y	2/200	0.13	0.35	0.048
D × F × Y	4/200	0.39	0.75	0.37
S × F × Y	4/200	0.018	0.040	0.73
D × S × F × Y	8/200	0.59	0.87	0.67

Note: Analyses were conducted using square-root-transformed data. Values in boldface type denote a significant effect ($\alpha = 0.05$).

Table 3. Analyses of variance with repeated measures (*p* values, MIXED procedure) for height of dominant seedlings of balsam fir, spruce (black and white), and white birch as a function of intensity of scarification intensity, presence or absence of a fence preventing deer browsing, and year after cutting in plots located 30 m from edge on Anticosti Island.

Source of variation	df/denominator df	Balsam fir ^a	Spruce ^b	White birch ^a
Scarification intensity (S)	2/40	<0.001	<0.001	0.56
Fence (F)	1/52	<0.001	0.19	<0.001
S × F	2/52	0.004	0.32	0.80
Year after cutting (Y)	2/224	<0.001	<0.001	<0.001
S × Y	4/224	0.07	0.22	0.52
F × Y	2/224	<0.001	0.75	<0.001
S × F × Y	4/224	0.07	0.98	0.65

Note: Values in boldface type denote a significant effect ($\alpha = 0.05$).

^aAnalyses were conducted using square-root-transformed data.

^bAnalyses were conducted using $y^{0.7}$ -transformed data.

3.3. Effect of distance to edge on seedling recruitment

The number of recruited balsam fir seedlings in unfenced plots varied as a function of distance to edge in interaction with level of scarification (Table 4), irrespective of year after cutting. However, recruitment was negative in all scarification treatments, and there was no clear pattern of decrease in balsam fir density with distance to edge. In unscarified areas, fir density varied from about 8000 to 16 000 seedlings/ha depending on distance to edge, whereas in scarified areas it ranged from about 2000 to 4000 seedlings/ha (results not shown). The number of recruited spruce seedlings in unfenced plots was influenced by distance to edge in interaction with year after cutting (Table 4). Seven years after cutting, the density of new seedlings decreased proportionally with distance to edge so that for a distance to edge >50 m, no difference in seedling density was detected be-

tween years 2 and 7 (Fig. 4). In contrast, scarification intensity and size of seed-tree group had no significant impact on spruce recruitment (Table 4). The number of recruited white birch seedlings was independent of distance to edge, since many seed trees were left on the cutover (data not shown).

3.4. Effects of deer browsing on vegetation cover

Cover of graminoids and ferns was approximately two times higher in unfenced plots than in fenced plots (Fig. 5), while percent cover of preferred browse species, such as American red raspberry and fireweed, was about 10 times higher in fenced plots than in unfenced plots (Fig. 5). Percent cover of Canada thistle was not influenced by deer browsing ($p = 0.19$). Mean cumulative cover of these five taxa in unfenced and fenced plots was 74% and 85%, respectively.

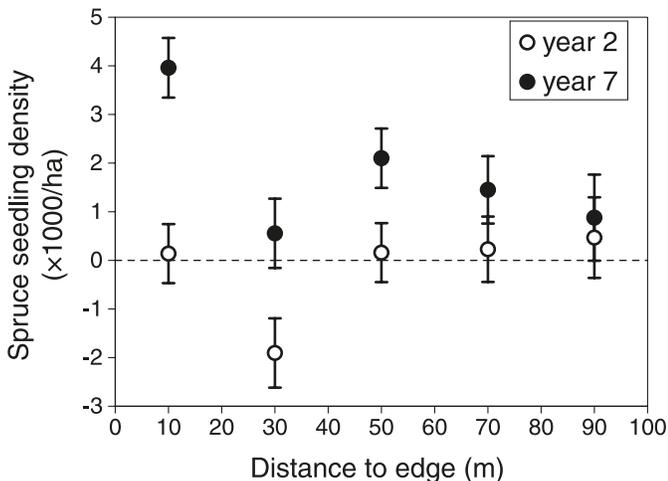
Table 4. Analyses of variance (*p* values, MIXED procedure) and orthogonal contrasts applied to the density of recruited seedlings 2 and 7 years after seed-tree-group cutting for balsam fir and spruce as a function of seed-tree-group diameter, scarification intensity, distance to edge, and year (2 or 7) after cutting on Anticosti Island.

Source of variation	df/denominator df	Balsam	
		fir	Spruce
Edge distance (E)	4/181	0.19	0.008
Dimension (D) × E	8/181	0.24	0.35
Scarification (S) × E	8/181	0.019	0.11
D × S × E	16/181	0.47	0.40
E × year (Y)	4/607	0.69	0.003
Y ₂ vs. Y ₇ at 10 m*	1/607	—	<0.001
Y ₂ vs. Y ₇ at 30 m*	1/607	—	0.001
Y ₂ vs. Y ₇ at 50 m*	1/607	—	<0.001
Y ₂ vs. Y ₇ at 70 m*	1/607	—	0.052
Y ₂ vs. Y ₇ at 90 m*	1/607	—	0.62
D × E × Y	8/607	0.97	0.12
S × E × Y	8/607	0.98	0.99
D × S × E × Y	16/607	0.99	0.55

Note: Only effects related to distance to edge are shown.

*Significance level corrected with the Bonferroni method ($\alpha = 0.05/5$) $P = 0.01$.

Fig. 4. Numbers (mean ± SE) of newly established spruce seedlings ($\times 1000/\text{ha}$) in unfenced plots 2 and 7 years after seed-tree-group cutting as a function of distance to edge and year after cutting on Anticosti Island.



4. Discussion

4.1. Establishment of regeneration in fenced areas

The establishment of natural regeneration after various soil-preparation treatments has been well studied in different forest ecosystems (Fredericksen and Pariona 2002; Karlsson et al. 2002; Yoshida et al. 2005). Improvement of seedbed receptivity through major changes in soil properties such as temperature, bulk density, moisture level, and hydraulic regime appears to be the key element explaining increased establishment of tree regeneration (Plamondon et al. 1980; Prévost 1992; MacKenzie et al. 2005). While the receptivity of seedbeds following treatments in our study appeared appropriate, our results concerning regeneration dynamics dif-

fered from this general pattern in that coniferous-species establishment decreased with increasing scarification intensity during the study period (Fig. 2).

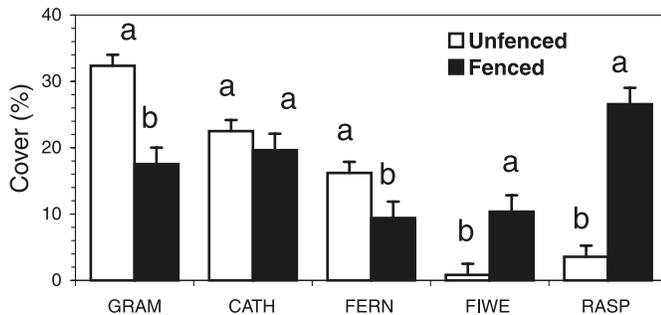
The low rate of conifer seedling establishment in fenced plots could have been due to different factors, such as a lack of seed availability or adverse seedbed moisture conditions (Bakuzis and Hansen 1965). Seedling mortality could have occurred as a result of desiccation (Kaufmann and Eckard 1977; Thomas and Wein 1984; Frank 1990) or competition with other plant species (Smith et al. 1997). Although we did not survey seed rain, most years for balsam fir usually occur at 2 to 4 year intervals (Frank 1990), whereas most years for white spruce can occur at 2 to 6 year intervals (Nienstaedt and Zasada 1990). This suggests that seed production should have taken place for both species at least once during the 8 year study. However, Frank (1990) reported that the germination rate for balsam fir seeds was only 10% when these seeds originated from trees older than 100 years, which was the case in the stands we studied. In addition, microsites might have become unreceptive with respect to germination (Coates et al. 1994) and seedling establishment, owing to increasing competition, especially by white birch (Fig. 3C) and raspberry (Fig. 5). Finally, the failure of conifer seedlings to establish 30 m from edge could also have been a random event, since it deviates from the trend illustrated in Fig. 4.

In contrast, establishment of white birch increased with time after cutting and with scarification intensity (Fig. 2C), supporting the results of Prévost (1997), who found that white birch establishment increased with scarification intensity. The proximity of mature white birch left throughout the cutover area probably favoured the availability and abundance of seeds. Seed crops for this species, like balsam fir, can range from 2 to 4 years (Perala and Alm 1990). Thus, the increase of birch density between years 2 and 7 after cutting was likely due to the production of a good seed crop during the intervening period.

4.2. Impact of deer browsing on the establishment of regeneration

In unfenced plots, browsing by white-tailed deer prevented height growth of palatable species such as balsam fir and white birch (Figs. 3A and 3C) in all scarification treatments. These results are consistent with those of other studies on Anticosti Island that have shown a significant impact of deer browsing on the establishment of palatable-tree regeneration (Potvin et al. 2003; Casabon and Pothier 2007, 2008; Tremblay et al. 2007). We hypothesized that when white birch regeneration is abundant, white-tailed deer decrease browsing pressure on balsam fir, but this pattern was not observed. This hypothesis was based on several studies which emphasized that the availability of high-quality forage had an effect on selection patterns and foraging behaviour of white-tailed deer (Murden and Risenhoover 1993; Berteaux et al. 1998; Coulombe et al. 2008). One possible explanation for these divergent results is that balsam fir and white birch seedlings were not abundant during the same year(s). Indeed, during years 1 and 2 after cutting, the density of white birch seedlings was low, whereas balsam fir density was at its highest. In year 7, when white birch density reached

Fig. 5. Percent cover (mean ± SE) of principal plant species or taxon groups competing with tree seedlings as a function of the presence or absence of a fence preventing deer browsing 7 years after seed-tree-group cutting on Anticosti Island. (GRAM, graminoids; CATH, Canada thistle; FERN, ferns; FIWE, fireweed; RASP, raspberry). For each taxon, a different letter indicates a significant difference ($p < 0.05$) between fenced and unfenced plots.



20 000 – 43 000 stems in unfenced areas, balsam fir density seemed to be at its lowest (Figs. 2A and 2C).

Although the height of white birch seedlings in unfenced plots was severely reduced by deer browsing (Fig. 3C), the density of seedlings did not differ between fenced and unfenced plots (Fig. 2C). This can be explained by the ability of white birch to survive in prostrate forms even after intensive damage by browsing or leaf-stripping, as Danell et al. (1994) have already noted for downy birch, *Betula pubescens* Ehrh. Therefore, in unfenced plots, white birch seedlings were limited to 20 cm in height and showed evidence of browsing, while in fenced plots, their dominant height reached more than 110 cm. Moreover, the height of white birch seedlings in fenced plots was reduced by deer browsing when they exceeded the grid height (1.5 m). This may have prevented us from detecting a significant effect of scarification on white birch height.

Deer browsing decreased neither the height of dominant seedlings nor seedling density for spruce. By removing many primary competitors, deer browsing maintained adequate growing conditions for unpalatable species such as white and black spruce. Graminoids and ferns also took advantage of selective deer browsing (Fig. 5), but their abundance was likely insufficient to limit the establishment of spruce species. Thus, if spruce stocking is adequate, we expect that over the medium term, white spruce will dominate the cutover area in association with unpalatable species such as graminoids, Canada thistle, and ferns.

4.3. Diameter of seed-tree groups and distance to edge

Our results showed that the size of seed-tree groups and distance to edge did not improve the establishment of balsam fir and white birch seedlings. The difference in balsam fir density as a function of scarification intensity and distance to edge was due to nonlinear effects in unscarified areas that likely originated from heterogeneous initial distribution of advance regeneration according to distance to edge. Our hypothesis that balsam fir establish at higher densities in closer proximity to the edge of seed-tree groups because some seedlings would be spared by deer browsing was

not supported. In unfenced plots, this is probably because white-tailed deer use all areas similarly, as Casabon and Pothier (2007) observed at the edge of large clearcuts.

In the case of spruce seedlings, we observed decreasing recruitment with increasing distance to edge, irrespective of scarification intensity. This indicates that natural seeding becomes negligible beyond 50 m from edge (Fig. 4). This might have important ecological consequences in a forest-harvesting context. Indeed, if advance regeneration of spruce is not adequate after clear-cutting, we expect that spruce density will decline with distance from seed sources. In closer proximity to the edge, we expect conversion from fir- to spruce-dominated stands (Potvin et al. 2003) because of the negative impact of deer browsing on balsam fir regeneration. But at greater distances we observed conversion from balsam fir stands to a prairie-like vegetation structure principally composed of graminoids, Canada thistle, and ferns, similar to that observed by Casabon and Pothier (2008) in the center of large clearcuts. Such conversions of vegetation composition and structure may occur on Anticosti Island if, firstly, deer population density remains high and, secondly, adequate seed sources are not left in the cutover area following clear-cutting.

5. Conclusion

Seed-tree-group cutting with or without scarification could not regenerate balsam fir stands in the presence of white-tailed deer densities averaging 20/km² locally. In contrast, white birch responded well to scarification treatment, indicating that a seed-tree cut may improve seed availability and seedling establishment. Our study thus revealed that the response of different species to scarification must be well understood before such treatment is applied in the context of severe herbivory. In a companion study, we used various silvicultural treatments on Anticosti Island and the results demonstrated that high deer densities prevented the establishment of balsam fir regeneration in all treatments (Beguín et al. 2009). Our results thus indicate that to be successful, these silvicultural treatments should be applied in combination with a reduction of deer density through intensive hunting and fencing of forest blocks.

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