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L'ÉTABLISSEMENT DU SAPIN BAUMIER EN PRÉSENCE DE DENSITÉS ÉLEVÉES DE CERF DE VIRGINIE À LA SUITE DE COUPES DE RÉGÉNÉRATION SUR L'ÎLE D'ANTICOSTI (QUÉBEC).

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Résumé

Les objectifs de ce projet étaient d'évaluer les effets de différents traitements sylvicoles sur l'établissement de la régénération naturelle en sapin baumier (*Abies balsamea* (L.) Mill.) qui est la cible d'un broutement intense de la part du cerf de Virginie (*Odocoileus virginianus* Zimmermann). Nos résultats montrent que l'utilisation de la coupe progressive d'ensemencement, de la coupe à blanc par bandes avec scarifiage et de la coupe avec réserve d'îlots semenciers avec scarifiage n'a pas permis l'établissement d'une banque suffisante de semis de sapin non broutés capable de succéder aux peuplements actuels. Toutefois, la coupe par bandes et la coupe avec réserve d'îlots semenciers, chacune jumelée avec une préparation de terrain, ont stimulé l'établissement du bouleau à papier (*Betula papyrifera* Marsh.), mais le broutement du cerf a prohibé sa croissance en hauteur, tout comme celle du sapin. Aucun de ces traitements sylvicoles n'apparaît donc approprié pour reconstituer les sapinières de l'île d'Anticosti en présence de densités de cerf aussi élevées.

Abstract

This project aims at evaluating the effects of several silvicultural treatments on the establishment of balsam fir (*Abies balsamea* (L.) Mill.) regeneration under severe white-tailed deer (*Odocoileus virginianus* Zimmermann) browsing. Our results show that the use of shelterwood seed cutting, strip clear-cutting with scarification and group seed-tree cutting with scarification did not allow the establishment of a sufficient unbrowsed balsam fir seedling bank to succeed to actual stands. However, strip clear-cutting and group seed-tree cutting together with scarification favoured the establishment of white birch (*Betula papyrifera* Marsh.) seedlings but deer browsing prevented their height growth, as for balsam fir. Therefore, none of these treatments will allow actual balsam fir stands to be regenerated as long as deer densities are not significantly lowered.

Avant-propos

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Introduction générale

L'île d'Anticosti abrite une importante population de cerf de Virginie dont la densité estimée est supérieure à 15 cerfs/ km² (Potvin et Breton, 2005) et peut atteindre plus de 30 cerfs/ km² localement. À de telles densités, la pression de broutement qu'exercent les cerfs sur la régénération naturelle en sapin empêche actuellement le renouvellement des vieilles sapinières (Tremblay et al., 2007, Casabon et Pothier, 2007). Sous ce type de couvert ou après la coupe, le sapin, qui est habituellement l'espèce ligneuse dominante dans la strate de régénération, laisse progressivement sa place au profit de l'épinette blanche (*Picea glauca* (Moench) Voss) et de l'épinette noire (*Picea mariana* (Mill.) B.S.P.), qui sont, elles-mêmes, peu broutées par le cerf de Virginie (Potvin et al., 2003). À la suite du broutement sélectif du cerf de Virginie, on assiste donc à une conversion des sapinières actuelles en pessières et ce, déjà depuis les années 1930 (Potvin et al., 2003). Cette transformation de la composition des peuplements soulève plusieurs enjeux pour les gestionnaires forestiers. D'une part, il y a une volonté de l'ensemble des acteurs pour conserver une densité de population de cerf compatible avec les activités de chasse automnale, qui, soulignons-le, constituent la cheville du développement économique local. D'autre part, pour soutenir des densités élevées de cerf, il est indispensable de maintenir des habitats qui permettent au cerf de satisfaire ses besoins biologiques, qui sont notamment l'accès à une nourriture suffisante et la quantité de couvert d'abri pour faire face aux stress environnementaux. Dans ce contexte, le développement de stratégies de gestion qui permettent le renouvellement des sapinières constitue l'objectif prioritaire pour les gestionnaires puisque ces peuplements fournissent l'essentiel de la nourriture hivernale aux cerfs (Sauvé et Côté, 2007) et servent de couvert d'abri principal durant l'hiver (Lefort et al., 2007).

Dans d'autres régions, les gestionnaires forestiers ont essayé différentes approches pour limiter les impacts du broutement causés par les cervidés sur le développement de la régénération forestière. Parmi ces approches, plusieurs études ont montré que le type de traitements sylvicoles influençait l'étendue des dommages causés par les cervidés en contrôlant la distribution spatiale et temporelle des ressources alimentaires (Reimoser et Gossow, 1996; Partl et al., 2002). En Autriche, Reimoser et Gossow (1996) ont observé que la régénération forestière avait une plus faible prédisposition aux dommages causés par le broutement des cervidés après l'application de traitements sylvicoles favorisant l'établissement d'une régénération naturelle abondante et diversifiée (ex : coupes progressives irrégulières) qu'après des coupes à blanc de petite superficie accompagnées d'une plantation monospécifique. Par ailleurs, l'utilisation de grandes coupes à blanc a été suggérée pour réduire les impacts du broutement sur la régénération préétablie au centre de celles-ci à cause de la longue distance que les cerfs ont à parcourir par rapport à la lisière boisée et de l'augmentation du risque de prédation qui y est associé (Drolet, 1978; Welch et al., 1991). Toutefois, sur l'île d'Anticosti, cette dernière approche s'est avérée inefficace pour régénérer adéquatement ces zones en sapin baumier. L'absence de prédateurs et la rareté des ressources alimentaires encouragent probablement les cerfs à utiliser toutes les zones régénérées, sans égard à la distance par rapport à la lisière boisée (Casabon et Pothier, 2007). Néanmoins, il est possible que certains traitements sylvicoles favorisent l'établissement d'une régénération naturelle abondante en sapin et en essences compagnes consommées par le cerf et permettent, le cas échéant, la croissance en hauteur d'un nombre adéquat de semis de sapin malgré le broutement sévère localisé sur une fraction de la banque de semis.

Selon l'autoécologie des essences forestières, la structure et la composition des peuplements et les politiques forestières locales, les forestiers ont à leur disposition une série d'outils sylvicoles capables d'influencer les conditions micro-environnementales du sous-bois et de favoriser ainsi l'établissement de la régénération naturelle. Il s'agit notamment des coupes de jardinage par pied d'arbre, des coupes progressives, des coupes de jardinage par groupe, des coupes à blanc par bandes, des coupes à blanc de petite superficie, des coupes avec réserve d'îlots semenciers ou de semenciers individuels. Parallèlement, une préparation de terrain peut aider à maîtriser le développement de la végétation compétitrice et améliorer la qualité du lit de germination ainsi que l'établissement des jeunes semis (Smith et al., 1997).

Nous avons donc expérimenté la capacité de plusieurs traitements sylvicoles à stimuler l'établissement du sapin. Nous avons émis l'hypothèse que l'utilisation de traitements sylvicoles, qui favorisent à la fois la disponibilité en semences de sapin et la germination de celles-ci, permettent l'établissement d'une banque de semis abondants. Par la suite, nous avons formulé l'hypothèse que malgré l'impact du broutement du cerf sur une fraction de cette banque de semis, une quantité suffisante de semis non broutés serait en mesure d'atteindre le stade du gaulis et d'assurer le renouvellement des sapinières étudiées, puisqu'ils seraient alors hors de portée du cerf. Pour tester ces hypothèses, nous avons étudié l'établissement à moyen terme du sapin et des essences compagnes dans un réseau de placettes clôturées et non clôturées situé dans des sapinières matures soumises à trois traitements sylvicoles différents : une coupe avec réserve d'îlots semenciers avec différentes préparations de terrain (pas de scarifiage, un passage du scarificateur et deux passages du scarificateur), une coupe à blanc par bandes avec un scarifiage et une coupe progressive d'ensemencement sans scarifiage. Le premier chapitre de ce mémoire traite des résultats obtenus après la coupe avec réserve d'îlots semenciers alors que le deuxième chapitre contient les résultats sur la coupe progressive d'ensemencement et la coupe à blanc par bandes.

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

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 pressure 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 high herbivory context. Consequently, we hypothesized that using group seed-tree cutting in conjunction with soil scarification might create favourable conditions for improving establishment of balsam fir regeneration. In 1998 and 1999, we set up three different sizes of circular forest groups (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 (Québec, Canada). Moreover, we used a network of fenced and unfenced regeneration plots to evaluate the impact of deer browsing. The results showed that, up to seven years after harvest, group seed-tree cutting did not improve conifer species establishment. Scarification negatively impacted the abundance of conifer species during the entire study period, while white birch (*Betula papyrifera* Marsh.) density was significantly higher in areas scarified twice than in unscarified areas. Overall, the development of palatable tree species appears unlikely at deer density >20 individuals/km² locally.

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 différent types de préparation de terrain, pour améliorer les conditions d'établissement du sapin baumier. En 1998 et 1999, nous avons installé trois tailles d'îlots semenciers (40, 60 et 80 m) 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 des cerfs. Sept ans après la coupe, les résultats ont montré que la coupe avec réserve d'îlots semenciers n'avait pas amélioré l'établissement des conifères. Le scarifiage a négativement influencé l'abondance des conifères durant toute la période d'étude mais a permis, par contre, d'augmenter significativement la densité de bouleau à papier (*Betula papyrifera* Marsh.). Toutefois, le développement des essences consommées par le cerf apparaît compromis à des densités locales >20 individus/km².

1.1. 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 (Risenhoover and Maass 1987). However, a number of deer populations in various regions have increased during the last few decades (Gill 1990; Rooney 2001), resulting in high local densities that can affect maintenance of many ecosystem components. Direct impacts of deer browsing have 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 as the main cause of forest 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 selective browsing include the direct killing of seedlings of preferred species, the reduction of seedling growth, or the introduction of an apparent advantage for herbaceous plant or tree species that are tolerant of browsing (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 a context of cervid overabundance, testing the use of silvicultural methods to reduce the extent of 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 were introduced to Anticosti Island about a century ago. During the first four decades following introduction, deer populations had increased to such a point that they limited the development of palatable regeneration, primarily the deciduous species. 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 activities, the main economic activity on the

Island. Indeed, the increased presence of unpalatable species could negatively impact deer population levels, which could decline in the near-future as foraging resources availability become scarce.

On Anticosti Island, the use of large clearcuts with protection of balsam fir advance regeneration did not mitigate deer browsing because nearly all palatable regeneration was severely browsed, irrespective of the distance to forest edge (Casabon and Pothier 2007). However, it is possible that some forms of tree retention treatments may create abundant regeneration of several palatable tree species and allow balsam fir seedlings to develop beyond the reach of deer. Abundant regeneration can be achieved by improving seed supply, the amount and distribution of the receptive seedbed, and 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 seed source (Greene and al. 1999). In addition, scarification may create a large number of receptive seedbeds for germination by improving soil properties such as soil moisture, soil temperature, bulk density and hydraulic regime (Plamondon et al. 1980; Prévost 1992; MacKenzie et al. 2005). However, little is known about the effect of scarification on balsam fir establishment, especially in a high herbivory context. Scarification was found to improve white birch (*Betula papyrifera* Marsh.) establishment (Perala and Alm 1990; Prévost 1997), which develops well after clearcutting (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 could feed on preferred species and decrease its pressure on less preferred species such as balsam fir, enabling some individuals to grow beyond the reach of deer.

The main objective of this study was to evaluate the efficiency of group seed-tree cutting at increasing the amount of dispersed seeds and established seedlings over the adjacent clearcut 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 high herbivory context. Our research hypotheses are that: *i*) the presence of a residual group of seed-trees combined with soil scarification allows production of abundant balsam fir regeneration, *ii*) some balsam fir seedlings may escape from deer browsing and be recruited to the sapling stage, and *iii*) scarification improves white birch establishment, altering, in turn, the foraging strategy of white tailed-deer towards the reduced use of balsam fir regeneration.

1.2. Material and Methods

1.2.1. Study area

The experiment was carried out on Anticosti Island (7943 km^2) 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 usually 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 (*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 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, each dominated by balsam fir (Table 1).

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

Seed-tree group diameter (m)	Stand density (stems/ ha)	Stand basal area (m²/ha)	% G Balsam fir	% G White spruce	Stand mean height (m)
40	2296 ± 690	40.7 ± 7.9	64 ± 21	25 ± 23	13.0 ± 1.5
60	2500 ± 696	41.2 ± 6.7	57 ± 25	25 ± 17	13.0 ± 1.1
80	2364 ± 938	38.4 ± 4.8	63 ± 15	34 ± 28	13.1 ± 1.5
Mean	2387 ± 748	41.0 ± 6.3	61 ± 20	28 ± 22	13.1 ± 1.1

Note: G corresponds to stand basal area (m²/ha)

Both sites were characterized by mesic conditions with shallow podzols and efficient drainage. Prior to cutting, ground vegetation was dominated by feather mosses, predominately *Hylocomium splendens* (Hedw.) B.S.G. and *Pleurozium schreberi* (Brid.) Mitt.

1.2.2. Experimental design

Two sites, 10 km apart, were harvested by the tree-length method in the fall of 1998 (Site 1) and 1999 (Site 2). In an effort to provide a seed supply for balsam fir natural regeneration, circular groups of trees were left unharvested. Each site contained three different seed-tree group diameters (40, 60 and 80 m) in a completely randomized design with three and four replications in Sites 1 and 2, respectively (Figure 1).

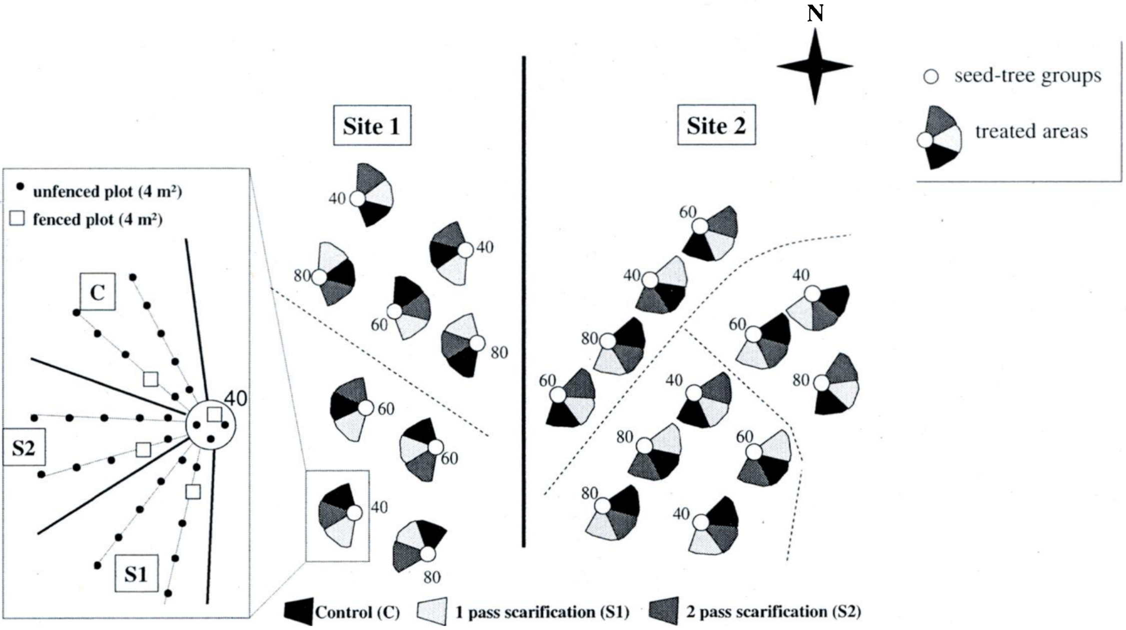

Figure 1. Experimental design showing the disposition of the 40-, 60-, and 80-m diameter seed-tree groups and the location of scarified areas within the two sites on Anticosti Island. The diagram on the left-hand side shows the organization of sampling plots in two transects by scarification level from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

The remaining seed-tree groups were at least 200 m apart from each other. In addition, white birch seed-trees were not harvested (density ≈ 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 twenty-one groups of trees. Three scarification levels were randomly applied around each group: a control (C) which was left undisturbed, a single-pass scarification (S1) and a double-pass scarification (S2) with the second pass perpendicular to the first. Each treatment was applied to a pie-slice shaped sub-plot covering a 60° angle from the centre of the seed-tree group and a distance of 100 m from the edge of the group (Figure 1). Within each sub-plot, ten circular regeneration sub-sub-plots (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-sub-plots 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.

1.2.3. 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 stems and seedling height (in six classes: <5 cm; 5–30 cm; 31–60 cm; 61–100 cm; 101–200 cm; 201–300 cm) for each tree species. In 2006, we also recorded herbaceous vegetation cover at the species level, except for graminoids, ferns and mosses where we restricted our classification to the family level. In order to evaluate the possible effects of competitive plant species on tree species establishment and height growth, we identified taxa that could compete directly with seedlings for light and soil nutrients based on their percent cover. There were five such species or taxon groups: graminoids, ferns, Canada thistle (*Cirsium arvense* (L.) Scop.), fireweed (*Epilobium angustifolium* L.), and raspberry (*Rubus idaeus* L.). We compared surveys conducted 1, 2, and 7 years after cutting. In the following paragraphs, year seven after cutting refers to both year seven for Site 1 and year eight for Site 2.

1.2.4. Statistical analyses

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

(Cochran and Cox 1992). Variation in plant cover was analysed as a split-plot but with a single measurement seven years after cutting. Seedling density was estimated according to seed-tree group dimension, scarification levels, presence of 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. Dimension of seed-tree groups, level of scarification, distance to edge, presence of 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 (Littell et al. 2006; SAS Institute 2003). The small number of black spruce seedlings did not permit reliable statistical analysis, so they were pooled with white spruce seedlings for the analyses. Seedling density was evaluated from regeneration sub-sub-plots (fenced vs. unfenced) located 30 meters 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 of all unfenced sampling plots within each pie-slice shaped area. We also estimated the dominant height in each fenced plot. To test the effect of distance to edge on regeneration establishment, we removed the confounding effect of advance regeneration present after cutting by subtracting the values of seedling density measured during the first survey after cutting from values measured in subsequent years. Moreover, we retained only unfenced plots in this analysis since fenced plots were restricted to 30 m from the edge. For all tests, we checked the normality of residuals and homogeneity of variance assumptions 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 the Akaike Information Criterion (AIC) (Littell et al. 2006). We removed seven exclosures (11%) from the analyses because they were damaged and browsing of vegetation inside 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 retransformation 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.

1.3. Results

1.3.1. Effects of group seed-tree 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).

Table 2. Analyses of variance with repeated measures (MIXED Procedure, SAS, p-values), using plots located 30 m from the edge, for seedling density (all height classes) of balsam fir, spruce, and white birch as a function of diameter of seed-tree groups (D), intensity of scarification (S), presence or absence of a fence preventing deer browsing (F) and year after cutting (Y) on Anticosti Island.

Sources of variation	d.f./den	Balsam fir [a]	Spruce [a]	White birch [a]
Dimension of groups (D)	2/18	0.20	0.14	0.80
Scarification (S)	2/36	**<0.001**	**<0.001**	0.11
Dimension x Scarification (D x S)	4/36	0.12	0.82	0.57
Fence (F)	1/46	**0.004**	0.21	0.18
Dimension x Fence (D x F)	2/46	0.13	0.08	0.15
Scarification x Fence (S x F)	2/46	0.11	0.70	0.76
Dimension x Scarification x Fence (D x S x F)	4/46	0.77	0.45	0.42
Year after cutting (Y)	2/200	**<0.001**	**<0.001**	**<0.001**
Dimension x Year (D x Y)	4/200	0.14	**0.042**	0.89
Scarification x Year (S x Y)	4/200	**<0.001**	0.23	**0.019**
Dimension x Scarification x Year (D x S x Y)	8/200	0.17	0.40	0.79
Fence x Year (F x Y)	2/200	0.13	0.35	**0.048**
Dimension x Fence x Year (D x F x Y)	4/200	0.39	0.75	0.37
Scarification x Fence x Year (S x F x Y)	4/200	**0.018**	**0.040**	0.73
Dimension x Scarif. x Fence x Year (D x S x F x Y)	8/200	0.59	0.87	0.67

Note: - values in bold character indicate significant effects (α =0.05)

- d.f.: numerator degree of freedom; den: denominator degree of freedom

[a] analyses were conducted using square-root transformed data

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, one 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 damaged a high proportion of the advance regeneration. Moreover, the negative impact of soil scarification persisted throughout the study (Fig. 2A).

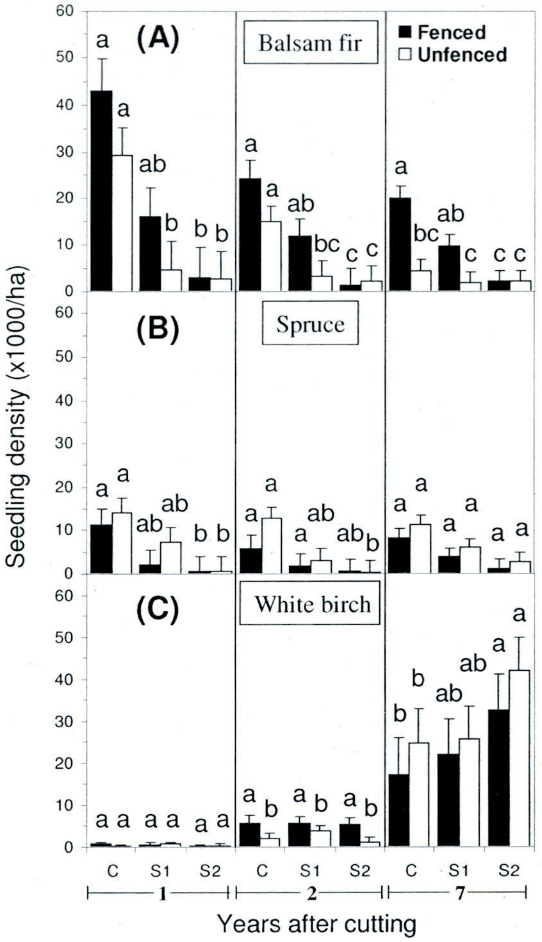

Figure 2. Seedling density (MEANS ± SE), using plots located 30 m from the edge, for (A) balsam fir, (B) spruce, and (C) white birch as a function of scarification intensity (C = control, S1 = single-pass scarification, S2 = double-pass scarification), presence or absence of a fence preventing deer browsing (F) and years after cutting on Anticosti Island. For each species and within each year after cutting, different letters indicate significant differences according to least square means comparisons corrected with the Bonferroni method.

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, damaged 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, seven years after cutting, we did not detect any effect of deer browsing on spruce density within any level of scarification (Fig. 2B). Instead, density of spruce seedlings 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 smallest seed-tree groups (40 m in diameter) than around larger tree groups.

In contrast with coniferous species, the impact of deer browsing on white birch seedlings was independent of soil scarification intensity throughout the study (Table 2). Two years after cutting, white birch density was relatively low but 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 seven years after cutting, white birch density was higher in areas scarified twice than in unscarified areas (Fig. 2C). Also, while not significant, birch density tended to be higher in areas scarified twice than in areas scarified once (Fig. 2C).

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

The effect of deer browsing on height of dominant balsam fir seedlings varied as a function of time after cutting (Table 3).

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

Sources of variation	d.f./den	Balsam fir [a]	Spruce [b]	White birch [a]
Scarification (S)	2/40	**<0.001**	**<0.001**	0.56
Fence (F)	1/52	**<0.001**	0.19	**<0.001**
Scarification x Fence (S x F)	2/52	**0.004**	0.32	0.80
Year after cutting (Y)	2/224	**<0.001**	**<0.001**	**<0.001**
Scarification x Year (S x Y)	4/224	0.07	0.22	0.52
Fence x Year (F x Y)	2/224	**<0.001**	0.75	**<0.001**
Scarif. x Fence x Year (S x F x Y)	4/224	0.07	0.98	0.65

Note: - values in bold character indicate significant effects (α =0.05)

- analyses were conducted using square-root ([a]) and $y^{0.7}$ ([b]) transformed data

- d.f.: numerator degree of freedom; den: denominator degree of freedom

Two years after cutting, height of dominant fir seedlings was less than 20 cm both in fenced and unfenced plots (Fig. 3A). Seven years after cutting, however, height of dominant fir seedlings was significantly higher 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 in areas scarified twice, no difference was detected between fenced and unfenced plots (Fig. 3A).

Height of dominant spruce seedlings was not statistically influenced by deer browsing (Table 3, Fig. 3B). However, spruce seedlings were taller in unscarified than in scarified areas and tended to be higher in areas scarified once rather than twice (Fig. 3B).

Height of dominant white birch seedlings was influenced by deer browsing in an interaction with time after cutting (Table 3). Deer browsing began to affect dominant height of white birch seedlings in the second year after cutting and this increased seven years after cutting (Fig. 3C). We did not detect any effect of scarification intensity on dominant height of white birch seedlings during the years after cutting.

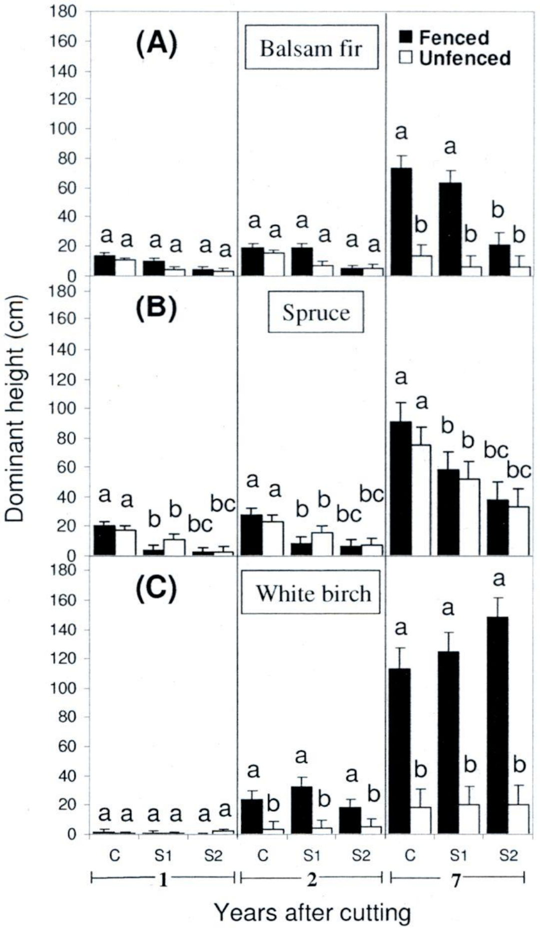

Figure 3. Dominant height (MEANS ± SE), using plots located 30 m from the edge, for (A) balsam fir, (B) spruce, and (C) white birch seedlings as a function of intensity of scarification (C = control, S1 = single-pass scarification, S2 = double-pass scarification), presence or absence of a fence preventing deer browsing and years after cutting on Anticosti Island. For each species and within each year after cutting, different letters indicate significant differences according to least square means comparisons corrected with the Bonferroni method.

1.3.3. 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.

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

Sources of variation	d.f./den	Balsam fir	Spruce
Edge distance (E)	4/181	0.19	**0.008**
Dimension x Edge (D x E)	8/181	0.24	0.35
Scarification x Edge (S x E)	8/181	**0.019**	0.11
Dimension x Scarif. x Edge (D x S x E)	16/181	0.47	0.40
Edge x Year (E x 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
Dimension x Edge x Year (D x E x Y)	8/607	0.97	0.12
Scarification x Edge x Year (S x E x Y)	8/607	0.98	0.99
Dimension x Scarif. X Edge x Year (D x S x E x Y)	16/607	0.99	0.55

Note: - only the effects related to distance to edge are shown

- d.f.: numerator degree of freedom; den: denominator degree of freedom

* significance level corrected with the Bonferroni method (α =0.05/5)=0.01

However, recruitment was negative in all scarification treatments, and there was no clear pattern of decrease in fir density with distance to edge. In unscarified areas, fir density varied from about 8 000 to 16 000 seedlings/ha depending on distance to edge, whereas in scarified areas, it ranged from about 2 000 to 4 000 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 larger than 50 m, no difference in seedling density was detected between years two and seven (Fig. 4). In contrast, scarification and size of seed-tree groups 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 cut-over (data not shown).

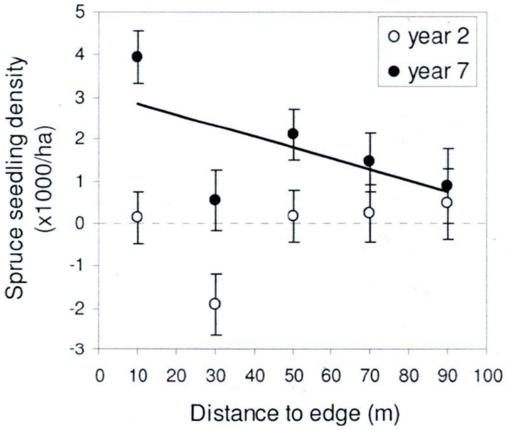

Figure 4. Number of newly established spruce seedlings (x 1000/ha) in unfenced plots (MEAN ± SE) two and seven years after group seed-tree cutting as a function of distance to edge (E) and year after cutting (Y) on Anticosti Island.

1.3.4. Effects of deer browsing on vegetation cover

Graminoid and fern cover was approximately two times higher in unfenced plots than in fenced plots (Figure 5), while percent cover of preferred browse species, such as raspberry (*Rubus idaeus* L.), and fireweed (*Epilobium angustifolium* L.), was about ten times higher in fenced plots than in unfenced plots (Figure 5). Percent cover of Canada thistle (*Cirsium arvense* (L.) Scop.) was not influenced by deer browsing ($p = 0.19$). The mean cumulative percent cover of these five taxa in unfenced and fenced plots was 74% and 85%, respectively.

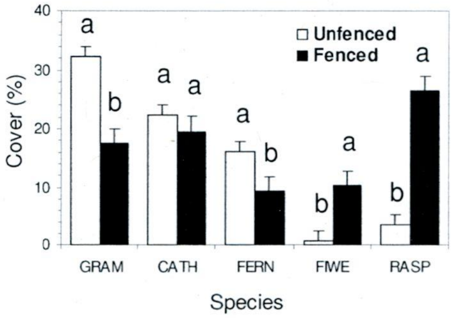

Figure 5. Percent cover (MEANS ± SE) of principal plant competitor species or taxon groups to tree seedlings as a function of presence or absence of a fence preventing deer browsing seven years after a seed-tree group cutting on Anticosti Island. (GRAM = Graminoids; CATH = Canada thistle; FERN = Ferns; FIWE = Fireweed; RASP = Raspberry). For each taxon, different letters indicate significant differences ($p < 0.05$) between fenced and unfenced plots.

1.4. Discussion

1.4.1. Establishment of regeneration in fenced areas

The establishment of natural regeneration after various soil preparations has been well studied in different forest ecosystems (Fredericksen and Pariona 2002; Karlsson et al. 2002; Yoshida et al. 2005), but little is known for balsam fir. In absence of deer browsing, increased establishment of natural regeneration following scarification has been found in different boreal regions (Putman and Zasada 1986; Prévost 1996 and 1997; Hanssen et al. 2003). Improvement of seedbed receptivity through major changes in soil properties such as soil temperature, bulk density, soil moisture, 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 receptive seedbeds following treatments appeared appropriate in our study, our results for regeneration dynamics differed from this general pattern in that coniferous establishment decreased with increasing scarification intensity during the study period (Fig. 2).

A low rate of conifer seedlings establishment in fenced plots could have occurred 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 plant competition (Smith et al. 1997). Although we did not survey seed rain, mast years for balsam fir usually occur at two to four year intervals (Frank 1990), whereas mast 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 eight-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 due to increasing plant competition, especially by white birch (Fig. 3C) and raspberry (Fig. 5). Finally, the failure of conifer seedling establishment at 30 m from the edge could also be a random event since it deviates from the trend illustrated in Fig. 4.

In contrast, white birch establishment increased with time after cutting and scarification intensity (Fig. 2C), supporting the results of Prévost (1997) who found an improvement of white birch establishment with increasing scarification intensity. The proximity of mature white birch trees left throughout the cut-over area probably favoured availability and abundance of seeds. As with balsam fir, seed crops for this species can range from two to four years (Perala and Alm 1990). Thus, the increase of birch density between years two and seven after cutting is likely due to the occurrence of a good seed crop during the intervening period.

1.4.2. Impact of deer browsing on regeneration establishment

In unfenced plots, white-tailed deer browsing prevented height growth of palatable species, such as balsam fir and white birch (Fig. 3A and 3C), in all scarification treatments. This result indicates that even when regeneration establishment is improved by scarification, the regeneration layer may be severely affected by browsing in forest systems where deer populations are overabundant. These results are consistent with those of other studies on Anticosti Island that have shown the significant impact of deer browsing on development of palatable tree regeneration (Potvin et al. 2003; Tremblay et al. 2007; Casabon and Pothier 2007 and 2008). We hypothesized that in the presence of abundant white birch regeneration, white-tailed deer would decrease browsing pressure on balsam fir, but this pattern was not observed. This hypothesis was based on several studies that 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. in press). 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 one and two after cutting, the density of white birch seedlings was low while balsam fir density was at its highest. In year seven, when white birch density reached 20 000 to 43 000 stems in unfenced areas, balsam fir density seemed to be at its lowest (Fig. 2A and 2C).

Although the height of white birch seedlings in unfenced plots was severely reduced by deer browsing (Fig. 3C), 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 *Betula pubescens* Ehrh.. Therefore, in unfenced plots, white birch seedlings were limited to a maximum of 20 cm in height and showed evidence of browsing, while in fenced plots, their dominant height reached more than 110 cm. Moreover, 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 neither decreased height of dominant seedlings nor the 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 establishment of spruces. Thus, if spruce stocking is adequate, we expect, over the medium-term, that white spruce will dominate the cut-over area in association with unpalatable species such as graminoids, Canada thistle, and ferns.

1.4.3. Group seed-tree dimension and distance to edge

Our results showed that the size of seed-tree groups and distance to edge did not improve the expected 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 non-linear effects in unscarified areas which likely originated from heterogeneous initial distribution of advance regeneration according to distance to edge. Our hypothesis that balsam fir would 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 similarly use all areas as Casabon and Pothier (2007) observed at the edge of large clearcuts.

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

1.5. Conclusion

Group seed-tree cutting with or without scarification could not regenerate balsam fir stands in the presence of white-tailed deer densities averaging 20 deer/km² locally. In contrast, white birch responded well to scarification treatments, 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 a high herbivory context. To be successful, however, our results indicate that these silvicultural treatments should be applied in combination with a reduction of deer density through intensive hunting and fencing of forest blocks. According to results from a control browsing experiment, it seems that balsam fir regeneration on Anticosti Island may be possible after clear-cutting at densities ≤15 deer/km² (Tremblay et al. 2007). However, it might be possible to use a silvicultural treatment that would increase the establishment of balsam fir and that could then increase the deer density threshold compatible with balsam fir recruitment. Such silvicultural treatments should reduce the distance between seed sources and seedbeds (e.g. narrow strip clearcutting) or maintain a continuous canopy over receptive seedbeds (e.g. shelterwood system). Because of the expansion of many deer populations in numerous regions, the response of palatable regeneration establishment after such silvicultural treatments needs to be tested in a context of deer overabundance.

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Using shelterwoods and strip clearcutting to promote natural regeneration under severe browsing pressure from white-tailed deer on Anticosti Island, Québec

Abstract

The use of silvicultural treatments creating large canopy openings was found to be inappropriate for regeneration of balsam fir (*Abies balsamea* (L.) Mill.) under severe 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. Results after eight years show that shelterwood seed cutting allows neither the establishment of new balsam fir seedlings nor the development of unbrowsed balsam fir seedlings. In the strip clearcutting, deer browsing halted height 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 not a promising option for promoting balsam fir establishment on Anticosti Island, as long as the deer population remains at such high densities.

Résumé

L'utilisation de coupes à blanc s'est avérée être inadéquate pour favoriser la régénération du sapin baumier (*Abies balsamea* (L.) Mill.) soumise à un broutement élevé de la part du cerf de Virginie (*Odocoileus virginianus* Zimmermann). Nous avons donc expérimenté deux autres traitements sylvicoles dans le but de favoriser l'établissement du sapin baumier. En 1998 et 1999, nous avons réalisé une coupe progressive d'ensemencement selon trois intensités de prélèvement (0, 25 et 40 % de la surface terrière) et une coupe à blanc par bandes avec scarifiage en utilisant trois largeurs de bande (15, 30 et 45 m) dans des sapinières matures. Pour chaque traitement, nous avons aussi installé un réseau de placettes clôturées et non clôturées pour évaluer l'effet du broutement. Huit ans après la coupe, les résultats montrent que la coupe progressive d'ensemencement n'a pas permis d'améliorer l'établissement du sapin baumier et le développement de semis non-broutés. Dans la coupe à blanc par bandes de toutes largeurs, le broutement du cerf a empêché la croissance en hauteur de la régénération de toutes les espèces comestibles par le cerf au profit d'espèces non-comestibles, dont l'épinette blanche (*Picea glauca* (Moench) Voss). Il apparaît donc que l'utilisation seule de traitements sylvicoles visant à stimuler l'établissement du sapin baumier sur l'île d'Anticosti ne constitue pas une avenue prometteuse aussi longtemps que les densités de cerf de Virginie ne seront pas significativement réduites.

2.1. Introduction

Managing forests for multiple purposes is essential to achieve sustainable forestry. In a context of deer overabundance, however, deer browsing can significantly influence the establishment and composition of natural regeneration as observed in several deer-forest systems (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 palatable species has important economic and ecological impacts (Côté et al., 2004) because of damages on economically valuable species and changes of natural succession pathways towards alternative states (Tremblay et al., 2006; Casabon and Pothier, in press). Moreover, a 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 sportive hunting represents a major source of income, a significant decrease of deer densities may result in major economic impacts, especially in rural areas.

On Anticosti Island, sportive hunting represents the main source of income for inhabitants. Maintaining adequate deer densities is a socio-economical 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 and their area decreases with the time because of recruitment failure from 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 as well as limiting damages on vegetation, especially on tree recruitment. Consequently, deer hunting and forest operations are used as wildlife management tools to maintain habitat suitability for deer compatible with recruitment of balsam fir.

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, likely due to the absence of natural predators and high deer densities increasing the use of all 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 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 improve seedling establishment by reducing the distance between seed sources and germination substrates (Greene and al., 1999). It is also possible to enhance the receptivity of germination substrates by improving seedbed quantity and quality through soil scarification (Jeglum, 1987). In addition, scarification may increase white birch (*Betula papyrifera* Marsh.) establishment (Perala and Alm, 1990; Prévost, 1997) that develops well after clearcutting (Harvey and Bergeron, 1989) and 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 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 damages on tree regeneration are 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 and 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 at the end of the 1990's: a strip clearcutting experiment with various strip widths and a shelterwood experiment with different intensities of seed cutting. We use seven 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.

2.2. Material and Methods

2.2.1. Study area

The experiments were conducted on Anticosti Island (7 943 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 usually 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 estimated at about 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 5). 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 efficient drainage. Before cutting, ground vegetation was dominated by feather mosses, mostly *Hylocomium splendens* (Hedw.) B.S.G. and *Pleurozium schreberi* (Brid.) Mitt.

Table 5. Stand characteristics (MEAN ± 1 SD) after shelterwood seed cutting and strip clearcutting (uncut strips) on Anticosti Island.

Silvicultural treatment	Stand density (n/ha)	Stand basal area (m²/ha)	% G fir	% G spruce	Stand mean height (m)
Seed cutting					
Control (0%)	1650±477	40.0±2.8	60±12	38±13	12.5±1.4
25%	1406±211	26.5±3.1	58±20	42±19	12.1±1.1
40%	1038±113	17.5±4.2	58±15	40±17	10.8±1.4
Strip clear-cutting					
15 m	1594±230	39.3±6.3	46±10	54±10	13.2±0.8
30 m	1353±323	36.3±4.3	69±10	30±11	12.6±1.0
45 m	1506±393	41.7±5.9	68±16	30±16	12.8±0.7

Note: G corresponds to stand basal area (m²/ha)

2.2.2. 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 planned a 2-cut shelterwood system. A seed cut was applied in 1998, using the tree-length method to remove 0, 25 and 40% of stand basal area (Table 5) in a completely randomized design with four replicates (12 experimental units of 2 500 m^2). We established a 400 m² 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 to dissociate the effect of deer browsing from that of harvest treatment. Accessible trails for machinery were left outside 400 m² main plots. Second, in 1999, we set up a strip clearcutting experiment (Table 5) using the tree-length method with three strip widths (15, 30 and 45 m) replicated four times in a completely randomized block design. After the cut, each 180-m-long strip was scarified using a Waddel disc trencher. Within each 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 m 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. 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.

2.2.3. 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: <5cm; 5–30 cm; 31–60 cm; 61–100 cm; 101–200 cm; 201–300 cm) were recorded for each tree species. The seed cutting experiment was established in autumn 1998, and regeneration was surveyed immediately after cutting and eight years later. The strip clearcutting experiment was established in autumn 1999, and regeneration was tallied 1, 2 and 7 years after cutting.

2.2.4. 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 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, 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 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 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 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). We removed six fenced plots (25%) from the analyses in the strip clearcutting experiment because they were damaged and browsing was apparent. 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.

2.3. Results

2.3.1. Shelterwood seed cutting experiment

The number of recruited seedlings and difference in height of dominant seedlings did not differ statistically among treatments for all species (Table 6). For balsam fir, the mean density of seedlings in control plots decreased by about 35 000 seedlings/ha after eight years in both fenced and unfenced areas (Fig. 6A). However, the number of recruited white birch seedlings in unfenced plots after eight years tended to be lower than in fenced plots for both intensities of seed cut (Fig. 6B).

Table 6. Analyses of variance (MIXED Procedure, SAS, p-values) 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.

		Balsam fir		White birch		Spruce	
Sources of variation	d.f./den	Density	Hdom	Density	Hdom*	Density	Hdom
Seed cutting intensity (I)	2/9	0.91	0.91	0.65	0.42	0.24	0.84
Fence (F)	1/7	0.17	0.15	0.26	0.16	0.50	0.15
Cutting Intensity x Fence (I x F)	2/7	0.47	0.28	0.73	0.64	0.43	0.42

Note: - d.f.: numerator degree of freedom; den: denominator degree of freedom

* Analyses were conducted using square-root transformed data

Although not statistically significant, 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. 7A and 7B). 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. 7C).

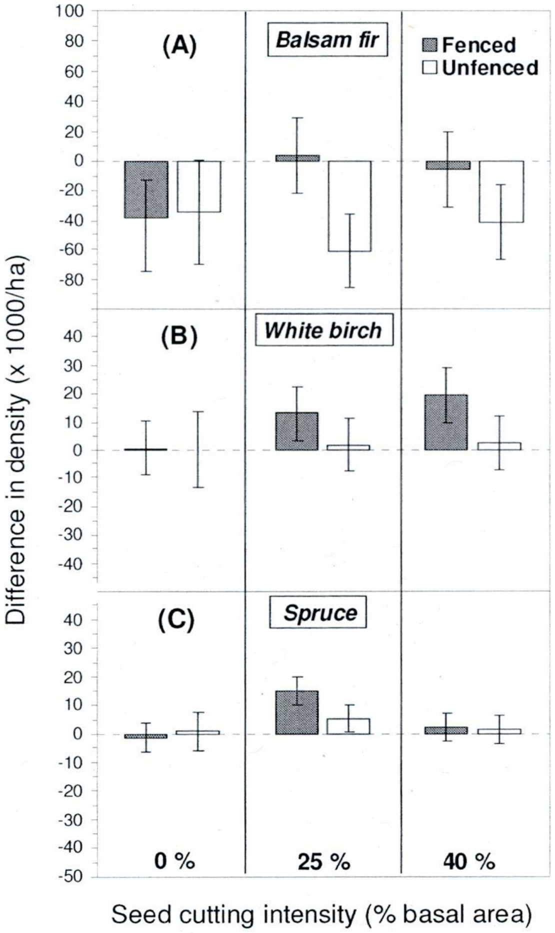

Figure 6. Difference in seedling density (x 1 000/ha) (MEAN ± 1 SE) between year 8 and immediately after shelterwood seed cutting as a function of seed cutting intensity and the presence or absence of a fence preventing deer browsing for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island.

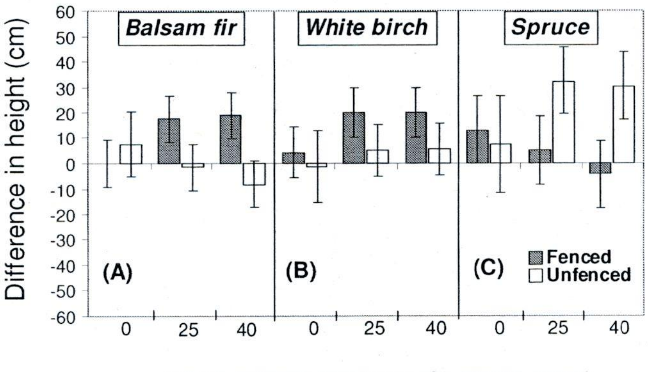

Figure 7. Difference in height of dominant seedlings (MEAN ± 1 SE) during the first eight years after shelterwood seed cutting as a function of seed cut intensity and presence or absence of a fence preventing deer browsing for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island.

2.3.2. Strip clearcutting experiment

One year after strip clearcutting, total balsam fir density ranged from 5 570 to 7 500 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 m 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 7; Fig. 8A). In contrast, difference in height of dominant fir seedlings in fenced plots was significantly higher than in unfenced plots seven years after cutting, whereas no differences were detected after two years (Table 7; Fig. 9A).

Table 7. Analyses of variance and orthogonal contrasts (MIXED Procedure, SAS, p-values) 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.

		Balsam fir		White birch		Spruce	
Sources of variation	d.f./den	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 x Fence (W x 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 x Year (W x Y)	2/151	0.16	0.10	0.49	0.16	0.87	0.41
Fence x Year (F x Y)	1/151	0.53	**<0.001**	**0.042**	**<0.001**	0.27	0.49
Y_2 x (F_N vs F_Y)*	1/151	-	0.62	0.99	0.36	-	-
Y_7 x (F_N vs F_Y)*	1/151	-	**<0.001**	**0.004**	**<0.001**	-	-
Width x Fence x Year (W x F x Y)	2/151	0.22	0.06	0.24	0.06	0.83	0.56

Note: d.f.: numerator degree of freedom; den: denominator degree 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 ($\alpha = 0.025$)

The number of recruited white birch seedlings was significantly higher in fenced than in unfenced plots seven years after cutting (Table 7; Fig. 8B). Moreover, seven years after cutting, difference in height of dominant white birch seedlings was higher in fenced than in unfenced plots (Table 7; Fig. 9B). No effect was detected two years after cutting (Table 7), at which time white birch density was less than 2 000 seedlings/ha in all experimental units (data not shown).

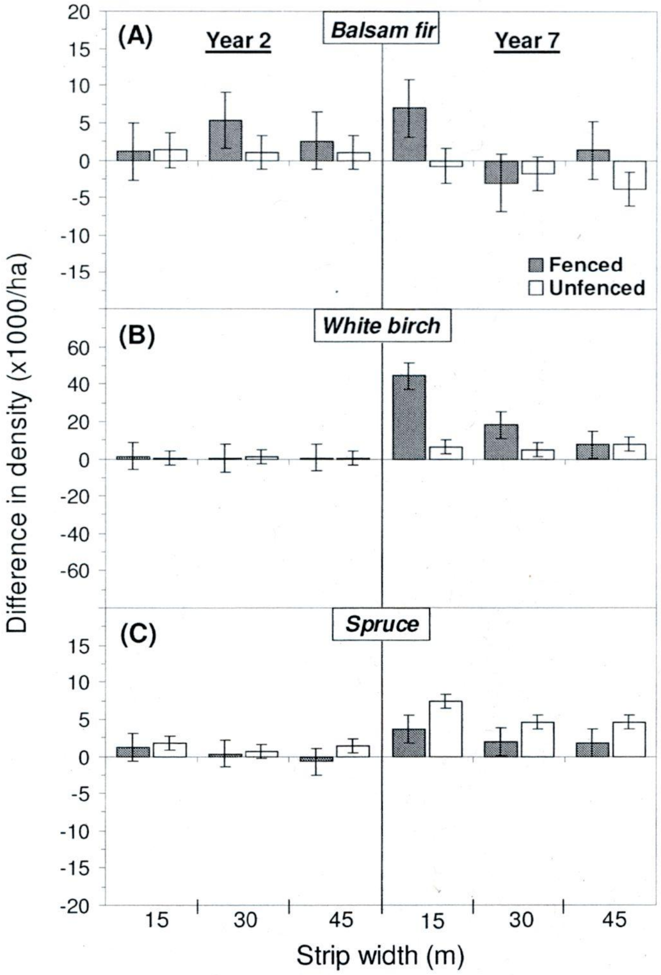

Figure 8. Difference in seedling density (x 1 000/ha) (MEAN ± 1 SE) 2 and 7 years after strip clearcutting as a function of strip width and presence of a fence preventing deer browsing for (A) balsam fir, (B) white birch, and (C) spruce on Anticosti Island. Difference was calculated by subtracting data one year after cutting from data at year 2 and year 7 after strip clearcutting.

The number of spruce recruits increased with time after cutting (Table 7; Fig. 8C) and was significantly higher in unfenced than in fenced plots (Table 7; Fig. 8C). Seven years after cutting, height growth of dominant spruce averaged 32 cm and 36 cm in fenced and unfenced plots, respectively (Fig. 9C), and no differences were detected between fencing treatments nor among strip widths (Table 7). At that point in time, total spruce seedling density ranged from 7 500 to 11 500 seedlings/ha in unfenced plots compared to less than 6 000 seedlings/ha in fenced plots (data not shown).

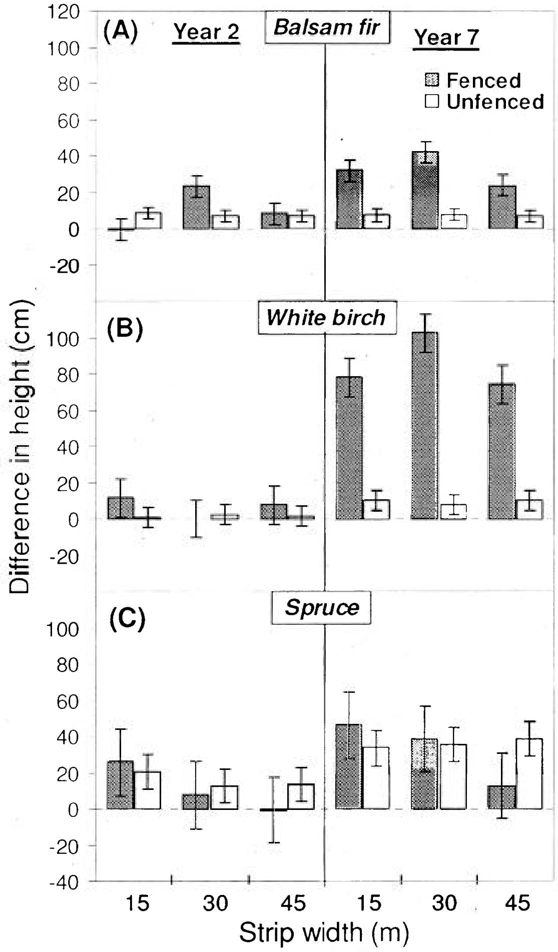

Figure 9. Difference in height of dominant seedlings (MEAN ± 1 SE) as a function of strip width, presence of a fence preventing deer browsing and time after cutting for (A) balsam fir (B), white birch, and (C) spruce on Anticosti Island.

2.4. Discussion

2.4.1. Shelterwood seed cutting

The number of recruited balsam fir seedlings eight 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, low germination rate and/or a consequence of a high seedling mortality rate. Mast years for balsam fir usually occur at intervals of 2–4 years (Frank, 1990), suggesting that good seed production should have taken place at least once during the eight year study. We did not survey balsam fir seed availability, but if seed production occurred, 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 removing 25% of the basal area in balsam fir stands did not affect seed availability, as compared with controls. Given an adequate seed supply, it seems that the spatial patterns and abundance of new seedlings are mostly driven by the availability of good seedbeds (Duchesneau and Morin, 1999). However, the quality and amount of adequate seedbeds have likely not 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.

2.4.2. 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 balsam fir since fir seed dispersal 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). Unfortunately, we did not survey seed rain, so we cannot determine whether proximity to seed trees improved seed dispersal. However, the strip widths used in our study were generally narrower than the effective distance of seed dispersal for balsam fir (25 to 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 various factors independent of deer browsing, such as viable seed availability, unfavourable seedbed conditions (Frank 1990), desiccation (Kaufmann and Eckard, 1977; Thomas and Wein, 1984) or plant competition (Coates et al., 1994). As with seed cutting, mast years for balsam fir should have occurred at least once during the seven-year study. Moreover, the soil scarification applied in the cut strips should have promoted establishment of natural regeneration, as observed by Prévost (1996 and 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., *Carex sp.*), ferns (e.g., *Dryopteris sp.*), 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. It has been suggested that dense herb layers can create a barrier to the establishment of seedlings (Coates, 1994) and may explain the lower regeneration densities found on rich sites (Harvey and Bergeron, 1989). Indeed, some studies have found that 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 positive impacts of scarification by reducing the window of opportunity for establishment of balsam fir regeneration. Moreover, since the positive effect of scarification on establishment of black spruce seedlings decreased over time (Jeglum, 1984), it is possible that seedbed receptivity was low when mast years occurred.

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. 9A and 9B). 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., in press). 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. 9C) and the number of spruce seedlings was even higher in unfenced areas (Fig. 8C). This suggests that increased competition from white birch and ground vegetation in fenced plots decreased microsite receptivity and likely prevented establishment of new spruce seedlings as already observed by Frisque and Vézina (1977) for black spruce seedlings. 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 predominately took advantage of selective 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).

2.4.3. Comparison between silvicultural treatments

Silvicultural treatments applied in the balsam fir forest–white-tailed deer system of Anticosti Island showed that deer browsing deeply affected height growth of balsam fir seedlings which stagnated over time in unfenced plots in all treatments (Table 8). 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/km². 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*) (density not mentioned). They argued that 'closer to nature' silvicultural treatments can reduce the risk of browsing damages both by decreasing habitat attraction for ungulates and favouring abundant regeneration establishment.

Table 8. Average density and height of balsam fir regeneration in fenced and unfenced areas 7 to 9 years after various silvicultural treatments on Anticosti Island.

		From 7 to 9 years after cutting			
		Seedling density (ha^{-1})		Height (cm)	
	Silvicultural treatment	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 1x)	9 808	1 905	64	7
	9) Group seed-tree cutting (scarification 2x)	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)
item 10: Refer to Casabon and Pothier (2007)

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 effect, 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/km²), 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 and al., 2007), could threaten the sustainability of deer population over the near-future. On the other hand, self-regulation of the deer population as a function of resource availability would have major economic consequences, since hunting activities represent the island's inhabitants' main source of income. 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.

2.5. 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 alternative because the major modifications of micro-climatic conditions related to clearcutting can cause extensive seedling mortality (e.g., litter drought) (Potvin and Laprise, 2002). On the other hand, if advance regeneration is abundant, clearcutting with careful logging around advance growth can be encouraged, as it has given adequate results in terms of stocking and regeneration density when balsam fir was protected from deer browsing (Casabon and Pothier, 2007).

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 may be possible after clear-cutting at densities ≤ 15 deer/km² (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/km². 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/km². 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/km²), together with the use of various silvicultural treatments.

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Conclusion générale

L'objectif principal de cette étude était d'étudier la capacité de la coupe avec réserve d'îlots semenciers, de la coupe à blanc par bandes et de la coupe progressive d'ensemencement à améliorer l'établissement du sapin baumier lorsque celui-ci est soumis au broutement intensif d'une densité élevée de population de cerfs de Virginie.

Les résultats, obtenus sept et huit ans après coupe, montrent que l'ensemencement à partir des semenciers résiduels a peu contribué à l'enrichissement de la banque de semis de sapin et cela, dans les trois dispositifs de coupe. Par ailleurs, le broutement du cerf a limité le développement en hauteur de la majorité des semis de sapin qui seront plus que probablement incapables de renouveler les peuplements actuels. Les différents traitements de scarifiage appliqués dans les bandes coupées et autour des îlots semenciers n'ont pas permis d'améliorer l'établissement du sapin comme escompté. Autour de ces derniers, l'établissement des semis de sapin était plus faible dans les zones scarifiées que dans les témoins, probablement parce que la majorité de la régénération en sapin était préétablie. Toutefois, l'établissement du bouleau à papier a été positivement influencé par l'intensité croissante du scarifiage, mais comme le sapin, sa croissance apicale a été stoppée par le broutement du cerf. Parmi les trois types de coupe que nous avons testés, la coupe progressive d'ensemencement s'est révélée contenir des densités supérieures de semis de sapin comparativement aux deux autres traitements sylvicoles sans toutefois permettre le recrutement suffisant de semis de sapin non broutés.

Il apparaît donc que l'utilisation seule des traitements sylvicoles testés ne permettra pas de régénérer les sapinières aussi longtemps que les densités de population de cerf de Virginie demeureront à un niveau aussi élevé. La diminution des densités de cerf à un niveau compatible avec la régénération des sapinières apparaît indispensable si l'on souhaite maintenir un habitat de qualité pour le cerf de Virginie ainsi qu'une activité de chasse durable. Actuellement, les gestionnaires forestiers de l'île d'Anticosti expérimentent l'utilisation de grands enclos de gestion (3-30 km²) à l'intérieur desquels les densités de cerf de Virginie sont substantiellement réduites. Le but de cette stratégie consiste à réduire temporairement (environ dix ans) la pression de broutement sur le développement de la régénération en sapin, le temps que celle-ci soit hors de portée des cerfs. Si la régénération naturelle en sapin n'est pas suffisante ou mal distribuée pour assurer le renouvellement des peuplements, les zones non régénérées sont alors regarnies par plantation. Dans ce contexte, l'utilisation de traitements sylvicoles favorisant l'établissement naturel du sapin pourrait constituer une solution de rechange à la plantation qui demeure un investissement financier important. Nos résultats indiquent que si la régénération préétablie n'est pas suffisante sous le couvert, l'utilisation de la coupe progressive d'ensemencement d'intensité modérée peut constituer une option appropriée pour favoriser l'établissement d'une banque abondante de semis avant la coupe finale. Si la régénération préétablie est abondante sous le couvert et suffisamment bien répartie dans l'espace, nos résultats suggèrent qu'une coupe avec protection de la régénération préétablie pourrait donner des résultats satisfaisants. Le maintien d'îlots ou de bandes résiduelles pourrait avoir peu d'effet sur l'établissement futur du sapin mais avoir un rôle important comme couvert d'abri pour les cerfs. Aussi, nos résultats ont montré que le scarifiage ne semble pas un moyen efficace pour stimuler l'établissement de la régénération naturelle en sapin.

Toutefois, le niveau de densité de cerf sous lequel ces traitements sylvicoles permettent un établissement adéquat du sapin n'est pas connu. Puisque notre étude ne visait pas à manipuler les densités de cerf, des expériences supplémentaires devront investiguer cet aspect en manipulant conjointement tant les densités de cerf que le type de traitement sylvicole. Cela permettrait d'établir si le seuil de densité de cerf compatible avec l'établissement du sapin est différent de celui établi dans le cadre d'une coupe avec protection de la régénération et des sols (15 cerfs/km², Tremblay et al., 2007). Aussi, cela permettrait d'améliorer notre compréhension des facteurs clefs qui influencent l'étendue des dommages causés par le broutement sur la régénération forestière. Finalement, puisque le développement des activités de récolte forestière à l'échelle du paysage semble étroitement lié à l'expansion des densités de cerf de Virginie en Amérique du Nord (Rooney, 2001), l'utilisation d'un tel dispositif pourrait être précieux pour orienter les stratégies d'aménagement forestier dans les régions forestières qui font, ou qui vont faire, face à la problématique de surabondance de cervidés.