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Browsing of tree regeneration by white-tailed deer in large clearcuts on Anticosti Island, Quebec

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Abstract

Browsing by the substantial population of white-tailed deer (*Odocoileus virginianus* Zimmermann) on Anticosti Island hampers the regeneration of balsam fir (*Abies balsamea* (L.) Mill.), which is both the deer's preferred food and shelter. The island's original fir stands have gradually been replaced by stands of white spruce (*Picea glauca* (Moench) Voss), as this species is rarely browsed by the deer. This project assesses the impact on the regeneration of balsam fir and companion species by large clearcuts performed using cutting with protection of regeneration and soils (CPRS). To this end, fenced-off areas adjacent to unfenced areas were established in 1995 and 1996 in large CPRS clearcuts. The results show that the distance from forest edge does not influence the stocking, number and height of seedlings, while browsing does reduce these variables in the case of fir and paper birch (*Betula papyrifera* Marsh.). However, stocking, number and height of white spruce seedlings were unaffected by both deer browsing and distance from forest edge. Woody debris seemed to protect balsam fir seedlings from browsing 8 years after cutting, but this protection should likely stop when seedlings will outgrow woody debris. It thus appears that large CPRS clearcuts will not permit the regeneration of balsam fir on a level sufficient for re-establishing fir stands on Anticosti Island.

Keywords: White-tailed deer; Browsing; High density; Tree regeneration; Clearcuts

1. Introduction

White-tailed deer (*Odocoileus virginianus* Zimmermann) populations have been increasing in North America for the past century and are presently at levels that have not been seen for the two last centuries (Rooney, 2001). The heavy browsing pressure imposed by a high density of deer can significantly modify an environment by inhibiting the growth of natural or artificial regeneration (Stoeckeler et al., 1957; Bellingham and Allan, 2003), by altering composition (Anderson and Loucks, 1979; Tilghman, 1989; Veblen et al., 1989; Anderson and Katz, 1993) and the structure of stands (Stewart and Burrows, 1989; Alverson and Waller, 1997; Healy, 1997; Rooney, 2001; Horsley et al., 2003), and even causing local extinction of plant species (Case and McCullough, 1987; Augustine and Frelich, 1998; Cornett et al., 2000; Russell and Fowler, 2004). The various effects of deer browsing can in turn produce a major negative impact on the forest industry and related economy in a given region (Tilghman, 1989; Conover, 1997).

White-tailed deer were introduced to Anticosti Island in the late 19th century. The island's population is now approaching 125,000 deer, and mean density is estimated at more than 15 deer/km^2 (Potvin and Poirier, 2004) and can be as high as 30 deer/km^2 in certain locations. At these densities, deer have a marked impact on the environment by limiting the development of regeneration and modifying ecosystems (Potvin et al., 2003; Potvin and Poirier, 2004). Excessive deer browsing on balsam fir (*Abies balsamea* (L.) Mill.) can transform the island's original fir stands into white spruce (*Picea glauca* (Moench) Voss) stands, as this species is rarely browsed by deer (Potvin et al., 2003). As a result, the island's deer population is projected to fall sharply due to the pronounced decline in the total area covered by fir stands over the next 40–50 years (Potvin et al., 2003). As Anticosti Island is a very popular hunting destination (this being its primary economic activity), it has become necessary to find a way of regenerating the island's fir stands in order to maintain quality

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deer habitat. The objective of preserving the initial ecosystems is also of primary importance.

In Quebec and elsewhere in the world, studies have shown that the centres of large clearcuts can be spared deer browsing due to the long distance from the forest edge and the consequent increase in predation risk (Drolet, 1978; Welch et al., 1991; Kay, 1993; Schmitz, 2005). Anticosti Island is characterized by the absence of predators, but the deer's instinct and the long hunting season – nearly 4 months – might lead to similar behaviours. This study is intended to test the impact of large clearcuts harvested by cutting with protection of regeneration and soils (CPRS) on the regeneration of balsam fir and companion species when deer density is high. The hypotheses to be tested are that: (1) the number of seedlings of balsam fir and companion species increases in keeping with their distance from the forest edge; (2) the presence of logging debris can temporarily protect seedlings from deer browsing; (3) deer reduce the number and stocking of seedlings of fir and companion species; (4) mean height growth of seedlings of fir and companion species is significantly reduced by deer browsing. These hypotheses will be tested using an experimental design comprising large cutblocks within which regeneration plots were established both inside and outside of fenced-off areas.

2. Material and methods

2.1. Study areas

Anticosti Island is located in the Gulf of St. Lawrence (49°28′N, 63°00′W) on the eastern edge of Quebec (Fig. 1). The island is 222 km long and has an area of 7943 km^2. The topography is generally even, with mean altitude being 126 m. The island's deposits are of post-glacial marine origin along the coast and at lower elevations, while the centre is covered with glacial till. Vast areas of organic deposits in peat bogs are found primarily in the eastern part of the island (Potvin and Poirier, 2004). Snowfall is abundant and approximately 20% higher than that measured in the white-tailed deer's range elsewhere in Quebec (Huot, 1982). The climate corresponds with that of the maritime sub-boreal bioclimatic, which is characterized by cool summers and relatively mild winters. The mean temperature is close to −11 °C in January and 16 °C in July (Environment Canada, 2006).

Anticosti Island is located in the balsam fir-white birch bioclimatic domain and in the eastern sub-domain of the lower boreal (Grondin et al., 1996). The primary tree species are white spruce, balsam fir and black spruce (*Picea mariana* (Mill.) B.S.P.). Species, such as trembling aspen (*Populus tremuloides* Michx), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.) and tamarack (*Larix laricina* (Du Roi) K. Koch) occur sporadically. Herbaceous vegetation is rich and diversified and dominated by *Clintonia borealis* (Ait.) Raf., *Maianthemum canadense* Desf., *Cornus canadensis* L., *Listera cordata* (L.) R. Br., *Dryopteris spinulosa* (O.F. Muell.) Watt and *Oxalis montana* Raf. The primary cause of forest disturbance is defoliation by hemlock looper (*Lambdina fiscellaria fiscellaria* (Guen.)). A very serious outbreak occurred from 1931 to 1936, and the most recent infestation, on a smaller scale, occurred from 1971 to 1973 (Dorais et al., 1996). Spruce budworm (*Choristoneura fumiferana* (Clem.)), which appeared for the first time in 1973 (Blais, 1983), is an additional source of damage. Windfall is another significant disturbance, while fire is of only secondary importance.

2.2. Experimental design

In 1995 and 1996, seven large CPRS clearcuts of approximately 3 km^2 were logged using tree-length harvesting,

Fig. 1. Localization of Anticosti Island and of the experimental clearcuts (circled area).

a technique that leaves logging debris on the site. All trees with diameter at breast height larger than 9.1 cm were harvested. In each of these CPRS clearcuts, all trees with diameter at breast height larger than 9.1 cm were harvested. Prior to felling, five to nine sampling plots were established per block at different distances from the predicted forest edge, for a total of 52 sampling plots. Each plot included a combination of a fenced area (deer exclusion area) and a unfenced area, each of which have a circular surface area of approximately 80 m^2. Fences of 3 m in height were installed immediately after logging in 1995 (three blocks) and 1996 (four blocks). Ten permanent circular quadrats of 4 m^2 were similarly established in each fenced and unfenced area. Following significant windfall in 1996, the dimensions of certain cutblocks were enlarged, which obliged us to re-measure the distances of the sampling plots from the nearest forest edges.

Sample plots were surveyed six times: prior to cutting and 1, 2, 3, 5.5 and 8.5 years after cutting. The surveys performed in 2001 and in 2004 were, respectively, 5 or 6 years and 8 or 9 years after cutting, depending on the year the block was logged. In each of these years the data from all logging blocks were pooled because otherwise too much data was missing when the clearcuts were analyzed separately. Accordingly, the combined data was assigned to the mean time period, that is, 5.5 and 8.5 years after cutting.

The regeneration survey was performed in early June of each year. This survey involved counting the number of commercial tree species by height class: <5, 5–30, 31–60, 61–100, 101–200, 201–300 and >301 cm. Three variables were calculated following data sampling: stocking (percentage of quadrats per sampling plot with at least one live seedling of the considered species), number of seedlings per hectare and mean height of seedlings per plot (group of 10 quadrats). Mean seedling height by species for each quadrat was calculated using the central value of each height class, which was weighted as a function of the number of seedlings by height class. An assessment of the percentage of ground area covered by obstacles and branches and the thickness and height from soil of piles of branches was performed at the same time as the regeneration survey. The percentage of ground covered by obstacles took into account the area covered by stumps, large boulders and snags that had fallen to the ground. The thickness of the accumulation of branches corresponded to the total mean thickness of branch cover on the ground in the quadrat, which excluded the empty space sometimes found between the ground and the bottom of the pile. Branch accumulation height can be defined as the distance between the ground and the top of the accumulation. In the case of each of the woody debris variables, the mean of the 10 quadrats determined during analysis served in calculating a mean value per plot.

2.3. Statistical analyses

An analysis of covariance for a repeated measurement design was performed using the MIXED procedure of SAS software (Milliken and Johnson, 2002). In order to take into account the correlation between repeated measurements of a plot, we tested seven variance–covariance structures and selected, for each analysis, the one that minimized the Akaike information criterion (AIC). Then, the constant part of the model (all interactions containing the edge variable) was minimized when non-significant in order to obtain the best model for explaining the response variables. The fenced and unfenced areas were compared over time while considering distance from forest edge. The covariables entered into the model corresponded to the data collected prior to application of CPRS for each variable analyzed, that is, regeneration stocking, number of seedlings per hectare and mean seedling height.

With respect to analysis of logging debris, the data were entered into the same statistical model in order to determine the impact of percentage of obstacles and percentage, height and thickness of branch cover on regeneration stocking and number of seedlings per hectare. Since logging debris was not measured in any way prior to application of CPRS, these data cannot be used in the form of covariables for variables related to logging debris in the statistical model.

3. Results

3.1. Effect of forest edges

Distance from forest edge failed to show a statistically significant impact ($p < 0.05$) for any of the variables analyzed. None of the variables relating to seedlings – stocking, number of seedlings per hectare and height – were influenced by distance from the forest in the unfenced plots. Since this held true for all species (Table 1), it would appear that deer browsed independently of distance from escape cover.

Furthermore, the absence of significant interaction between distance from forest edge and fencing indicates that distance from the forest does not have an influence on seeding in plots, such as would be apparent from the fenced plots but to much lesser degree in unfenced plots owing to deer grazing. The seeding of plots by the adjacent forest is therefore not a variable to consider when interpreting the statistical analyses.

3.2. Stocking and number of tree seedlings

The analysis of covariance shows that the interaction between fencing and time is statistically significant ($p < 0.001$) for balsam fir with respect to stocking and number of seedlings per hectare. This indicates that differences were observed between the fenced and unfenced plots, but not for all the years under study. Thus, Fig. 2A shows that fir stocking is significantly higher in fenced areas than in unfenced areas

Table 1
Significance level (p) of distance from forest edge on variables measured for various species as calculated by the SAS MIXED procedure

	Stocking	Number of seedlings per hectare	Mean height
Balsam fir	0.112	0.164	0.078
White spruce	0.118	0.172	0.560
Paper birch	0.905	0.638	0.916

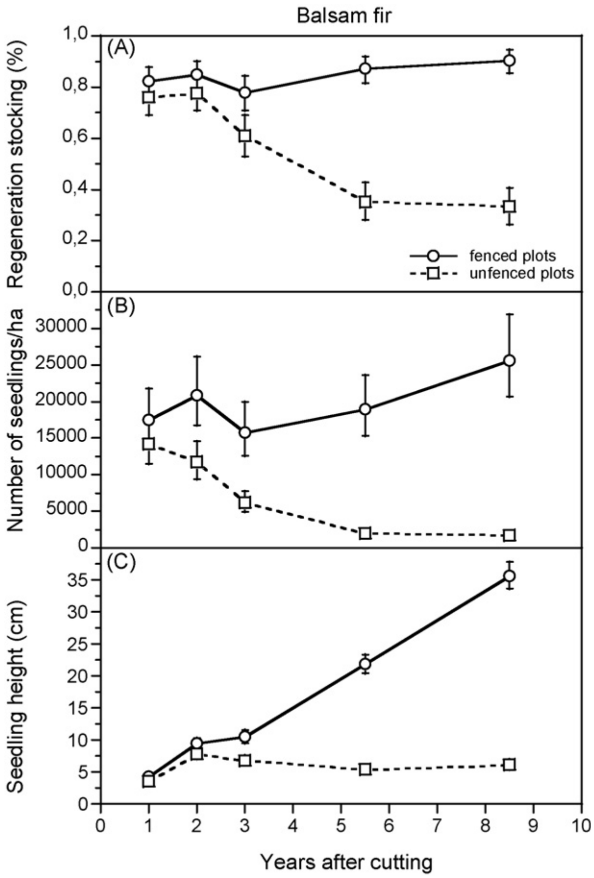

Fig. 2. Changes over time of (A) regeneration stocking, (B) number of seedlings per hectare, and (C) mean seedling height of balsam fir regeneration after clearcutting. Vertical bars correspond to standard errors.

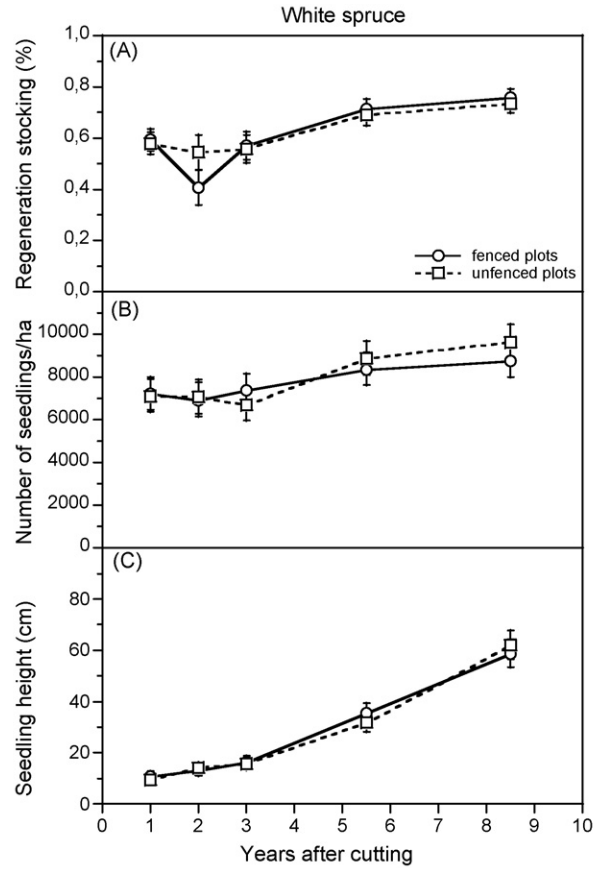

Fig. 3. Changes over time of (A) regeneration stocking, (B) number of seedlings per hectare, and (C) mean seedling height of white spruce regeneration after clearcutting. Vertical bars correspond to standard error.

beginning 5.5 years after cutting ($p < 0.001$). Number of fir seedlings per hectare is higher in fenced areas than in unfenced areas from the 2nd year after cutting (year 2, $p = 0.003$; year 3, 5.5 and 8.5, $p < 0.001$), and the difference between the two treatments increase over time (Fig. 2B).

In the case of white spruce, for both stocking and number of seedlings per hectare, only the year was highly significant ($p < 0.001$). The positive value of the parameter obtained for each of the years reveals that these variables increase over time and at the same rate for fenced and unfenced plots (Fig. 3A and B).

Stocking and number of seedlings per hectare of paper birch showed highly significant variation as a function of year and between fenced and unfenced areas ($p < 0.001$), with the exception of the number of seedlings per hectare 1 year after cutting (Table 2). Thus, the number of seedlings per hectare of birch between fenced and unfenced areas was different beginning in the 2nd year after cutting, with the difference between the two treatments subsequently increasing over time (Fig. 4A and B).

3.3. Height of tree seedlings

Balsam fir and paper birch seedlings were significantly taller in fenced areas than in unfenced areas for every year after cutting, except the 2nd year in the case of balsam fir (Table 3). The mean height of seedlings in the unfenced areas stagnated at 5 cm for balsam fir (Fig. 2C) and at 2.5 cm for paper birch (Fig. 4C), while height increased over time inside the fenced areas. The difference in the mean height of white spruce seedlings between fenced and unfenced areas was not statistically significant in any of the years (Table 3), suggesting that the growth of this species was unaffected by deer browsing.

3.4. Impact of woody debris

The impact of woody debris was analyzed on the basis of stocking and number of seedlings per hectare of balsam fir

Table 2
Significance level (p) of fencing (fenced and unfenced areas) in relation to paper birch stocking and number of seedlings per hectare in different years, as calculated using the SAS MIXED procedure

Years after cutting	Stocking	Number of seedlings per hectare
1	0.001	0.068
2	0.009	0.002
3	<0.001	<0.001
5.5	<0.001	<0.001
8.5	<0.001	<0.001

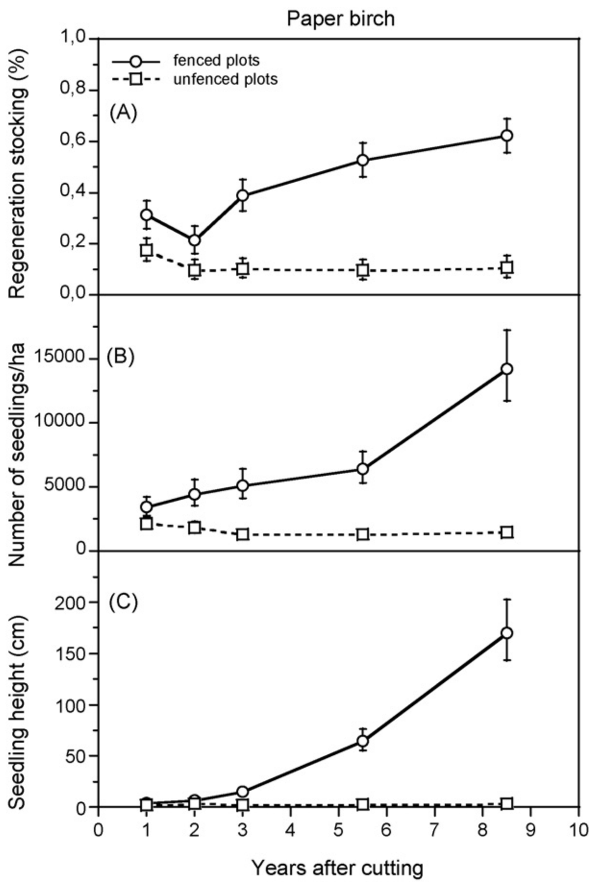

Fig. 4. Changes over time of (A) regeneration stocking, (B) number of seedlings per hectare, and (C) mean seedling height of paper birch regeneration after clearcutting. Vertical bars correspond to standard error.

only. The percentage of cover by branches and thickness of branch accumulation did not have a significant medium-term impact on stocking and survival of fir seedlings. However, 8.5 years after cutting, statistical analyses show that higher percentage cover by large woody debris, which includes stumps, is associated with a higher number of seedlings per hectare of balsam fir ($p = 0.016$). The number of seedlings per hectare observed in the absence of large woody debris is approximately 2000 and increases to 13,000 with 70% cover by large woody debris.

Table 3
Significance level (p) of fencing (fenced and unfenced areas) in relation to mean height of balsam fir, white spruce and paper birch in different years as calculated using the SAS MIXED procedure

Years after cutting	Mean height		
	Balsam fir	White spruce	Paper birch
1	0.039	0.317	<0.001
2	0.057	0.589	0.029
3	0.001	0.853	<0.001
5.5	<0.001	0.326	<0.001
8.5	<0.001	0.571	<0.001

4. Discussion

4.1. Effect of forest edges

The distance to escape cover did not influence the browsing behaviour of white-tailed deer, which seem to make equal use of the entire surface area of large clearcuts. The initial hypothesis that the centre of large clearcuts would be spared deer browsing was thus disproved. This hypothesis was based on several studies showing a decline in browse use with distance from forest edge in clearcuts subject to the influence of cervids (Drolet, 1978; Welch et al., 1991; Kay, 1993; Schmitz, 2005). However, all studies showing an effect relating to distance from forest edge were conducted in environments where predators were present, which contrasts sharply with conditions on Anticosti Island. Bergquist and Örlander (1998) raised the possibility that as visual exposure to predators is much higher in recent clearcuts, it probably becomes very costly in terms of energy and increased predation risk for a deer to feed in these locations.

In the long-term absence of predators, such as on Anticosti Island, it is possible that this behaviour could be modified, which would enable the deer to venture into the centre of large clearcuts (Andrén and Angelstam, 1993; Reyes and Vasseur, 2003). On the other hand, this behaviour could be driven by the pressure exerted on the environment by high-density ungulate populations. Several authors have observed that distance from forest edge does not influence browsing by various ungulate species when populations are dense (Williamson and Hirth, 1985; Andrén and Angelstam, 1993; Cadenasso and Pickett, 2000; Reyes and Vasseur, 2003). Drawing on the density-dependent habitat selection theory (e.g., Fretwell and Lucas, 1970), it is possible that certain individuals in a high-density population are forced to feed in habitats presenting greater limitations, which includes locations far from forest edges. As a result, on Anticosti Island, the lack of food resources associated with high deer densities may oblige the deer to move further from forest cover to feed themselves, regardless of theoretically higher risks of predation at these locations than at those closer to the forest edge.

4.2. Stocking and number of tree seedlings

The results obtained show that white-tailed deer have a marked short- or medium-term impact on stocking and number of seedlings per hectare of balsam fir and paper birch. In fenced plots, these variables tend to gradually increase while decline or stagnation is observed in unfenced plots (Figs. 1 and 3). The impact of deer is thus increasingly evident over time and is more obvious among species most sought after as browse, such as paper birch (Case and McCullough, 1987; Tilghman, 1989). A decline in the number of seedlings and their stocking has previously been observed when large ungulate population are present following clearcutting (Tilghman, 1989; Martin and Baltzinger, 2002) and under forest cover (Frelich and Lorimer, 1985; Veblen et al., 1989; Brandner et al., 1990; Witmer and deCalesta, 1991; Alverson and Waller, 1997; Healy, 1997; Cross, 1998; Cornett et al., 2000; Rooney, 2001; Rooney and Waller, 2003; Russell and Fowler, 2004).

In addition, the absence of significant differences between the fenced and unfenced areas in the case of white spruce reveals that the deer avoid browsing this species. High deer densities have no effect on stocking and number of seedlings per hectare of this species in large clearcuts. White spruce has an acceptable level of stocking (75%) and a fairly high number (between 8500 and 9500) of seedlings per hectare, all heights combined, 8.5 years after cutting (Fig. 2). Consequently, if clearcutting continues to be the principal harvesting method and if it is applied without fencing, the balsam fir stands on Anticosti Island will gradually be replaced by white spruce stands, as was already proposed by Potvin (1992) and Potvin et al. (2000, 2003). This replacement of balsam fir by white spruce was also observed on Isle Royale, Michigan, due to a large moose population (McInnes et al., 1992). Black spruce, which is also little browsed by deer, can be a companion to white spruce in forest types characterized by poorer drainage. As long as the deer density does not decline on Anticosti Island, it is likely that logging of fir stands will favour the establishment of spruce stands. Furthermore, where spruce was not able to regenerate, we observed that clearcuts had a prairie structure with scattered white spruce saplings. Several authors noted this tendency to transition from a forest to a prairie or a savannah, with the initial species often being replaced by herbaceous plants or trees not browsed by deer (Jane, 1994; Healy, 1997; Putman and Moore, 1998; Russell and Fowler, 2004). This transformation could occur on Anticosti Island after clearcutting of locations presenting minimal spruce regeneration if the deer population density continues to remain at its current high levels.

4.3. Height of tree seedlings

According to our findings, balsam fir and paper birch seedlings were shorter in unfenced plots than in fenced plots for all measurement periods. Thus, white-tailed deer have a marked impact on the height growth of these species which stagnate over time in unfenced areas. Browsing in the latter areas prevents seedlings from growing higher than approximately 5 cm in the case of fir and 2.5 cm in the case of birch. As suggested by Stoeckeler et al. (1957) and Whitney (1984), recruitment of saplings of intermediate height classes is problematic in the presence of high deer densities.

Several experiments have also shown a decline in height and retardation of seedling growth due to browsing by high populations of large herbivores in clearcuts (Tilghman, 1989; Cooke and Farrell, 2001; Kullberg and Bergström, 2001; Horsley et al., 2003; Reyes and Vasseur, 2003) and under tree cover (Stoeckeler et al., 1957; Brandner et al., 1990; Alverson and Waller, 1997; Cornett et al., 2000; Opperman and Merenlender, 2000; Harmer, 2001). As a result, deer browsing can retard forest succession (Gill and Beardall, 2001). Furthermore, the reduction in height growth of desirable seedlings due to browsing can lead to a situation in which seedlings are surpassed by competing non-browsed vegetation, placing them at risk of ultimately experiencing a higher mortality rate (Gill and Beardall, 2001).

4.4. Impact of woody debris

Fir seedlings counted 8.5 years after cutting increased with the percentage of obstacles in the logged area. Many authors have observed that woody debris has a positive effect on forest regeneration (Tilghman, 1989; Kay, 1993; Bergquist et al., 1999). Stumps, fallen snags and large boulders seem to create a visual obstruction that protects the seedlings, at least until they grow above these obstacles. Smaller woody debris (branches) does not have a significant medium-term impact, probably because it decomposes much more rapidly than does large woody debris. The more pronounced presence of seedlings near debris may be the result of improved visual protection (Bergquist and Örlander, 1998) or of better moisture conditions provided by obstacles, which favour seedling establishment and growth.

5. Conclusion

This study shows that large clearcuts harvested by CPRS in balsam fir stands are not a solution that will ensure fir regeneration, given the current density of the island's deer populations. The impact of deer is quite marked even at significant distances from the forest edge. Deer browsing has had the effect, on the one hand, of limiting regeneration and the growth of fir and paper birch, and, on the other, of encouraging the growth of white spruce. The net result has been to profoundly alter the island's ecosystem. The high deer population, absence of predators and limited browse supply help explain the failure of large clearcuts to regenerate Anticosti Island's fir stands. Deer densities should be reduced to ensure the maintenance of fir stands and the plant species native to the island. It is possible that lower deer densities could make large CPRS clearcuts an effective way of fostering the establishment and growth of fir seedlings and associated plant species. A deer density of between 7 and 15 deer/km^2 attained in less than 3 years after cutting is required to maintain the natural community of ground plants found in fir stands (Tremblay et al., 2006). These authors believe, however, that densities approaching 7 deer/km^2 would be required to maintain the diversity of plant communities characteristic of the Eastern balsam fir-white birch domain.

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