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Can the impact of deer browsing on tree regeneration be mitigated by shelterwood cutting and strip clearcutting?

Julien Beguin [a,*], David Pothier [b], Marcel Prévost [c]

[a] Chaire de recherche industrielle CRSNG-Produits forestiers Anticosti, Département de biologie, 1045 ave. de la Médecine, Université Laval, Québec, Québec G1V 0A6, Canada
[b] Centre d'étude de la forêt, Département des Sciences du Bois et de la Forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, Québec G1V 0A6, Canada
[c] Ministère des Ressources naturelles et de la Faune, Forêt Québec, Direction de la recherche forestière, 2700 rue Einstein, Québec, Québec G1P 3W8, Canada

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ABSTRACT

Silvicultural treatments creating large canopy openings failed to restore regeneration of balsam fir (*Abies balsamea* (L.) Mill.) due to browsing pressure from white-tailed deer (*Odocoileus virginianus* Zimmermann). Consequently, we tested two alternative silvicultural treatments aimed at improving balsam fir establishment on Anticosti Island (Québec, Canada). In 1998 and 1999, we set up shelterwood seed cutting using three harvest intensities (0, 25 and 40% of basal area) and strip clearcutting with scarification using three different strip widths (15, 30 and 45 m), both with fenced and unfenced regeneration plots, in balsam fir stands. After 8 years, shelterwood seed cutting did not allow the establishment of new balsam fir seedlings, nor the development of unbrowsed balsam fir seedlings. In the strip clearcutting, deer browsing suppressed growth of palatable species in all strip widths. This favoured the development of unpalatable species, especially white spruce (*Picea glauca* (Moench) Voss). Our study demonstrates that the use of silvicultural treatments alone is unlikely to restore balsam fir regeneration on Anticosti Island, as long as the deer population remains higher than 20 deer/km^2.

1. Introduction

Deer browsing influences the establishment and composition of natural regeneration (Rooney et al., 2002; Danell et al., 2003; Husheer et al., 2003; Potvin et al., 2003; Barrett and Stiling, 2006; Long et al., 2007). Recruitment failure of tree species preferred by deer has important economic and ecological impacts (Côté et al., 2004) because of damage to economically valuable species and changes of natural succession pathways towards alternative states (Tremblay et al., 2006; Casabon and Pothier, in press). Moreover, chronic browsing on vegetation due to high deer densities may decrease habitat suitability in the long term (Tremblay et al., 2005) and could threaten indirectly the sustainability of deer population size because of a growing lack of resources (Caughley, 1970; Forsyth and Caley, 2006). In regions where sport hunting represents a major source of income, a decrease of deer densities may result in major economic impacts, especially in rural areas.

On Anticosti Island, sport hunting is the main source of income for inhabitants. Maintaining adequate deer densities is a socio-economic priority. However, the actual white-tailed deer densities ($\geq$20 deer/km^2) prevent the establishment of palatable tree species such as balsam fir (*Abies balsamea* (L.) Mill.) and deciduous species (Potvin et al., 2003; Casabon and Pothier, 2007; Tremblay et al., 2007). In addition, actual balsam fir stands are becoming old ($\geq$100 years) and their area decreases with time because of recruitment failure from the seedling bank. Hence, the decrease of balsam fir, the main winter forage for white-tailed deer (Lefort et al., 2007), could threaten the long-term viability of their population because of a lack of food. In this context, forest managers are facing trade-offs between maintaining suitable habitat for deer and limiting damage to vegetation, especially seedlings. Consequently, deer hunting and forest operations are used as wildlife management tools to restore balsam fir regeneration and to maintain habitat suitability for deer.

Some authors have suggested using large clearcuts with protection of advance regeneration to reduce browsing impact in the centre of those areas because the long distance from the forest edge entails a consequent increase in predation risk (Drolet, 1978; Welch et al., 1991). On Anticosti Island, this approach has failed to promote balsam fir regeneration, due to the absence of natural predators and high deer densities increasing the use of all

* Corresponding author at: Département des Sciences du Bois et de la Forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, Québec G1V 0A6, Canada. Tel.: +1 418 656 2131x2620; fax: +1 418 656 5262.
E-mail address: julien.beguin.1@ulaval.ca (J. Beguin).

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regenerated areas (Casabon and Pothier, 2007). One disadvantage of large clearcuts is that they limit seedling establishment in areas located beyond the effective distance of seed dispersal for many desirable species (Greene and Johnson, 1996). If advance regeneration, i.e. seedlings established before logging, is browsed in those areas, there will likely be a lack of seedlings. To avoid this problem, some form of tree retention harvesting could help to improve seedling establishment by reducing the distance between seed sources and seedbeds (Greene et al., 1999). It is also possible to enhance the receptivity of seedbeds, both by improving their quantity and quality through soil scarification (Jeglum, 1987). In addition, scarification after clearcutting may increase white birch (*Betula papyrifera* Marsh.) establishment (Perala and Alm, 1990; Prévost, 1997). This is important because white birch is high-quality winter forage for white-tailed deer (Crawford, 1982; Dumont et al., 2005). Some studies have pointed out that white-tailed deer fed more selectively in response to an increased abundance of high-quality foods (Murden and Risenhoover, 1993; Berteaux et al., 1998). If browsing is concentrated on preferred species, the pressure on balsam fir may be reduced and some individuals could grow beyond the reach of deer. However, few experimental studies have investigated the establishment success of natural regeneration after tree retention harvests in a deer overabundance context (e.g. Reimoser and Gossow, 1996). Such studies are particularly relevant since browsing damage on tree regeneration is increasing, or will increase in the near future, in several regions because of expansion of many deer populations (Rooney, 2001).

Among tree retention treatments, we can distinguish the shelterwood system, in which the seed cut results in a homogeneous canopy cover, from strip clearcutting, in which residual seed-trees are spatially restricted to unharvested strips. Both of these treatments can be effective in reducing the distance between seedbeds and seed sources when strip clearcutting are narrower than 100 m (Greene et al., 1999). Moreover, the shelterwood system can also promote balsam fir regeneration by taking advantage of its high shade tolerance and its ability to germinate on many substrates (Weetman and Algar, 1976; Baldwin, 1977; Frank, 1986; Hannah, 1988).

To investigate the effects of various silvicultural treatments on the establishment of natural regeneration under severe browsing pressure from deer, we set up two experiments in 1998 and 1999: a shelterwood experiment with different intensities of seed cutting and a strip clearcutting experiment with various strip widths, respectively. We use 7 years of data to test the following hypotheses: (1) abundant regeneration can be established by using a tree retention treatment and improving seedbed quality; (2) abundant regeneration of balsam fir will allow some individual seedlings to develop despite deer browsing; and (3) scarification will improve white birch establishment, reducing, in turn, browsing on balsam fir regeneration.

2. Material and methods

2.1. Study area

The experiments were conducted on Anticosti Island (7943 km^2), located in the Gulf of St. Lawrence, Québec, 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 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 (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) B.S.P.). 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 white-tailed deer population density is $\geq$20 individuals/km^2 (Potvin and Breton, 2005), but local density can be higher. The shelterwood and strip clearcutting experiments were conducted 10 km apart on two sites dominated by balsam fir stands (Table 1). The shelterwood and strip clearcutting experiments were established within a 25 ha and a 72 ha area, respectively. Both sites were characterized by mesic conditions with shallow podzols and good drainage. Before cutting, ground vegetation was dominated by feather mosses, mostly *Hylocomium splendens* (Hedw.) B.S.G. and *Pleurozium schreberi* (Brid.) Mitt.

2.2. Experimental designs

We conducted two separate multi-factorial experiments in these stands to investigate the impacts of various canopy removals on the establishment and development of tree species in interaction with deer browsing. First, we designed a two-cut shelterwood system using two different seed cutting intensities. A seed cut was applied in 1998, using the tree-length method to remove 25 or 40% of stand basal area. In addition, some areas were left unharvested as a control treatment (Table 1). The three levels of cutting intensity (0, 25, and 40%) were organised in a completely randomized design with four replicates (12 experimental units of 2500 m^2). We established a 400 m^2 main plot in the centre of each of these 12 experimental units. Within each main plot, we set up one fenced 4 m^2 sub-plot surrounded by a 1.5 m high fence and two unfenced 4 m^2 sub-plots. Sampling size was identical for the three intensities of seed cut: each level of intensity contained four fenced and eight unfenced plots. Accessible trails for machinery were left outside 400 m^2 main plots. Second, in 1999, we set up a strip clearcutting experiment (Table 1) using the tree-length method with three strip widths (15, 30 and 45 m) replicated four

Table 1
Stand characteristics (mean $\pm$ 1 S.D.) after shelterwood seed cutting and strip clearcutting (uncut strips) on Anticosti Island

Silvicultural treatment	Stand density (n/ha)	Stand basal area (m^2/ha)	% G fir	% G spruce	Stand mean height (m)
Seed cutting					
Control (0%)	1650 $\pm$ 477	40.0 $\pm$ 2.8	60 $\pm$ 12	38 $\pm$ 13	12.5 $\pm$ 1.4
25%	1406 $\pm$ 211	26.5 $\pm$ 3.1	58 $\pm$ 20	42 $\pm$ 19	12.1 $\pm$ 1.1
40%	1038 $\pm$ 113	17.5 $\pm$ 4.2	58 $\pm$ 15	40 $\pm$ 17	10.8 $\pm$ 1.4
Strip clearcutting					
15 m	1594 $\pm$ 230	39.3 $\pm$ 6.3	46 $\pm$ 10	54 $\pm$ 10	13.2 $\pm$ 0.8
30 m	1353 $\pm$ 323	36.3 $\pm$ 4.3	69 $\pm$ 10	30 $\pm$ 11	12.6 $\pm$ 1.0
45 m	1506 $\pm$ 393	41.7 $\pm$ 5.9	68 $\pm$ 16	30 $\pm$ 16	12.8 $\pm$ 0.7

Note: G corresponds to stand basal area (m^2/ha).

times in a completely randomized block design. After the cut, each 180-m-long strip was scarified using a Waddel disc trencher. Within each cut strip, unfenced regeneration sub-plots (4 m^2) were established 3 m apart along six transects perpendicular to the strip at 30, 50, 80, 100, 130 and 150 m along the strip length. Therefore, each transect within the 15 m strips contained five regeneration sub-plots, while in the 30 and 45 m strips, each transect contained 10 and 15 regeneration sub-plots, respectively. In addition, two fenced 4 m^2 sub-plots 10 m apart were established near the centre of each strip at a distance of 40 m along the strip length to evaluate the impact of deer browsing in each strip width. Since some fenced plots were damaged (25%) and browsing was apparent, we retained only 18 fenced plots for further analyses. Sampling size was thus composed of 6 fenced plots by strip width and 120, 240, and 360 unfenced plots in the 15, 30, and 45 m strip width, respectively. Each cut strip was surrounded by unharvested strips of equal width to reproduce an operational strip cut system, which would use only one strip width. Unlike the seed cutting experiment, no control was used in the analyses of the strip clearcutting experiment.

2.3. Data collection

In each experiment, regeneration surveys were conducted from July to August during which the number of stems and seedling height (in six classes: <5 cm; 5–30 cm; 31–60 cm; 61–100 cm; 101–200 cm; 201–300 cm) were recorded for each tree species. The dominant height of each species was assessed for every plot by retaining the mid-point of the tallest height class for each species. If a species was absent, its dominant height was zero. The seed cutting experiment was established in autumn 1998, and regeneration was surveyed immediately after cutting and 8 years later. The strip clearcutting experiment was established in autumn 1999, and regeneration was tallied 1, 2 and 7 years after cutting.

2.4. Statistical analyses

The treatment applications resulted in different mean seedling sizes and distributions among seed cutting intensities and strip widths immediately after treatment. To remove these biases, we subtracted the seedling density and dominant height values measured during the first survey after cutting from the values measured in subsequent years. Differences in seedling density and height of dominant seedlings were analysed according to a split-plot design with repeated measures in the case of strip clearcutting (Cochran and Cox, 1992). In the seed cutting analyses, seed cutting intensity (0, 25, and 40%) and the presence or absence of a fence were used as fixed factors, whereas replications in cutting treatments were used as random effects. In the strip clearcutting analyses, strip width (15, 30, and 45 m), presence or absence of a fence and year after cutting were used as fixed factors, while the blocks in interaction with fixed factors were used as random factors. All data were analysed using the MIXED procedure in the SAS system (Littell et al., 2006; SAS Institute, 2003). In both experiments, the small number of black spruce seedlings did not permit statistical analyses, so they were pooled with white spruce in the analyses.

For the strip clearcutting statistical analyses, we averaged the data from the regeneration plots per transect for a total of five unfenced and a maximum of two fenced experimental units (EU) for each replication of each strip width. In the seed cutting analyses, we averaged the data from the regeneration plots for a total of one EU in both the fenced and unfenced portions of each replication within which each of the seed cutting intensities was applied. For all tests, we checked the normality of residuals and homogeneity of variance assumptions and applied square root or natural logarithm transformations when needed. To take into account the temporal correlation between strip clearcutting surveys, we introduced nine different variance–covariance matrix structures into the models (variance components, compound symmetry, heterogeneous compound symmetry, spatial power, toeplitz, heterogeneous toeplitz, autoregressive (1), heterogeneous autoregressive (1) and unstructured). We selected the structure that minimized the Akaike Information Criterion (AIC). Means between treatments were compared using protected *a posteriori* orthogonal contrasts and we adjusted the level of significance (α-value) with the Bonferroni correction when the number of contrasts exceeded the number of degrees of freedom. Since retransformation did not give reliable estimates of standard error using smearing estimates (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. However, all statistical tests of mean comparisons were performed on transformed variables.

3. Results

3.1. Shelterwood seed cutting experiment

Immediately after treatment application, balsam fir density in fenced plots was 186 875, 94 375, and 57 500 seedlings/ha in controls, 25% seed cutting, and 40% seed cutting, respectively. For the same treatments, balsam fir density in unfenced plots was 70 312, 74 375, and 47 500 (data not shown). In all plots, seedlings were shorter than 20 cm and no deciduous species were present in both fenced and unfenced plots. Moreover, spruce density in fenced plots was 5625, 5625, and 9375 seedlings/ha in control plots, 25% seed cutting, and 40% seed cutting, respectively, compared to 938, 3125, and 4675 seedlings/ha in unfenced plots for the same treatments (data not shown).

The number of recruited seedlings and difference in height of dominant seedlings did not differ statistically among treatments for all species (Table 2). For balsam fir, the mean density of

Table 2
Analyses of variance (*p*-values, MIXED procedure, SAS) applied to the difference in seedling density (all height classes) and height of dominant seedlings (Hdom) between year 8 and just after shelterwood seed cutting for balsam fir, white birch, and spruce as a function of the seed cut intensity (0% or control, 25% and 40% of the basal area) and the presence or absence of a fence preventing deer browsing on Anticosti Island

Sources of variation	d.f./den	Balsam fir		White birch		Spruce	
		Density	Hdom	Density	Hdom[a]	Density	Hdom
Seed cutting intensity (*I*)	2/9	0.91	0.91	0.65	0.42	0.24	0.84
Fence (*F*)	1/9	0.17	0.15	0.26	0.16	0.50	0.15
Cutting intensity × fence ($I \times F$)	2/9	0.47	0.28	0.73	0.64	0.43	0.42

Note: d.f.: numerator degree of freedom; den: denominator degree of freedom.
[a] Analyses were conducted using square-root transformed data.

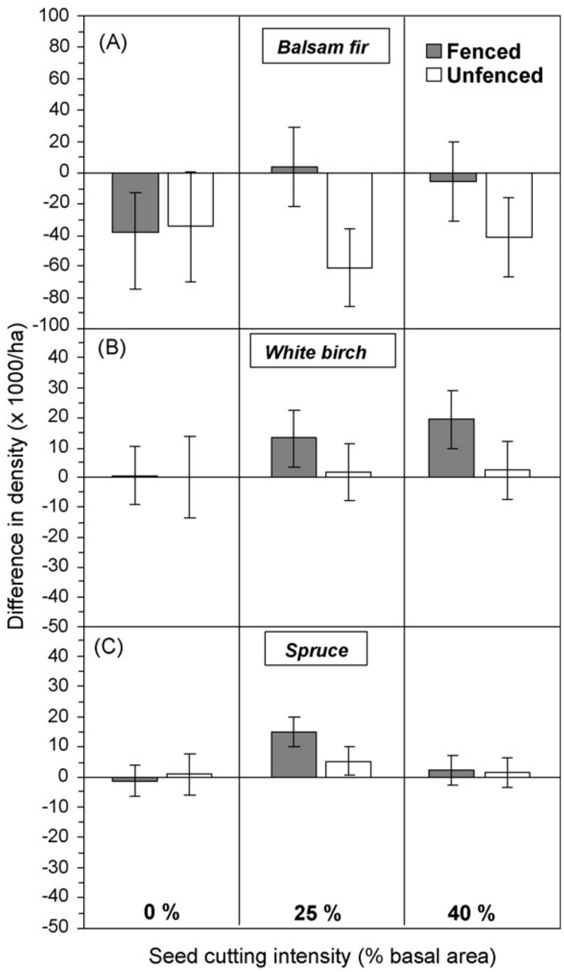

Fig. 1. Difference in seedling density ($1000\times$/ha) (mean $\pm$ 1 S.E.) between year 8 and immediately after shelterwood seed cutting as a function of seed cutting intensity and the presence or absence of a fence preventing deer browsing for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island.

seedlings in control plots decreased by about 35 000 seedlings/ha after 8 years in both fenced and unfenced areas. However, the number of recruited white birch seedlings in unfenced plots after 8 years tended to be lower than in fenced plots for both intensities of seed cut (Fig. 1A and B). Although not statistically significant,

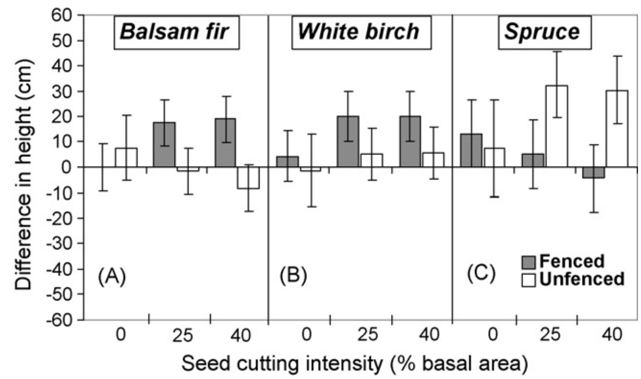

Fig. 2. Difference in height of dominant seedlings (mean $\pm$ 1 S.E.) during the first 8 years after shelterwood seed cutting as a function of seed cut intensity and presence or absence of a fence preventing deer browsing for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island.

differences in height of dominant balsam fir and white birch seedlings in fenced plots tended to be higher in areas in which seed cutting was applied than in the controls (Fig. 2A and B). For spruce, however, difference in height of dominant seedlings in both seed cut treatments tended to be higher in unfenced than in fenced plots (Fig. 2C).

3.2. Strip clearcutting experiment

One year after strip clearcutting, total balsam fir density ranged from 5570 to 7500 seedlings/ha in unfenced plots for all strip widths. In fenced plots, fir density was 14 120 seedlings/ha in the 30 m strips compared with less than 560 seedlings/ha in 15 and 45 m strips (data not shown). Two and seven years after cutting, no difference was detected among strip widths and between fenced and unfenced plots in the number of recruited fir seedlings (Table 3; Fig. 3A). In contrast, difference in height of dominant fir seedlings in fenced plots was significantly higher than in unfenced plots 7 years after cutting, whereas no differences were detected after 2 years (Table 3; Fig. 4A).

The number of recruited white birch seedlings was significantly higher in fenced than in unfenced plots 7 years after cutting (Table 3; Fig. 3B). Moreover, 7 years after cutting, difference in height of dominant white birch seedlings was higher in fenced than in unfenced plots (Table 3; Fig. 4B). No effect was detected 2 years after cutting (Table 3), at which time white birch density was

Table 3

Analyses of variance and orthogonal contrasts (p-values, MIXED procedure, SAS) applied to the number of recruited seedlings (density) and the difference in height of dominant seedlings (Hdom) 2 and 7 years after strip clearcutting for balsam fir, white birch, and spruce as a function of strip width (15, 30 and 45 m), presence (F_Y) or absence (F_N) of a fence preventing deer browsing, and year after cutting on Anticosti Island

Sources of variation	d.f./den	Balsam fir		White birch		Spruce	
		Density	Hdom[a]	Density[b]	Hdom[c]	Density[d]	Hdom[a]
Strip width (W)	2/6	0.68	0.13	0.50	0.59	0.26	0.22
Fence (F)	1/8	0.11	**<0.001**	0.07	**<0.001**	**0.040**	0.32
Width $\times$ fence ($W \times F$)	2/8	0.84	0.06	0.29	0.47	0.84	0.16
Year after cutting (Y)	1/151	0.16	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Width $\times$ year ($W \times Y$)	2/151	0.16	0.10	0.49	0.16	0.87	0.41
Fence $\times$ year ($F \times Y$)	1/151	0.53	**<0.001**	**0.042**	**<0.001**	0.27	0.49
$Y_2 \times (F_N$ vs. $F_Y)$*	1/151	–	0.62	0.99	0.36	–	–
$Y_7 \times (F_N$ vs. $F_Y)$*	1/151	–	**<0.001**	**0.004**	**<0.001**	–	–
Width $\times$ fence $\times$ year ($W \times F \times Y$)	2/151	0.22	0.06	0.24	0.06	0.83	0.56

Note: d.f.: numerator degrees of freedom; den: denominator degrees of freedom.

Analyses were conducted using $(y + 50)^{0.1}$ (a), $\ln(y + 6)$ (b), $(y + 50)^{0.2}$ (c), and $(y + 10)^{0.5}$ (d) transformed data.

* Bonferroni correction with a level of significance (α = 0.025).

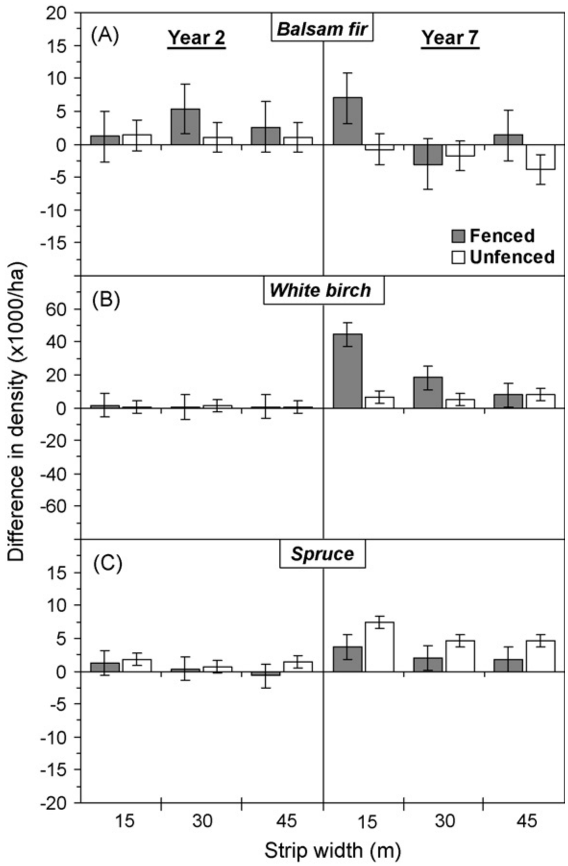

Fig. 3. Difference in seedling density (1000×/ha) (mean ± 1 S.E.) 2 and 7 years after strip clearcutting as a function of strip width and presence of a fence preventing deer browsing for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island. Difference was calculated by subtracting data 1 year after cutting from data at year 2 and year 7 after strip clearcutting.

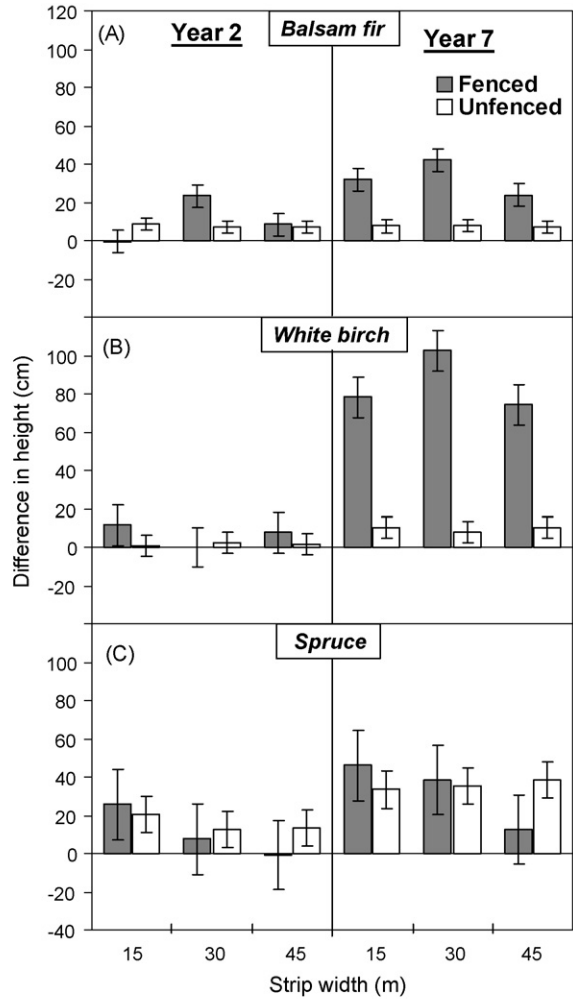

Fig. 4. Difference in height of dominant seedlings (mean ± 1 S.E.) as a function of strip width, presence of a fence preventing deer browsing and time after cutting for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island.

less than 2000 seedlings/ha in all experimental units (data not shown).

The number of spruce recruits increased with time after cutting (Table 3; Fig. 3C) and was significantly higher in unfenced than in fenced plots (Table 3; Fig. 3C). Seven years after cutting, height growth of dominant spruce averaged 32 and 36 cm in fenced and unfenced plots, respectively (Fig. 4C), and no differences were detected between fencing treatments nor among strip widths (Table 3). At that point in time, total spruce seedling density ranged from 7500 to 11 500 seedlings/ha in unfenced plots compared to less than 6000 seedlings/ha in fenced plots (data not shown).

4. Discussion

4.1. Shelterwood seed cutting

The number of recruited balsam fir seedlings 8 years after cutting was not influenced by the intensity of seed cutting, even in fenced plots that prevented deer browsing. Our hypothesis that partial removal of the canopy would produce abundant balsam fir regeneration was not supported by the results. This hypothesis was based on several experimental studies showing that seed cutting had a positive effect on balsam fir establishment (Weetman and Algar, 1976; Baldwin, 1977; Frank, 1986; Hannah, 1988).

The near absence of new balsam fir seedlings in fenced plots after seed cutting may be the result of low balsam fir seed availability, unfavourable seedbed conditions (Frank, 1990), desiccation (Kaufmann and Eckard, 1977; Thomas and Wein, 1984) and/or plant competition (Coates et al., 1994). We did not survey balsam fir seed availability, but it is unlikely that the reduced number of seed trees after seed cutting prevented adequate seed supply. Indeed, Raymond et al. (2000) found that seed cutting of 25% of the basal area in balsam fir stands did not affect seed availability, as compared with controls. Moreover, the quality and amount of adequate seedbeds are unlikely to have limited establishment of new germinants in our study because the ground was covered by a continuous carpet of feather mosses, which are known to be receptive seedbeds for balsam fir seed germination (Côté and Bélanger, 1991; McLaren and Janke, 1996; Duchesneau and Morin, 1999). In addition, germination and survival of young balsam fir were found to be highest under 40–79% canopy cover (McLaren and Janke, 1996), which corresponds to the removal of 25 and 40% of stand basal area in our study.

It is possible that the number of balsam fir seedlings before cutting was near carrying capacity so that new seedlings were compensated for by mortality of others and, consequently, little differences were observed in fenced plots. Finally, the apparent failure of balsam fir seedling establishment in fenced areas in which seed cutting was applied may be related to the limited number of treatment replications and/or of fenced sub-plots within each treatment. According to the regeneration development results of the seed cutting experiment, it seems that balsam fir and white birch can dominate the regeneration stratum in fenced areas whereas spruce will likely dominate the future stand if the stand is left unfenced.

4.2. Strip clearcutting

Strip widths of 15, 30 and 45 m had no significant effect on the number of recruited balsam fir seedlings and the height growth of dominant seedlings over time, irrespective of the presence of fences. Our hypothesis that the narrowest strips would promote balsam fir regeneration by reducing the distance between receptive seedbeds and seed trees was thus rejected. This hypothesis was based on several studies that showed the positive short-term response of black spruce regeneration after strip clearcutting (Ruel, 1989; Pominville and Ruel, 1995; Pothier, 2000), especially in narrow strips within which abundant establishment was related to increasing seed supply as compared with wider strips (Frisque and Vézina, 1977; Jeglum, 1987; Jeglum and Kennington, 1993). We expected a similar pattern for fir since seed dispersal distance is shorter for balsam fir than for black spruce (Viereck and Johnston, 1990) and also decreases proportionally with increasing distance of seed trees (Frank, 1990). Moreover, the strip widths used in our study were generally narrower than the effective distance of seed dispersal for balsam fir (25–60 m, Frank, 1990) and the maximum openings of 125–150 m recommended by Frank and Bjorkbom (1973).

The modest rate of balsam fir establishment in fenced plots may have been caused by the same factors mentioned above for seed cutting. Soil scarification applied in the cut strips should have promoted establishment of natural regeneration, as observed by Prévost (1996, 1997) and Hanssen et al. (2003). Indeed, scarification is known to improve soil properties such as moisture, temperature, and bulk density (Plamondon et al., 1980; Prévost, 1992; MacKenzie et al., 2005). Also, the protection against the drying effects of sun and wind afforded by the leave strips should have limited desiccation (Jeglum and Kennington, 1993).

Growth of herbaceous species was rapid after cutting, especially in fenced plots where ground vegetation was mainly composed of graminoids (e.g., *Cinna latifolia* (Trev.) Griseb, *Schizachne purpurascens* (Torr.) Swallen), ferns (e.g., *Pteridium aquilinum* (L.) Kuhn), raspberry (*Rubus idaeus* L.), fireweed (*Epilobium angustifolium* L.), northern bush-honeysuckle (*Diervilla lonicera* Mill.) and bunchberry (*Cornus canadensis* L.). The swift colonization by herbaceous plants could have prevented the development of new balsam fir seedlings by occupying available microsites and competing directly for resources. Indeed, from 1 to 9 years after clearcutting in Anticosti Island, percent cover of vegetation in fenced plots was roughly twice as high as in unfenced plots (Casabon and Pothier, in press). Moreover, the time elapsed to reach 100% of ground cover was 3 years in fenced plots compared to 8 years in unfenced plots. This vegetation can create a barrier to the establishment of seedlings (Coates et al., 1994) and may explain the lower regeneration densities found on rich sites (Harvey and Bergeron, 1989). Moreover, soil preparation may increase the aggressiveness of plant competition (Durand et al., 1998) and stimulate the germination of invasive competitors (Prévost, 1992). This may have reduced the window of opportunity for establishment of balsam fir regeneration.

Given the low establishment in all cut strips, it seems that strip clearcutting failed to produce unbrowsed balsam fir seedlings, even when more palatable white birch seedlings were present. Indeed, deer browsing kept both balsam fir and white birch seedlings from reaching 10 cm in height (Fig. 4A and B). The availability of high-quality forage was found to affect the selection patterns and foraging behaviour of white-tailed deer (Murden and Risenhoover, 1993; Berteaux et al., 1998; Coulombe et al., 2008). In our study, it is possible that the limited establishment of new white birch seedlings together with high deer densities prevented any significant changes in diet selection by white-tailed deer.

Unlike balsam fir and white birch, height growth of dominant spruce seedlings was not affected by deer browsing (Fig. 4C) and the number of spruce seedlings was even higher in unfenced areas (Fig. 3C). In unfenced plots, deer browsing prevented development of white birch and other palatable plant species. By removing these species, deer browsing maintained the availability of microsites for unpalatable species such as white and black spruce. Although graminoids, Canada thistle (*Cirsium arvense* (L.) Scop.) and ferns were advantaged by deer browsing, they might have been not sufficiently abundant to limit establishment of spruce. Therefore, we expect that spruce will dominate the cutover areas in association with unpreferred species such as graminoids, Canada thistle and ferns. These results suggest that there will be a conversion from fir- to spruce-dominated stands as long as deer density remains high (Potvin et al., 2003), even if residual strips are left after cutting as seed sources. Conversion of tree species composition of this sort as a result of severe deer browsing has been observed in clearcuts on Anticosti Island (Casabon and Pothier, 2007; Tremblay et al., 2007) as well as on Isle Royale (McInnes et al., 1992) and in Newfoundland (Thompson and Curran, 1993).

4.3. Comparison between silvicultural treatments

Silvicultural treatments applied in the balsam fir forest–white-tailed deer system of Anticosti Island showed that deer browsing strongly affected height growth of balsam fir seedlings which stagnated over time in unfenced plots in all treatments (Table 4). In addition, the treatments intended to improve natural seeding and seedbed quality did not perform better than the standard clearcutting system with protection of advance regeneration. In the spruce-fir-beech forest–roe deer (*Capreolus capreolus*) system in Austria, Reimoser and Gossow (1996) reported that the predisposition of the regeneration layer to browsing damages was higher in small clearcuts than in partial cuts when roe deer densities ranged from 7 to 13 deer/km^2. They reported similar results comparing clearcuts with shelterwoods and strip-clearcuttings from several areas in Austria, Liechtenstein, and Switzerland for red deer (*Cervus elaphus*), roe deer, and chamois (*Rupicapra rupicapra*). They argued that 'closer to nature' silvicultural treatments can reduce the risk of browsing damage both by decreasing habitat attraction for ungulates and favouring abundant regeneration establishment. In our study, we did not find such patterns for balsam fir and white birch. This suggests that if interactions between food-independent factors (e.g. edge effects, thermal and hiding cover, climate, terrain conditions) and food supply may play an important role in the extent of browsing damages at low and medium deer densities, they become secondary when deer densities are high. Indeed, at current deer density on Anticosti Island ($\geq$20 deer/km^2), none of the silvicultural treatments produced the expected abundant establishment of balsam fir and white birch regeneration. Instead, spruce seedlings tended to take advantage of severe deer browsing on palatable species to dominate tree regeneration, irrespective of the size of canopy openings.

Our results suggest that spruce-dominated stands will succeed the present fir stands. The stand conversion will probably be associated with significant changes in the ecosystem dynamics of Anticosti Island. Among these changes, minimal availability of balsam fir, the main foraging resource in winter (Sauvé and Côté, 2007; Lefort et al., 2007), could threaten the sustainability of the deer population over the near-future. On the other hand, self-

Table 4
Average density and height of balsam fir regeneration in fenced and unfenced areas 7–9 years after various silvicultural treatments on Anticosti Island

Silvicultural treatment	From 7 to 9 years after cutting			
	Seedling density (ha^{-1})		Height (cm)	
	Fenced	Unfenced	Fenced	Unfenced
Gradient of canopy opening				
(1) Control (untreated)	148 750	35 625	18	13
(2) Shelterwood seed cutting (25% of b.a.)	98 125	21 875	31	16
(3) Shelterwood seed cutting (40% of b.a.)	51 875	11 875	36	9
(4) Strip clearcutting (width of 15 m)	11 500	6 081	32	11
(5) Strip clearcutting (width of 30 m)	17 500	4 915	42	12
(6) Strip clearcutting (width of 45 m)	2 917	3 200	24	11
(7) Group seed-tree cutting (no scarification)	20 105	4 850	74	13
(8) Group seed-tree cutting (scarification l×)	9 808	1 905	64	7
(9) Group seed-tree cutting (scarification 2×)	2 111	2 143	21	6
(10) Large clearcuts (CLAAG)	25 000	2 000	35	5

Note: items 7, 8, 9: refer to Beguin et al. (submitted for publication); item 10: refer to Casabon and Pothier (2007).

regulation of the deer population as a function of resource availability would have major economic consequences, since hunting activities represent the main source of income for the island's inhabitants. Recently, scientists and managers have implemented integrated forest management strategies using sport hunting and large enclosures to both maintain the ecological processes and components present in the ecosystem prior to the introduction of deer, and sustain development of the island's economy in the long-term.

5. Conclusion

Our results suggest that managers should lower the white-tailed deer population on Anticosti Island if their goal is to sustain the present forest composition. In an integrated forest management system where deer densities are reduced by hunting in large fenced enclosures, it is possible to apply silvicultural treatments that will optimize fir establishment and development. If there is a lack of balsam fir advance regeneration, seed cutting may be the best silvicultural treatment, but if advance regeneration is abundant, clearcutting with careful logging around advance growth can be encouraged.

The deer density at which these silvicultural treatments can produce adequate balsam fir regeneration is still unknown. According to results from a controlled browsing experiment, it seems that balsam fir regeneration on Anticosti Island can be successful after clear-cutting at densities $\leq$15 deer/km^2 (Tremblay et al., 2007). However, it may be possible to use silvicultural treatments that improve natural seeding to increase this threshold to deer densities ranging, for instance, from 15 to 18 deer/km^2. Indeed, successive seeding from seed sources may increase establishment of balsam fir (Hughes and Bechtel, 1997) and white birch (Prévost, 1997) regeneration. This could allow an adequate density of balsam fir seedlings to be spared by browsing, while at the same time, the additional food supply could make it possible to support deer densities higher than 15 deer/km^2. To explore the relationship between the amount of food supply and extent of damages caused by browsing, future research should involve development of large-scale experiments in which white-tailed deer densities are controlled at various levels (e.g., from 15 to 18 deer/km^2), together with the use of various silvicultural treatments.

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