ÉCOSCIENCE
10 (4): 487-495 (2003)

The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Québec: A 150-year process[1]

François POTVIN[2], Société et de la faune et des parcs du Québec, 675 boul. René-Lévesque est, Boîte 92, Québec, Québec G1R 5V7, Canada, e-mail: fpotvin@fapaq.gouv.qc.ca
Pierre BEAUPRÉ, Ministère des Ressources naturelles, 880 chemin Sainte-Foy, Québec, Québec G1S 4X4, Canada.
Gaétan LAPRISE, Société et de la faune et des parcs du Québec, C.P. 159, Port-Menier, Anticosti, Québec G0G 2Y0, Canada.

Abstract: White-tailed deer (*Odocoileus virginianus*) were introduced 100 y ago on Anticosti, a 7,943-km^2 island located in the Gulf of St. Lawrence, Québec. The forest of the island is typically boreal and, at the time of the introduction, was dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*). Since then, the vegetation has been modified as a result of high deer density (16 deer·km^{-2}) and heavy browsing. The most important change is the progressive decline of balsam fir stands, formerly the prevalent forest type. We describe that process at three spatial and time scales. On the largest scale (whole island, 100 y), we examined the age and species composition of stands on recent forest maps as well as the age structure of 2,555 individual balsam fir and white spruce trees. Balsam fir was largely dominant before 1930, but was replaced by white spruce afterwards. We also estimated that fir stands, which now cover 20% of the island, occupied about 40% of the total area initially. On an intermediate scale (1,200 km^2, 30 y), we examined the natural regeneration established after an insect outbreak that took place in 1971-1972 and massively killed predominantly balsam fir forests. In that area, white spruce regeneration now largely replaces that of balsam fir. On a finer scale (< 1 km^2, 3 y), we monitored 1,800 balsam fir seedlings (2-5 cm high) individually tagged. Seedlings were browsed throughout the snow-free season, and the annual browsing incidence in forest was estimated at 26%. Considering the present age of remnant fir stands, we estimate that most of these will have been eradicated in 40-50 y.
Keywords: *Abies balsamea*, balsam fir, herbivory, île d'Anticosti, *Picea glauca*, white spruce, white-tailed deer.

Résumé : Il y a 100 ans, le cerf de Virginie (*Odocoileus virginianus*) a été introduit sur Anticosti, une île de 7943 km^2 située au Québec dans le golfe du Saint-Laurent. La forêt y est de type boréal et, au moment de l'introduction du cerf, était dominée par le sapin baumier (*Abies balsamea*), l'épinette blanche (*Picea glauca*) et l'épinette noire (*P. mariana*). La population de cerfs a depuis augmenté de façon telle (densité actuelle de 16 individus·km^{-2}) que le broutement intense a modifié la végétation. Le déclin progressif des sapinières, le type de peuplement le plus abondant à l'origine, constitue le principal changement observé. Nous décrivons ce processus à trois échelles spatio-temporelles. À l'échelle la plus large (ensemble de l'île, 100 ans), nous avons examiné l'âge et la composition en espèces des peuplements sur les cartes forestières récentes ainsi que la structure d'âge de 2555 sapins et épinettes blanches. Avant 1930, le sapin dominait largement les forêts mais il a été remplacé par l'épinette blanche. Nous avons évalué que les sapinières, qui occupent actuellement 20 % de la superficie de l'île, étaient présentes sur environ 40 % de cette superficie avant l'introduction du cerf. À une échelle intermédiaire (1200 km^2, 30 ans), nous avons examiné la régénération naturelle qui s'est installée après une importante épidémie d'insectes survenue en 1971 et 1972 dans des peuplements composés surtout de sapin. Dans ce secteur, la régénération en épinette blanche est nettement supérieure à celle du sapin. À une échelle plus fine (<1 km^2, 3 ans), nous avons suivi 1800 petites plantules de sapin (2 à 5 cm de hauteur), marquées individuellement. Les plantules ont été broutées durant toute la saison sans neige et le taux annuel de broutement des plantules a atteint 26 % en forêt. Compte tenu de l'âge des sapinières actuelles, nous estimons que la plupart de ces peuplements auront disparu dans 40 à 50 ans.
Mots-clés : *Abies balsamea*, cerf de Virginie, épinette blanche, herbivorie, île d'Anticosti, *Picea glauca*, sapin baumier.

Nomenclature: Marie-Victorin, 1964; Banfield, 1974.

Introduction

Islands have long been a source of fascination and inspiration for naturalists and ecologists. Their finite size, isolation, and limited flora and fauna facilitate testing hypotheses on ecological processes in a unique way. Fundamental theories such as natural selection (Darwin, 1859) and island biogeography (MacArthur & Wilson, 1967) or long-term studies such as predator-prey-vegetation relationships (Peterson, 1977) are all associated with island situations. Islands are particularly suited for analyzing plant-herbivore interactions, because ungulate introductions quite often have resulted in a heavy impact on native vegetation. Well known examples are Isle Royale (McLaren & Peterson, 1994), Newfoundland (McLaren *et*

[1]Rec. 2002-12-04; acc. 2003-04-28.
[2]Author for correspondence.

al., 2000), New Zealand (Howard, 1967), and South Georgia (Leader-Williams, 1988).

Increasing densities of ungulates are becoming a widespread problem (Alverson, Waller & Solheim, 1988; Gill, 1992a,b; Angelstam *et al.,* 2000; Fuller & Gill, 2001). White-tailed deer (*Odocoileus virginianus*) populations in particular have increased in North America and now might have detrimental effects on whole forest ecosystems (McShea & Rappole, 1997; Waller & Alverson, 1997; Rooney, 2001). Such problems have been reported in the past (Leopold, Sowls & Spencer, 1947; Graham, 1954), but they tended to be restricted to local areas. With the main large predators of white-tailed deer reduced or extirpated long ago, declining interest in hunting and, in the north, milder winters have resulted in deer densities increasing to record levels. Even areas recognized as marginal for white-tailed deer less than 30 y ago in Québec now face overpopulation (Potvin *et al.,* 1977; Huot, Lamontagne & Goudreault, 2002).

Islands where deer have been at high density for many years can be used to help understand the processes of intensive herbivory and to experiment with original solutions. Anticosti is a large island where white-tailed deer were introduced 100 y ago and have been very numerous since about 1930 (Potvin *et al.,* 2000). In the absence of predators of deer, the boreal forest system, where balsam fir (*Abies balsamea*) stands were once the prevalent forest type, is gradually being transformed by selective deer herbivory. This paper describes that process at three spatial and temporal scales.

Methods

STUDY AREA

Anticosti (49° 28' N, 63° 00' W) is a 7,943-km^2 island located in the Gulf of St. Lawrence, Québec. Port-Menier, with a population of 275, is the only permanent human settlement. During the snow-free season, lodges distributed throughout the island receive some 10,000 visitors for hunting, fishing, and recreation activities. At the time of deer introduction, the forest was dominated by balsam fir, white spruce (*Picea glauca*), and black spruce (*P. mariana*) (Martin-Zédé, 1938; Pimlott, 1963). Deciduous species were more abundant than they are now (Hébert & Jobin, 2001). Commercial logging has been active on the western portion of the island for the past 100 y. Insect outbreaks and fires are the main natural factors driving the dynamics of the forest.

The native mammalian fauna was limited to seven species: red fox (*Vulpes vulpes*), black bear (*Ursus americanus*), river otter (*Lontra canadensis*), deer mouse (*Peromyscus maniculatus*), American marten (*Martes americana*), and two bat species, *Myotis lucifugus* and *M. keenii* (Newsom, 1937; Cameron, 1958; Potvin *et al.,* 2000). Species that were successfully introduced include white-tailed deer, beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), snowshoe hare (*Lepus americanus*), and moose (*Alces alces*). Some 150-220 deer were introduced between 1896 and 1900, and they rapidly occupied the whole island (Potvin *et al.,* 2000). The population was estimated at 125,000 deer (16 deer·km^{-2}) in recent aerial surveys (Potvin, Breton & Gingras, 1991; Rochette, Gingras & Potvin, 2003). The density of moose is about 0.8 animal·10 km^{-2} (MLCP, 1987), and their impact on vegetation is minimal compared to deer. Deer-hunting success has remained stable over the last 30 y, and the number of deer seen per hunter-day has been increasing recently (Potvin *et al.,* 2000). After a severe winter, these two indices of deer abundance decrease temporarily but they resume their former level after one or two hunting seasons. Based on limited empirical data and on Caughley's ungulate-vegetation model (Caughley, 1976), deer number probably peaked at a record level in the early 1930s and then gradually stabilized at the current level (Figure 1).

Winters are long on the island, usually with 6 months of snow on the ground. The winter severity index on Anticosti is among the highest for Québec (Huot, Lamontagne & Goudreault, 2002), and there are on average 49 d with a snow depth > 50 cm (A. Gingras, pers. comm.). The success of the deer introduction in such a poor habitat (boreal forest) coupled with harsh winter conditions is amazing. The absence of predators and a low hunting harvest rate (< 8% annual rate over the past 20 y and much less before) are part of the explanation. Facing no predator or human harassment, deer have adopted a winter-survival strategy that involves catabolizing their body reserves to the ultimate limit (Huot, 1982).

The impact of such high deer density on the vegetation has been tremendous. The shrub layer is totally absent, except for regenerating spruces. Most deciduous species, such as mountain maple (*Acer spicatum*), beaked hazelnut (*Corylus cornuta*), and red-osier dogwood (*Cornus stolonifera*) have been nearly extirpated (Pimlott, 1963; Potvin *et al.,* 2000). The most important change is the progressive decline of balsam fir stands, once the

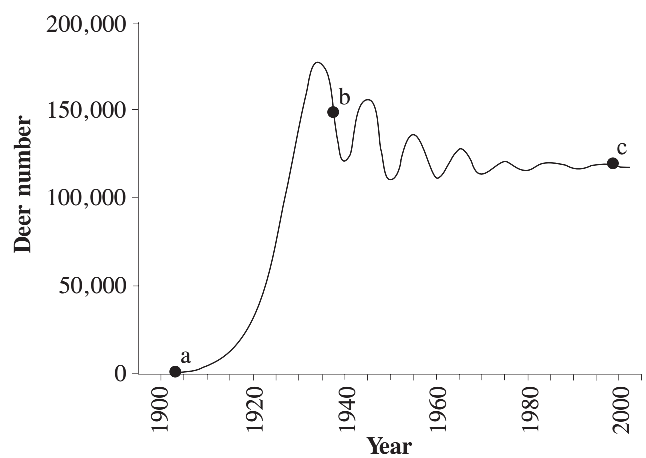

FIGURE 1. Theoretical evolution of white-tailed deer number on Anticosti Island from introduction to year 2000. Three points on the curve are derived from empirical data: a) some 150-220 deer were introduced between 1896-1900, b) an important decline occurred in 1934 (D. H. Pimlott, unpubl. data; Huot, 1982), and c) the population was estimated at 125,000 deer by two recent aerial surveys (Potvin, Breton & Gingras, 1991; Rochette, Gingras & Potvin, 2003). Variations in between are based on Caughley's ungulate-vegetation model (Caughley, 1976), assuming an initial growth rate (λ) of 1.23 and a carrying capacity (K) of 250,000 animals from 1896 to 1930 and 70,000 afterwards.

prevalent forest type. Although usually considered a minor browse species, balsam fir makes up 70% to 80% of the deer diet in winter on Anticosti (Huot, 1982; Lefort, 2002). In stands that have been logged or opened by insect outbreaks, white spruce, an unpalatable browse species, has replaced balsam fir.

VEGETATION SURVEYS

We studied the effect of deer herbivory on balsam fir at three spatial and time scales: whole island (100 y), a 1,200-km^2 zone (30 y), and < 1-km^2 sites (3 y). On the largest scale (whole island, 100 y), we used data from a recent provincial forest survey. In Québec, forest surveys are based on the interpretation of aerial photos to build forest maps (1:20,000) and ground surveys to evaluate the wood volume of tree stands (MRN, 1995). Aerial photos for the last survey were taken in 1997 and 1998, at a scale of 1:10,000 (panchromatic colour photos) or 1:15,000 (black and white). The ground survey was conducted in 2000. To assess how forest composition changed after the deer introduction, we used the digitized forest maps to measure the age distribution of the principal forest types. Each polygon on the map is described according to different attributes, including landcover type (water, forest, non productive land such as bogs), dominant and codominant tree species of the canopy (balsam fir, white spruce, black spruce, etc.), height class (< 1.5, 1.5-4, 4-7, 7-12, > 12 m), age class (10, 30, 50, 70, 90, and > 100 y), stand origin (insect outbreak, clear-cut, fire), and ecological type (see Table I).

Because the age classes of forest stands on the maps are large (20 y) and do not subdivide stands that are over 100 y old into separate age classes, we also examined data from the ground survey. Stands for which the height class was > 7 m were grouped into 97 forest strata for the survey, and an average of 14 sampling units were allocated per stratum. For each unit, a 0.04-ha circular plot was established to count the number of trees by species and by 2-cm DBH (diameter at breast height) class. Three dominant or codominant trees were selected at each plot for dendrometric measurements, including age determination with a Pressler increment borer at 1 m above ground level. We used a three-step procedure to compute the relative proportion of balsam fir and white spruce by age class (in 10-y increments) in this sample. These steps were designed to correct for the allocation of sampling units by strata, which is not proportional to the area they occupy on the island, and for the selection of stems, which favours larger trees because selection is limited to dominants and codominants. In the first step, we built a weighted table of the number of stems by species and DBH class for the whole island. This stand table involved summing the stem counts in the 0.04-ha plots by species and DBH class for each stratum, dividing it by the respective number of units per stratum, and weighting it by the proportion of the area occupied by each stratum on the whole island. In the second step, we used the three selected trees per sampling unit to calculate the number of stems by 10-y age class and DBH class for balsam fir and white spruce separately. The final step involved extracting the data for balsam fir and white spruce from the stand table and combining it with the two tables from the second step. The relative proportion of balsam fir or white spruce could then be obtained by age class, on a stem basis. We added 10 y to compensate for the fact that ages were measured at 1 m (MRN, unpubl. data).

Finally, on the largest scale, we built two forest maps for the island. The first approximated the general forest composition before deer were introduced. We used the ecological types identified on the forest maps (MER, unpubl.; Saucier *et al.,* 1998) and assumed that all MS2 and RB5 units were then occupied by balsam fir stands (Table I). This estimate is conservative, because RS2 and RS3 types can also contain balsam fir. The second map, showing the present forest, was obtained by using the dominant tree species of the canopy of the recent survey (forest maps from aerial photos) to identify the main forest types.

On an intermediate scale (1,200 km^2, 30 y), we examined natural regeneration established after a hemlock looper (*Lambdina fiscellaria*) outbreak that occurred in 1971-1972 and massively killed predominantly balsam fir forests (Figure 2). In that 1,172-km^2 area, photointerpretation of 1:10,000 colour photos enabled us to add two attributes to the forest polygons describing the tall regeneration (1.5-7 m): abundance of total coniferous regeneration and abundance of balsam fir only (absence, < 5, 5-25, 25-40, 40-60, 60-80, 80-100% cover density). In that area, we selected stands that had been totally destroyed by the outbreak, as indicated by the origin attribute on the map. For those stands (n = 4,783; 691 km^2), we then computed the proportion of the area occupied by each regeneration density class. We also evaluated for the same stands the composition of the new forest, based on

TABLE I. Definition of the ecological forest types used in the 1997-2000 forest survey on Anticosti Island (MER, unpubl. data; Saucier *et al.,* 1998).

Ecological type	Definition
MS2	Balsam fir stand with white birch
RB5	White spruce stand originating from deer browsing of MS2 type
RE2	Black spruce stand (moss or Ericacae)
RE3	Black spruce stand (*Sphagnum*)
RS2	Balsam fir stand with black spruce
RS3	Balsam fir stand with black spruce (*Sphagnum*)

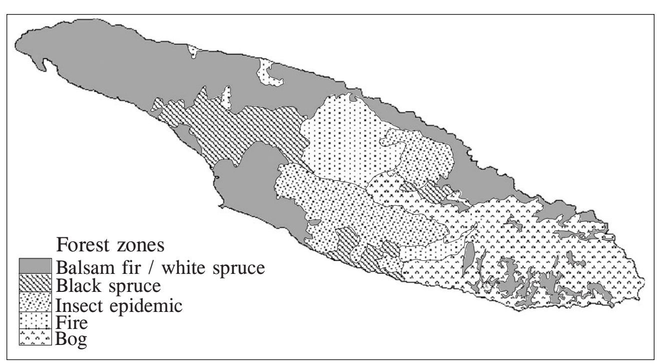

FIGURE 2. Principal forest zones on Anticosti Island (adapted from Nadeau & Beaupré, 1991). The insect epidemic zone corresponds to the hemlock looper 1971-1972 mortality area.

the dominant and codominant tree species of the canopy (> 4 m high) on the forest maps.

An intensive experimental design was established to measure the effects of herbivory on a local scale (< 1 km^2, 3 y). We tagged 1,800 small seedlings at 10 different sites, five in uncut balsam fir stands and five in recent clear-cut blocks (1995-1996, 3 km^2) of the same forest type. These seedlings were 2-5 cm high and had a single, unbrowsed stem. They were not covered by branches or cutting slash, in order to be accessible to deer. Each seedling was identified by a glass rod with a unique number. Seedlings were monitored for 3 y during the snow-free season at 2-4 week intervals. At each visit, each seedling was tallied as follows: (1) alive and unbrowsed, (2) dead (dried), (3) browsed, or (4) disappeared. New seedlings were also tallied and added to the monitoring experiment as they became established. Browsed seedlings, even those partially browsed, were eliminated because rapid healing in summer might have caused erroneous interpretation in the following visits. Some of these partially browsed seedlings might have survived, so their elimination must be taken into account when interpreting the results. All the terminal tips of browsed seedlings were chewed, which is typical of deer, and did not show an angular clean cut, typical of snowshoe hare. There are no other mammals likely to browse seedlings on the island besides deer mice, a species considered omnivorous more than herbivorous.

Data on tagged seedlings were analyzed both as absolute values, (*i.e.,* number of seedlings) and relative values, (*i.e.,* browsing rate). Seedlings that disappeared were lumped with browsed seedlings because we assume that they were extirpated by deer. The browsing rate at each visit was computed as the percentage of seedlings browsed over a 30-d period:

$$\text{Rate}_t(\%) = 100 \times \frac{\text{NBR}_{t-1,t}}{\text{NALIVE}_{t-1}} \times \frac{30}{\text{DAYS}_{t-1,t}} \qquad [1]$$

where NBR $_{t\text{-}1,\,t}$ = number of browsed (and disappeared) seedlings between visits t-1 and t, NALIVE $_{t\text{-}1}$ = number of seedlings alive at visit t-1, and DAYS $_{t\text{-}1,\,t}$ = number of days between visits t-1 and t. For the first annual visit in May, the period corresponds to the number of days since the last visit (October or November of the previous year) when there was no snow on the ground. Browsing rates were transformed with an arcsine function (x + 1) before applying a statistical test, as suggested for a percentage scale (Snedecor & Cochran, 1967). We used an ANOVA to test for the effect of site and period (year, month) on the browsing rate. Significant results (P < 0.05) were followed by an *a posteriori* Scheffé test to identify the groups that were statistically different from the others.

Results

WHOLE ISLAND SCALE

Balsam fir and white spruce stands occupied 3,403 km^2 on Anticosti Island according to the recent forest survey. The most abundant age class was > 100 y (40%), followed by 30 y (26%), 50 y and 90 y (13% each), and 70 y (8%). The 10-y class was very rare (< 1%). The relative proportion of balsam fir or white spruce as the dominant species (> 50% basal area for either species) has changed since deer introduction. While stands established before 1930 were mostly balsam fir (77-84% for age classes 90 and > 100 y), younger stands are now dominated almost entirely by white spruce (92-99% for age classes 50 y and less) (Figure 3).

When allocated to the recruitment y, the species composition from individual balsam fir and white spruce trees aged in the ground survey shows the same pattern as in forest stands (Figure 4). Balsam fir was the most frequent species up to 1910. A shift happened from 1920 to 1930, after which more than 90% of recruited trees were white spruce.

Our estimation based on the ecological forest type shows that about 40% of the island was occupied by balsam fir stands in 1896, before deer were introduced (Figure 5). Balsam fir-dominated stands now make up only 20% of the area.

INTERMEDIATE SCALE

The density of the coniferous tall regeneration (1.5-7 m) in the zone of the 1971-1972 hemlock looper epidemic suggests adequate stocking, with the 40-60% class being most common (Figure 6). Balsam fir makes up a very small fraction of this regeneration, with only 13% of the area having a density ≥ 5% in balsam fir. Based on the canopy composition (> 4 m high), the forest in this area is now largely dominated by pure white spruce stands (76%) or white spruce-dominated stands (15%), while balsam fir-dominated stands are rare (6%) (Figure 7).

LOCAL SCALE

Tagging indicated that the number of balsam fir seedlings would have increased 153% in the uncut forest sites after 3 y, due to new seedling establishment, had deer been absent (Table II). In the clear-cut blocks, the absence of seed trees resulted in a low establishment of new seedlings. In this case, a higher natural mortality

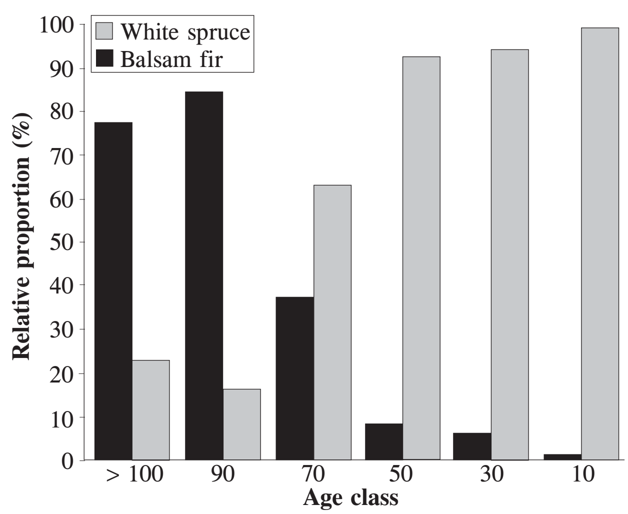

FIGURE 3. Relative proportion of balsam fir and white spruce dominated stands (> 50% basal area) by age class on Anticosti Island, according to a 1997-2000 forest survey.

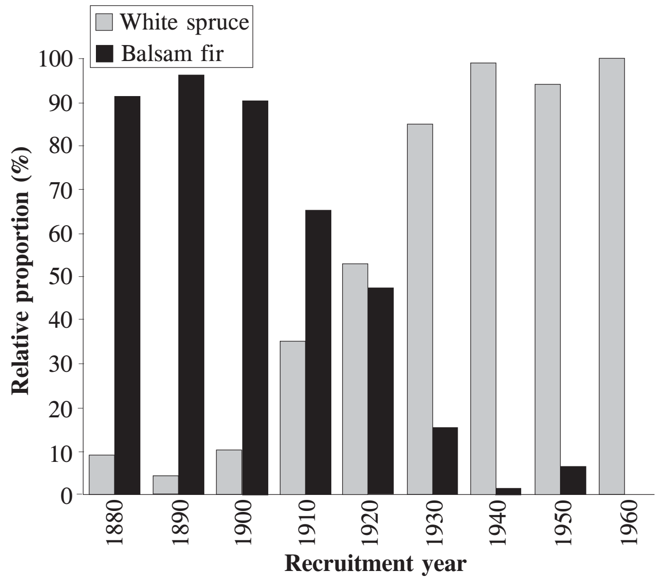

FIGURE 4. Species composition by age class (10-y intervals) of 2,555 balsam fir and white spruce trees studied in the ground surveys of a 1997-2000 forest inventory on Anticosti Island. Age classes are converted to the recruitment year (2000 minus age class).

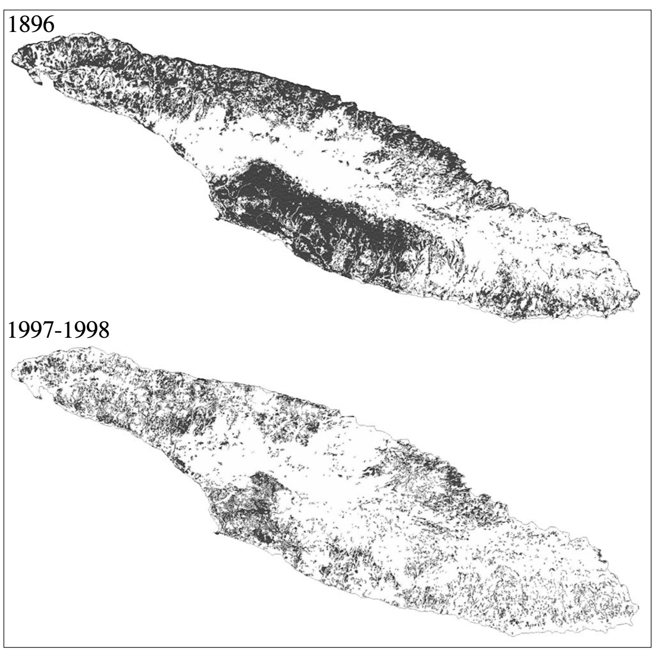

FIGURE 5. Distribution of balsam fir stands (black) on Anticosti Island before the deer introduction (1896) and recently (1997-1998). The historic map is based on the ecological types of the recent forest survey best suited for balsam fir stands (MS2, RB5). The recent map is based on balsam fir-dominated stands (> 50% basal area) on the forest maps from the same survey.

than in uncut forest would have caused the number of seedlings to decrease to 57% of the initial value in a deer-free scenario. Deer herbivory had a clear impact both in forest sites and in clear-cut blocks: only 59% and 3% of the initial number of small seedlings were still present after the last monitoring in each area, respectively. Since the partially browsed seedlings that we eliminated represent 66% of the total number of browsed seedlings, sur-

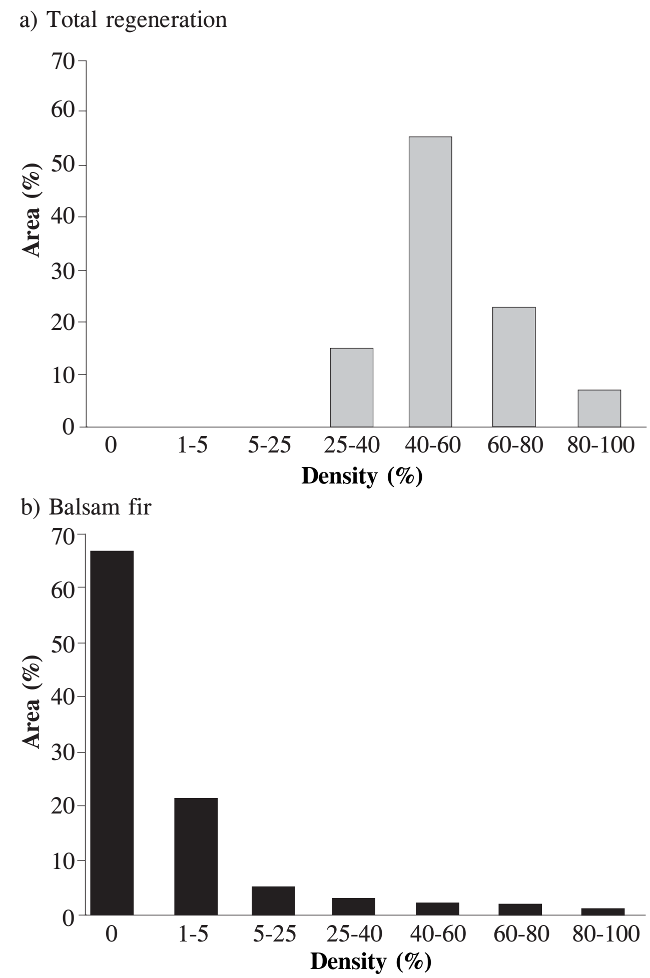

FIGURE 6. Cover density class of tall regeneration (1.5-7 m) in the area of the 1971-1972 hemlock looper outbreak on Anticosti Island, based on the interpretation of 1:10,000 colour photos from a 1997-2000 forest survey.

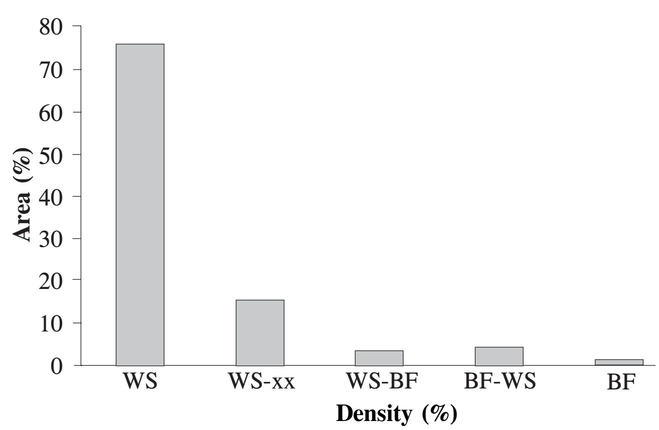

FIGURE 7. Forest composition in the area of the 1971-1972 hemlock looper outbreak on Anticosti Island, based on the dominant or codominant tree species in the 1997-2000 forest survey (WS = white spruce > 75% basal area; WS-xx = white spruce > 50% and balsam fir < 25%; WS-BF = white spruce > 50% and balsam fir > 25%; BF-WS = balsam fir > 50% and white spruce > 25%; BF = balsam fir > 75%).

vival should be higher because a proportion of the eliminated seedlings would have survived.

TABLE II. Dynamics of balsam fir tagged seedlings on Anticosti Island monitored over a 3-y period at 10 sites: five balsam fir forest sites and five clear-cut blocks of the same forest type.

Number of seedlings	Forest sites (n = 5)	Clear-cut blocks (n = 5)
Tagged seedlings - initially (1)	398	1,421
New seedlings (2)	329	176
Dead seedlings - not related to deer (3)	120	783
Partial total (1 + 2 - 3)	607 (153%)[a]	814 (57%)[a]
Browsed seedlings - deer (4)	373[b]	765[c]
Final result - seedlings alive after 3 y (1 + 2 - 3 - 4)	234 (59%)[a]	49 (3%)[a]

[a] Proportion of the initial number.
[b] Includes 131 seedlings that were partially browsed and that we eliminated to avoid erroneous interpretation in the following visits. A portion of those seedlings would probably have survived.
[c] Includes 617 seedlings that were partially browsed and that we eliminated to avoid erroneous interpretation in the following visits. A portion of those seedlings would probably have survived.

The mean annual browsing rate was 26% in the uncut forest sites and 48% in the clear-cut blocks. In the forest sites, the browsing rate was not influenced by the site ($P = 0.588$) and was higher in the last 2 y ($P < 0.001$) than previously. In the clear-cut blocks, blocks that were harvested in 1996 also had a higher rate in recent years, while this was not the case for those harvested in 1995. On a monthly basis (30-d rate), the browsing rate in forest sites tended to be higher in May (7%) and September and October (6%), as opposed to June, July, or August (3-4%) ($P = 0.079$) (Figure 8). In the clear-cut blocks, it was definitely higher in May (18%) and lower in June (5%) than in the other months ($P = 0.037$).

Discussion

IMPACT OF DEER ON ANTICOSTI ISLAND

Since their introduction some 100 y ago, white-tailed deer have had a measurable impact on the forest of Anticosti Island. Once dominated by balsam fir, the forest composition began to change as early as 1910 to 1920. White spruce has become the dominant species of the forest recruits since 1930 (Figure 3). Over the last 50 y, the relative proportion of balsam fir stands in the recruited forest, as compared to white spruce, has never exceeded 10%. In 1971-1972, a hemlock looper outbreak affected an area of 1,200 km^2, massively killing balsam fir stands in only 2 y. Even in such a large area, deer were able to control balsam fir regeneration, so that the new forest taking its place is almost entirely white spruce. After visiting the island in 1953, Pimlott (1963) reported that 40-y old balsam fir stands were common, but that he was unable to locate a single stand originating from seedlings after 1930. More recently, Chouinard and Filion (2001) used dendrochronology to study a semi-open stand originating from a clear-cut followed by a fire in 1959. Most balsam fir stems on this site had a low height or radial growth, except when they reached > 110 cm and could escape deer browsing. Conversely, white spruce was not affected.

The severe impact by white-tailed deer on balsam fir is unique since this browse species is normally considered of low nutritional value (Ullrey *et al.,* 1968). Large-scale

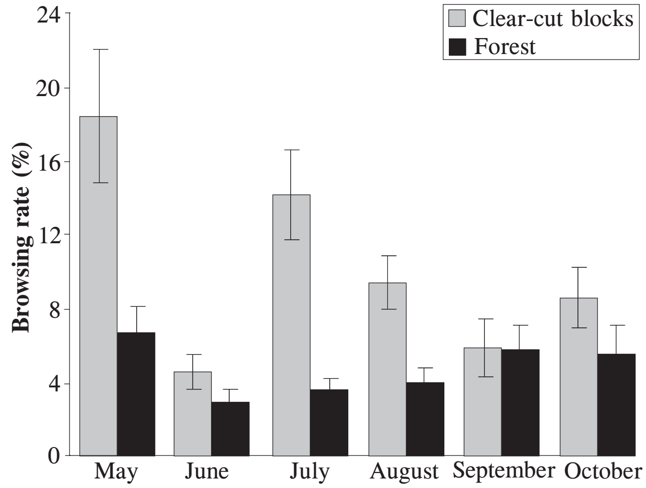

FIGURE 8. Mean browsing rate by month (± SE) of tagged balsam fir seedlings at 10 sites on Anticosti Island (five uncut sites in balsam fir forest, five clear-cut blocks of the same forest type).

negative effects by white-tailed deer have been reported on yew (*Taxus canadensis*) (Alverson *et al.,* 1988; Gill, 1992b; Waller & Alverson, 1997), white cedar (*Thuja occidentalis*) (van Deelen, 1999), eastern hemlock (*Tsuga canadensis*) (Anderson & Loucks, 1979; Anderson & Katz, 1993; Mladenoff & Stearns, 1993; Rooney *et al.,* 2000), and deciduous species (Stewart & Burrows, 1989). Black-tailed deer (*Odocoileus hemionus sitkensis*), introduced prior to 1901 on the Haida Gwaii archipelago, have a similar impact on western redcedar (*Thuja plicata*) (Martin & Baltzinger, 2002). Even for those species, small seedlings (< 15-30 cm) are rarely browsed in favour of larger saplings (Stewart & Burrows, 1989; Rooney *et al.,* 2000). Small seedlings also are rarely browsed by other cervids (Gill, 1992a; Bergstrom & Bergqvist, 1997). On Anticosti, 26% of our tagged small seedlings were browsed each year during the snow-free season, so very few ever reach 30 cm. In their study on the same island, Chouinard and Filion (2001) observed browsing on 37% of seedlings (< 30 cm) and 100% of saplings (> 30 cm). Deer herbivory behaviour on Anticosti is in fact closer to that of goats (*Capra* spp.), which consume even young seedlings (Holdgate, 1967).

Damage to balsam fir has typically been reported for moose (*Alces alces*) on Isle Royale, Michigan (Brandner, Peterson & Risenhoover, 1990; McLaren, 1996) and Newfoundland (Bergerud & Manuel, 1968; Thompson & Curran, 1993; Connor *et al.,* 2000; McLaren *et al.,* 2000). Occurring mostly in winter time, this damage is different and less severe than that produced by deer on Anticosti, which takes place year round. On Isle Royale, Brandner, Peterson, and Risenhoover (1990) reported that continuous browsing by moose kept balsam fir forests in earlier successional stages. On Newfoundland, moose have changed species composition in boreal forest (Connor *et al.,* 2000), but balsam fir still remains common in the overstory or understory (Thompson & Curran, 1993). We agree with Crête, Ouellet, and Lesage (2001), who compared herbivory by caribou/reindeer (*Rangifer tarandus*), moose, and white-tailed deer and concluded that deer were most destructive. Moose do not browse close to the ground, unlike deer, and therefore cannot reach small seedlings.

Changes in the composition of the dominant forest as a result of selective herbivory have been observed elsewhere. In northern Europe, hardwoods and Norway spruce (*Picea abies*) have increased, while Scots pine (*Picea sylvestris*) has decreased (Gill, 1992b). On the Haida Gwaii archipelago, current regeneration of secondary forests will result in a species composition that is deficient in redcedar, as opposed to Sitka spruce (*Picea sitkensis*) and western hemlock (*Tsuga heterophylla*) (Martin & Baltzinger, 2002). In northern Wisconsin, second-growth hardwoods, mainly sugar maple (*Acer saccharum*), have replaced stands once dominated by eastern hemlock (Anderson & Loucks, 1979). In this case, Mladenoff and Stearns (1993) have argued that deer browsing was not the sole factor responsible for the hemlock decline. They suggested that other conditions have worked to suppress hemlock regeneration recently, such as less favourable climatic conditions and less suitable seedbeds. Such alternatives to herbivory are ruled out on Anticosti, because balsam fir regeneration is much more prolific than that of white spruce (Doucet *et al.,* 1996).

Besides effects on tree regeneration, intensive herbivory can have other ecological consequences (Angelstam *et al.,* 2000; Fuller & Gill, 2001). As mentioned earlier, the shrub layer is totally absent, except for regenerating spruces, and most deciduous species have been nearly extirpated (Pimlott, 1963; Potvin *et al.,* 2000). Exclosure experiments and comparison with the neighbouring Mingan Islands, which are devoid of deer, also have shown severe impacts on herbaceous plants (Potvin & Breton, 1992; Moore, Pothier & Potvin, 2001; Viera, 2003). In areas accessible to deer, fireweed (*Epilobium angustifolium*), raspberry (*Rubus idaeus*), and yellow clintonia (*Clintonia borealis*) are rare or absent, while Canada reed-grass (*Calamagrostis canadensis*) and thistles (*Cirsium vulgare* and *C. arvense*) become dominant species. Common when deer were introduced, black bear began to decline 20 y later (McKay, 1979) and are now almost extinct, probably because fruit-plants have disappeared. Insect diversity (*e.g.,* Carabidae) also has been impoverished on Anticosti as a result of replacement of balsam fir by spruce (Hébert & Jobin, 2001).

THE FUTURE

The future of balsam fir on Anticosti is at risk. Most stands (88%) belong to the 90- and > 100-y age classes. Although balsam fir can reach 200 y, this species becomes susceptible to decay and insect outbreaks after 70 y (Doucet *et al.,* 1996). Over the past 10-20 y, we have observed that older balsam fir stands have accelerated in decay, becoming more open as individual trees gradually fall down. In December 1996, a large-scale blowdown (*ca* 400 km^2) took place in the western portion of the island. Local-scale blowdowns have also been reported more recently. Considering the age of remnant fir stands, we estimate that under the present situation of herbivory, most of these will be eradicated and not replaced in 40-50 y. Scattered stands of balsam fir and individual trees will persist, but the large stands that were once dominant will have been almost totally replaced by spruce-dominated stands.

Eradication of balsam fir stands represents the third phase of a process started with deer introduction. Following Caughley's model (Caughley, 1976), we suggest that the population went through a first phase characterized by a rapid increase (Figure 1). After the destruction of the shrub layer, a second phase took place, when the deer density and the vegetation were rather stable. The third phase will start with the eradication of the last large balsam fir stands. Between the second and third phases, the deer population will probably increase in the short term, as fallen trees provide an abundant winter food source (twigs, lichens). This increase may have started already, as indicated by the number of deer seen per hunter-day, which has recently been rising (Potvin *et al.,* 2000). In the long term, a marked decrease in deer numbers will certainly happen, and a new equilibrium level may develop between vegetation and deer, one that is much lower than the recent one.

The eradication of balsam fir stands is a process that will have taken some 150 y and is directly linked to the ecological characteristics of this tree species, especially to its longevity and regeneration strategy. The regeneration strategy of balsam fir is similar to that of hemlock. It is based on an abundant seedling bank that is favoured by the strong shade tolerance of this species (Doucet *et al.,* 1996; Rooney *et al.,* 2000). Because the viability of balsam fir seeds is less than one year, no re-establishment is possible after seed trees have been removed by insect outbreaks, blowdown, or clear-cutting, even if the amount of herbivory decreases.

Deer hunting and recreation tourism are the main economic activities on Anticosti. It is doubtful that the island can remain an attractive destination for hunters over the long term if most balsam fir stands become eradicated, because this change would be related to a large drop of deer population. Is it possible to change the trend created by deer overabundance? In reaction to the negative effects of white-tailed deer, which they consider to be a keystone herbivore, Waller and Alverson (1997) have made two proposals: to expand research and monitoring and to extend our ability to manipulate the populations. In order to protect sensitive species, Alverson, Waller, and Solheim (1988) suggested building exclosures, increasing hunting, and managing the habitat in such a way as to decrease animal densities. Large exclosures and important population reductions have already been applied to some areas (Leader-Williams, Walton & Prince, 1989).

On Anticosti, a forest-deer monitoring program is already in place, part of it having been reported in this paper. Habitat management initiatives have been applied since 1995 and are still being evaluated. Trials include large clear-cuts (Moore, Pothier & Potvin, 2001), seed-tree cuttings (M. Prévost, pers. comm.), and strip clear-cuttings (D. Pothier, pers. comm.). Clear-cut areas also were fenced in 2000 and 2001 and subjected to hunting to decrease deer density. More recently, deer reduction by intensive hunting in local areas is also being tested. In order to manage the scientific program related to those experiments, a research chair was established in 2001, the Chaire de recherche industrielle CRSNG-Produits forestiers Anticosti. For scientists, Anticosti remains a challenge that should help provide solutions to the widespread and increasing problem of herbivore effects on ecosystems.

Acknowledgements

This paper is a contribution from the Chaire de recherche industrielle CRSNG-Produits forestiers Anticosti of Université Laval, Québec. The study was financed by Société de la faune et des parcs du Québec, Ministère des Ressources naturelles du Québec and Produits forestiers Anticosti. We wish to thank J. Huot, D. Pothier, and two anonymous reviewers for their helpful comments on the manuscript.

Literature cited

Alverson, W. S., D. W. Waller & S. L. Solheim, 1988. Forests too deer: Edge effects in northern Wisconsin. Conservation Biology, 2: 348-358.

Anderson, R. C. & A. J. Katz, 1993. Recovery of browse-sensitive tree species following release from white-tailed deer (*Odocoileus virginianus* Zimmerman) browsing pressure. Biological Conservation, 63: 203-208.

Anderson, R. C. & O. L. Loucks, 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology, 16: 855-861.

Angelstam, P., P. E. Wikberg, P. Danilov, W. E. Faber & K. Nygren, 2000. Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russia Karelia. Alces, 36: 133-145.

Banfield, A. W. F., 1974. Les mammifères du Canada. Les Presses de l'Université Laval, Québec, Québec.

Bergerud, A. T. & F. Manuel, 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. Journal of Wildlife Management, 32: 729-746.

Bergstrom, R. & G. Bergqvist, 1997. Frequencies and patterns of browsing by large herbivores on conifer seedlings. Scandinavian Journal of Forest Research, 12: 288-294.

Brandner, T. A., R. O. Peterson & K. L. Risenhoover, 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. Ecology, 71: 155-164.

Cameron, A. W., 1958. Mammals of the islands of the Gulf of St. Lawrence. National Museum of Canada, Bulletin 154, Ottawa, Ontario.

Caughley, G., 1976. Wildlife management and the dynamics of ungulate populations. Pages 183-246 *in* T. H. Coaker (ed.). Applied Biology. Volume I. Academic Press, New York, New York.

Chouinard, A. & L. Filion, 2001. Detrimental effects of white-tailed deer browsing on balsam fir growth and recruitment in a second-growth stand on Anticosti Island, Québec. Écoscience, 8: 199-210.

Connor, K. J., W. B. Ballard, T. Dilworth, S. Mahoney & D. Anions, 2000. Changes in structure of a boreal forest community following intense herbivory by moose. Alces, 36: 111-132.

Crête, M., J. P. Ouellet & L. Lesage, 2001. Comparative effects on plant of caribou/reindeer, moose and white-tailed deer herbivory. Arctic, 54: 407-417.

Darwin, C., 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. John Murray, London.

Doucet, R., M. Pineau, J.-C. Ruel & G. Sheedy, 1996. Sylviculture appliquée. Pages 965-1004 *in* Ordre des ingénieurs forestiers du Québec (éd.). Manuel de foresterie. Les Presses de l'Université Laval, Québec, Québec.

Fuller, R. J. & R. M. A. Gill, 2001. Ecological impacts of deer in woodland. Forestry, 74: 189-192.

Gill, R. M. A., 1992a. A review of damage by mammals in north temperate forests 1. Deer. Forestry, 65: 145-169.

Gill, R. M. A., 1992b. A review of damage by mammals in north temperate forests 3. Impact on trees and forest. Forestry, 65: 363-388.

Graham, S. A., 1954. Changes in northern Michigan forests from browsing by deer. Transactions of the North American Wildlife Conference, 19: 526-533.

Hébert, C. & L. Jobin, 2001. Impact du cerf de Virginie sur la biodiversité des forêts de l'île d'Anticosti. Les insectes comme indicateurs. Naturaliste Canadien, 125(3): 96-107.

Holdgate, M. W., 1967. The influence of introduced species on the ecosystems of temperate oceanic islands. IUCN Publication, New Series, 9: 151-176.

Howard, W. E., 1967. Ecological changes in New Zealand due to introduced mammals. IUCN Publication, New Series, 9: 219-240.

Huot, J., 1982. Body condition and food resources of white-tailed deer on Anticosti island, Québec. Ph.D. thesis, University of Alaska, Fairbanks, Alaska.

Huot, M., G. Lamontagne & F. Goudreault, 2002. Plan de gestion du cerf de Virginie 2002-2008. Société de la faune et des parcs du Québec, Rapport 8047-02-03, Québec, Québec.

Leader-Williams, N., 1988. Reindeer on South Georgia: The Ecology of An Introduced Population. Cambridge University Press, New York, New York.

Leader-Williams, N., D. W. H. Walton & P. A. Prince, 1989. Introduced reindeer in South-Georgia – A management dilemma. Biological Conservation, 47: 1-12.

Lefort, S., 2002. Habitat hivernal du cerf de Virginie (*Odocoileus virginianus*) à l'île d'Anticosti. M.Sc. thesis, Université Laval, Québec, Québec.

Leopold, A., L. K. Sowls & D. L. Spencer, 1947. A survey of overpopulated deer ranges in the United States. Journal of Wildlife Management, 11: 162-177.

MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

Marie-Victorin, F., 1964. Flore laurentienne. Les Presses de l'Université de Montréal, Montréal, Québec.

Martin, J. L. & C. Baltzinger, 2002. Interaction among deer browsing, hunting, and tree regeneration. Canadian Journal of Forest Research, 32: 1254-1264.

Martin-Zédé, G., 1938. L'île ignorée – Journal de l'île d'Anticosti 1895-1926. Archives nationales du Québec, Québec, Québec.

McKay, D., 1979. Anticosti – The Untamed Island. McGraw-Hill Ryerson, Toronto, Ontario.

McLaren, B. E., 1996. Plant-specific response to herbivory: Simulated browsing of suppressed balsam fir on Isle Royale. Ecology, 77: 228-235.

McLaren, B. E., S. P. Mahoney, T. S. Porter & S. M. Oosenbrug, 2000. Spatial and temporal patterns of use by moose of pre-commercially thinned, naturally-regenerating stands of balsam fir in central Newfoundland. Forest Ecology and Management, 133: 179-196.

McLaren, B. E. & R. O. Peterson, 1994. Wolves, moose, and tree rings on Isle Royale. Science, 266: 1555-1558.

McShea, W. J. & J. H. Rappole, 1997. Herbivores and the ecology of forest understory birds. Pages 298-309 *in* W. J. McShea & J. H. Rappole (eds.). The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institute Press, Washington, D.C.

Mladenoff, D. J. & F. Stearns, 1993. Eastern hemlock regeneration and deer browsing in the Great Lakes region - A reexamination and model simulation. Conservation Biology, 7: 889-900.

MLCP, 1987. Plan de gestion de l'orignal. Ministère du Loisir, de la Chasse et de la Pêche, Québec, Québec.

Moore, J. D., D. Pothier & F. Potvin, 2001. La coupe de grande superficie: une solution pour régénérer les sapinières de l'île d'Anticosti en présence de densités élevées de cerfs? L'Aubelle, 137: 16-18.

MRN, 1995. Norme de stratification écoforestière. Troisième programme de connaissance de la ressource forestière. Rapport RN95-3025, Ministère des Ressources naturelles, Service de l'inventaire forestier, Québec, Québec.

Nadeau, G. & P. Beaupré, 1991. Carte des zones forestières de l'île d'Anticosti. Ministère des Forêts, Région de la Côte-Nord, Québec, Québec.

Newsom, W. M., 1937. Mammals on Anticosti island. Journal of Mammalogy, 18: 435-442.

Peterson, R. O., 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service, Scientific Monograph Series 11, Washington, D.C.

Pimlott, D. H., 1963. Influence of deer and moose on boreal forest vegetation in two areas of eastern Canada. Transactions of the International Union of Game Biologists, 6: 105-116.

Potvin, F., P. Beaupré, A. Gingras & D. Pothier, 2000. Le cerf et les sapinières de l'île d'Anticosti. Rapport 4286-00-02, Société de la Faune et des Parcs du Québec, Québec, Québec.

Potvin, F. & L. Breton, 1992. Impact du cerf sur la succession végétale après coupe à Anticosti: suivi d'un ensemble d'exclos de 1984 à 1989. Rapport 1932, Ministère du Loisir, de la Chasse et de la Pêche, Québec, Québec.

Potvin, F., L. Breton & A. Gingras, 1991. La population de cerfs d'Anticosti en 1988-1989. Rapport SP 1779, Ministère du Loisir, de la Chasse et de la Pêche, Québec, Québec.

Potvin, F., R. Joly, M. Bélanger, J. M. Brassard, S. Georges & P. Lessard, 1977. Problématique de la chasse du cerf au Québec. Rapport spécial 8, Ministère du Tourisme, de la Chasse et de la Pêche, Québec, Québec.

Rochette, B., A. Gingras & F. Potvin, 2003. Inventaire aérien du cerf de Virginie de l'île d'Anticosti. Société de la faune et des parcs du Québec, Québec, Québec.

Rooney, T. P., 2001. Deer impacts on forest ecosystems: A North American perspective. Forestry, 74: 201-208.

Rooney, T. P., R. J. McCormick, S. L. Solheim & D. M. Waller, 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper Great Lakes, U.S.A. Ecological Applications, 10: 1119-1132.

Saucier, J. P., J. F. Bergeron, P. Grondin & A. Robitaille, 1998. Les régions écologiques du Québec méridional (3e version): un des éléments hiérarchiques de classification écologique du territoire mis au point par le ministère des Ressources naturelles du Québec. L'Aubelle, 124 (Supplément): 1-12.

Snedecor, G. W. & W. G. Cochran, 1967. Statistical Methods. 6th edition. Iowa State University Press, Ames, Iowa.

Stewart, G. H. & L. E. Burrows, 1989. The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island, New Zealand. Biological Conservation, 49: 275-294.

Thompson, I. D. & W. J. Curran, 1993. A reexamination of moose damage to balsam fir - white birch forests in central Newfoundland - 27 years later. Canadian Journal of Forest Research, 23: 1388-1395.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, B. E. Brent & K. E. Kemp, 1968. Digestibility of cedar and balsam fir browse for the white-tailed deer. Journal of Wildlife Management, 32: 162-171.

van Deelen, T. R., 1999. Deer-cedar interactions during a period of mild winters: Implications for conservation of conifer swamp deeryards in the Great Lakes Region. Natural Areas Journal, 19: 263-274.

Viera, V., 2003. Effets à long terme du cerf de Virginie (*Odocoileus virginianus*) sur les communautés végétales d'un milieu boréal. M. Sc. thesis, Université Laval, Québec, Québec.

Waller, D. M. & W. S. Alverson, 1997. The white-tailed deer: A keystone herbivore. Wildlife Society Bulletin, 25: 217-226.