Fairy slipper (*Calypso bulbosa*) on Anticosti Island: the occurrence of a rare plant in an environment strongly modified by white-tailed deer

Ève-Marie Morissette, Claude Lavoie, and Jean Huot

Abstract: The introduction of white-tailed deer (*Odocoileus virginianus* Zimm.) at the end of the 19th century, and their subsequent proliferation on Anticosti Island (Quebec) has had a strong impact on forest vegetation. Only 50% of the original balsam fir (*Abies balsamea* (L.) Mill.) cover remains on the island, and fir has been progressively replaced by white spruce (*Picea glauca* (Moench) Voss) because of browsing. This phenomenon may have an impact on rare species, such as the fairy slipper orchid (*Calypso bulbosa* (L.) Oakes; Orchidaceae), associated with old fir stands. In this study, we mapped fairy slipper populations on Anticosti Island and collected data on its habitat. We developed a statistical model to identify key environmental characteristics predicting the presence or the absence of the species. We hypothesized that on Anticosti Island, the fairy slipper is restricted to old-growth fir stands located on calcareous soils; consequently, this orchid is endangered because its habitat is gradually disappearing. A total of 69 sampling stations were surveyed along three transects crossing the island. The fairy slipper was present in 19 of the 69 stations. A fir stand, with a large quantity of dead logs and low levels of tree and moss cover, is more likely to harbour a fairy slipper population than any other forest stand. It is possible that on Anticosti Island, the presence of the fairy slipper is associated with forest age and structure (the latter being strongly influenced by deer) rather than with fir per se. Moreover, deer, by browsing shrubs and fir seedlings and saplings, have apparently had a positive impact on the fairy slipper population by eliminating competition between this orchid and other understory plants. On the other hand, deer have hampered the regeneration of fir forests; old fir stands that were eliminated by blowdowns, insect outbreaks, fires or logging have been replaced by spruce stands. This may have an impact on the long term survival of the fairy slipper, unless spruce stands soon provide suitable habitats for the species as they mature.

Key words: Anticosti Island, *Calypso bulbosa*, fairy slipper, *Odocoileus virginianus*, rare plant, white-tailed deer.

Résumé : L'introduction, à la fin du 19^{e} siècle, et la prolifération subséquente du cerf de Virginie (*Odocoileus virginianus* Zimm.) sur l'île d'Anticosti (au Québec) a eu un impact important sur la végétation forestière de l'île. Les forêts de sapins baumiers (*Abies balsamea* (L.) Mill.) sur l'île occupent de nos jours moins de 50 % de leur superficie originale; en raison du broutement du cerf, elles sont progressivement remplacées par des pessières. Ce phénomène pourrait avoir des répercussions sur les espèces rares associées aux vieilles sapinières, notamment sur le calypso bulbeux (*Calypso bulbosa* (L.) Oakes; Orchidaceae). Dans ce travail, nous avons cartographié les populations de calypso de l'île d'Anticosti et prélevé des données sur son habitat. Nous avons construit un modèle statistique pour circonscrire les caractéristiques environnementales favorables à la présence du calypso. Nous avons émis l'hypothèse que cette orchidée ne se trouve sur l'île d'Anticosti que dans les vieilles sapinières reposant sur sol calcaire. En conséquence, l'espèce serait en danger puisque son habitat disparaît peu à peu. Soixante-neuf stations d'échantillonnage ont été inventoriées le long de trois transects traversant l'île. Le calypso était présent dans 19 des 69 stations. Une sapinière avec une grande quantité de troncs morts et un faible couvert arborescent et muscinal est plus susceptible d'abriter une population de calypso que tout autre peuplement forestier. Cela dit, la présence du calypso sur l'île d'Anticosti pourrait être davantage associée à l'âge avancé d'une forêt (et avec sa structure particulière fortement influencée par le cerf) qu'à la présence du sapin en soi. De plus, le cerf a apparemment un impact positif sur le calypso car il élimine par broutement la compétition entre l'orchidée et les autres espèces de plantes (arbustes, plantules et gaules de sapin). Par contre, le cerf empêche la régénération des sapinières; ces dernières ne se reconstituent pas une fois éliminées par des chablis, des épidémies d'insectes, des feux ou la coupe de bois. Cela pourrait donc avoir un impact sur la survie à long terme des populations de calypso, à moins que les pessières qui vieillissent ne fournissent très bientôt des habitats favorables à l'orchidée.

Mots-clés : île d'Anticosti, calypso bulbeux, *Calypso bulbosa*, cerf de Virginie, *Odocoileus virginianus*, plante rare.

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Introduction

The population density of white-tailed deer (*Odocoileus virginianus* Zimm.) in the eastern part of North America has significantly increased during the 20th century (Horsley et al. 2003; Côté et al. 2004). Changes in agricultural and forestry practices, and the reduction of natural predator populations and hunting pressure, are mainly responsible for this expansion (Côté et al. 2004). In several regions, deer browsing has had an impact on plant cover, vegetation structure, and successional patterns of forest communities (Russell et al. 2001; Horsley et al. 2003; Côté et al. 2004; Kraft et al. 2004). A high-density deer population can also decrease plant diversity at a local scale, and eventually be responsible for the extirpation of native species (Anderson 1994; Augustine and Frelich 1998; Fletcher et al. 2001; Stockton et al. 2005; Forrester et al. 2006). Russell et al. (2001) estimated that a deer density > $8.5{\cdot}km^{-2}$ may significantly affect the recruitment of some tree species.

In 1896 and 1897, 220 white-tailed deer were introduced for hunting on Anticosti Island, which is located in the Gulf of St. Lawrence, Quebec (Fig. 1). The deer population rapidly expanded because of the absence of natural predators on the island (Cameron 1958). This population is currently (2006) estimated at 166 000 individuals (Ministère des Ressources naturelles et de la Faune du Québec, unpublished data). The deer density ($21{\cdot}km^{-2}$) is much higher than the critical threshold suggested by Russell et al. (2001) for tree recruitment. The cover of small shrubs and forest herbs on the island has been severely reduced following deer introduction, but the most remarkable vegetation change observed was the decline of balsam fir (*Abies balsamea* (L.) Mill.) forests, and their gradual replacement by white spruce (*Picea glauca* (Moench) Voss) stands (Chouinard and Filion 2001). During winter, fir and spruce are the only available food sources for deer, but fir is preferred over spruce because fir twigs are less fibrous and, consequently, more digestible (Lefort et al. 2007; Sauvé and Côté 2007). The survival of large fir forests on Anticosti Island is at risk: they now cover only 20% of the area of the island, i.e., less than half the area they occupied before deer introduction (Potvin et al. 2003). Most residual fir stands are 90–120 years old, and are particularly vulnerable to natural disturbances, such as blowdowns or insect outbreaks (Potvin et al. 1999). Stands are also cut for lumber. Rare plant species associated with old fir stands may be threatened, and could be extirpated from the island in the next 40–50 years (Potvin et al. 2003); such is the case of the fairy slipper (*Calypso bulbosa* (L.) Oakes; Orchidaceae).

The fairy slipper is an orchid with a circumboreal distribution (Luer 1975; Higman and Penskar 1996). This species is mainly found in peatlands or in old-growth forest stands dominated by conifers such as eastern white cedar (*Thuja occidentalis* L.), fir, or spruce (Case 1987; Higman and Penskar 1996; Reddoch and Reddoch 1997). A mature individual produces a single flower from May to June (Mosquin 1970; Luer 1975; Higman and Penskar 1996). The flower is pollinated by bumblebees (Mosquin 1970; Boyden 1982), but because this plant does not provide any reward (nectar) to visitors, which are therefore deceived, the pollination rate is usually low (Boyden 1982; Proctor and Harder 1995). Although this plant can produce a large amount of seeds once pollinated (Boyden 1982), that does not necessarily ensure the emergence of new individuals, because the fairy slipper is dependant on symbiotic fungi to initiate seed germination and seedling development (Zettler 1996).

Fairy slipper populations are declining in northeastern North America (Caljouw 1981; Case 1987; Higman and Penskar 1996; Reddoch and Reddoch 1997; Dignard and Pouliot 2004). Orchids are removed by plant collectors or lost through logging of old-growth forests (Caljouw 1981; Case 1987; Higman and Penskar 1996). The fairy slipper is possibly more widespread on Anticosti Island than elsewhere in the eastern part of North America, owing to the abundance of calcareous soils on which the orchid is often confined (Reddoch and Reddoch 1997; Dignard and Pouliot 2004). On the other hand, vegetation changes on the island associated with the prolific white-tailed deer may have had an impact on the distribution, abundance, and long-term viability of fairy slipper populations.

The deer invasion on Anticosti Island provides an excellent opportunity to study the impact of an invader on a rare plant species. Do deer have any direct (browsing) or indirect (habitat transformation) impacts on the fairy slipper? In this study, we mapped fairy slipper populations on Anticosti Island and collected data on its habitat. We developed a statistical model to identify key environmental characteristics predicting the presence or absence of the species. We hypothesized that on Anticosti Island, the fairy slipper is strictly found in old-growth fir stands located on calcareous soils. Consequently, this orchid may be endangered because its habitat is gradually disappearing.

Methods

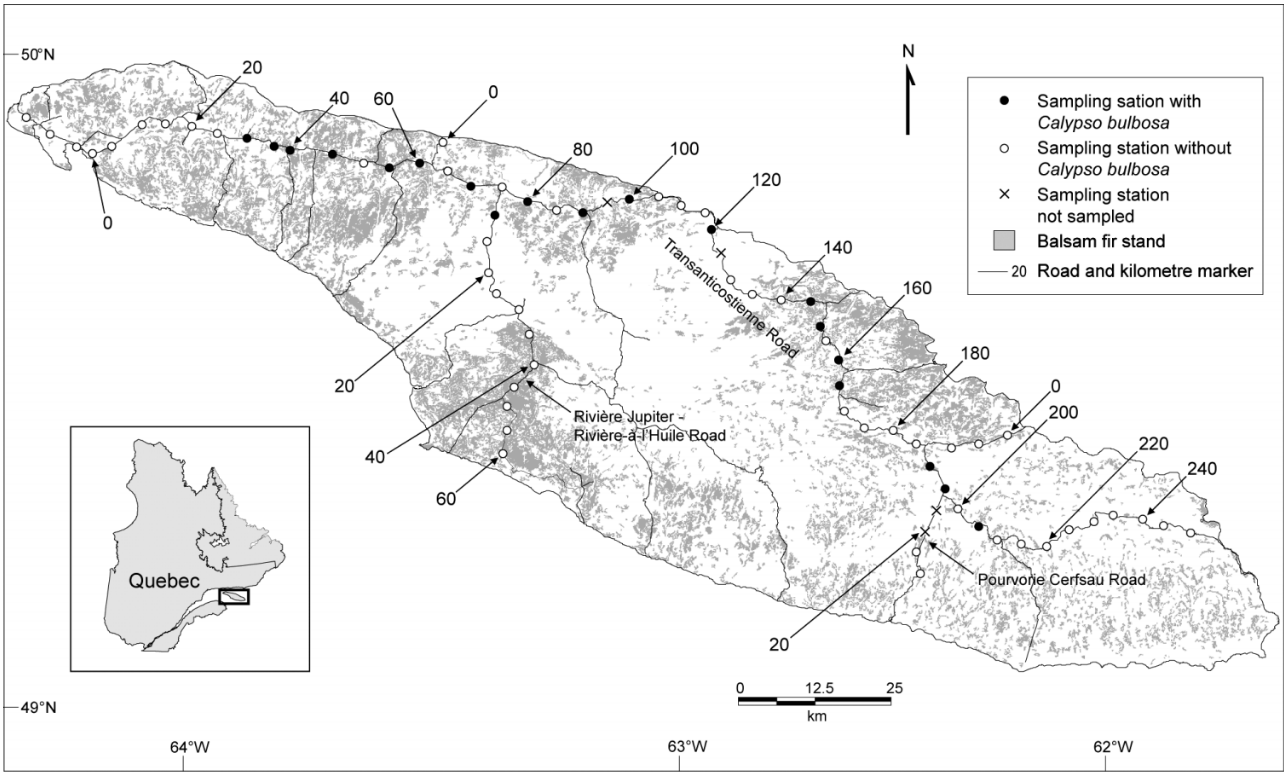
Study area

Anticosti Island covers an area of 7943 km^2 (Fig. 1). The island is located in the boreal forest zone, more specifically in the balsam fir – white spruce or black spruce (*Picea mariana* (Mill.) BSP) bioclimatic domain (Robitaille and Saucier 1998). Fir and spruce forests are widespread, but ombrotrophic and minerotrophic peatlands are also important components of the island. Peatlands cover nearly one third of the area of the island, especially in its southeastern part (Pellerin et al. 2006). The mean annual temperature on the island is 2 °C. The mean annual precipitation totals 1000 mm. About 430 cm of snow fall each year on the island (Environnement Canada 2005).

Spatial distribution of fairy slipper populations around the Gulf of St. Lawrence

To gain a broader perspective on the distribution and abundance of fairy slipper populations around the Gulf of St. Lawrence (USA: Maine; Canada: New Brunswick, Newfoundland, Nova Scotia, Prince Edward Island, and Quebec), we collected information from herbarium specimens of this species sampled in this region and stored in the main herbaria of eastern Canada (Acadia University; Agriculture and Agri-Food Canada; Bishop's University; Canadian Museum of Nature; Gouvernement du Québec; McGill University; Memorial University; New Brunswick Museum; Université Laval; Université de Montréal; Université de Sherbrooke; University of New Brunswick) and Maine (University of

Fig. 1. Spatial distribution of sampling stations, with or without the fairy slipper orchid (*Calypso bulbosa*), surveyed in June 2004 on Anticosti Island (Quebec). Four stations were not sampled because the sites were too heavily disturbed by fire or logging.



Maine). Each herbarium specimen was checked for possible misidentification, and the specimen number, sampling location, year of sampling, habitat characteristics, and name of collector(s) were recorded. Geographic coordinates (latitude, longitude) of sampling sites were identified as precisely as possible using the "TOPOS sur le web" database (Commission de toponymie du Québec 2008) for Quebec locations, the Querying geographical names of Canada database for other Canadian locations (Natural Resources Canada 2008), and the Geographic names information system for Maine locations (United States Board on Geographic Names 2008). Any duplicates or specimens lacking precise information about sampling location or date were discarded. Additional data from Bouchard et al. (1991), Reddoch and Reddoch (1997) and the Centre de données sur le patrimoine naturel du Québec (2004) were also used to map the distribution of the fairy slipper. All data were incorporated into a geographical information system, MapInfo Professional© (MapInfo Corporation 2005).

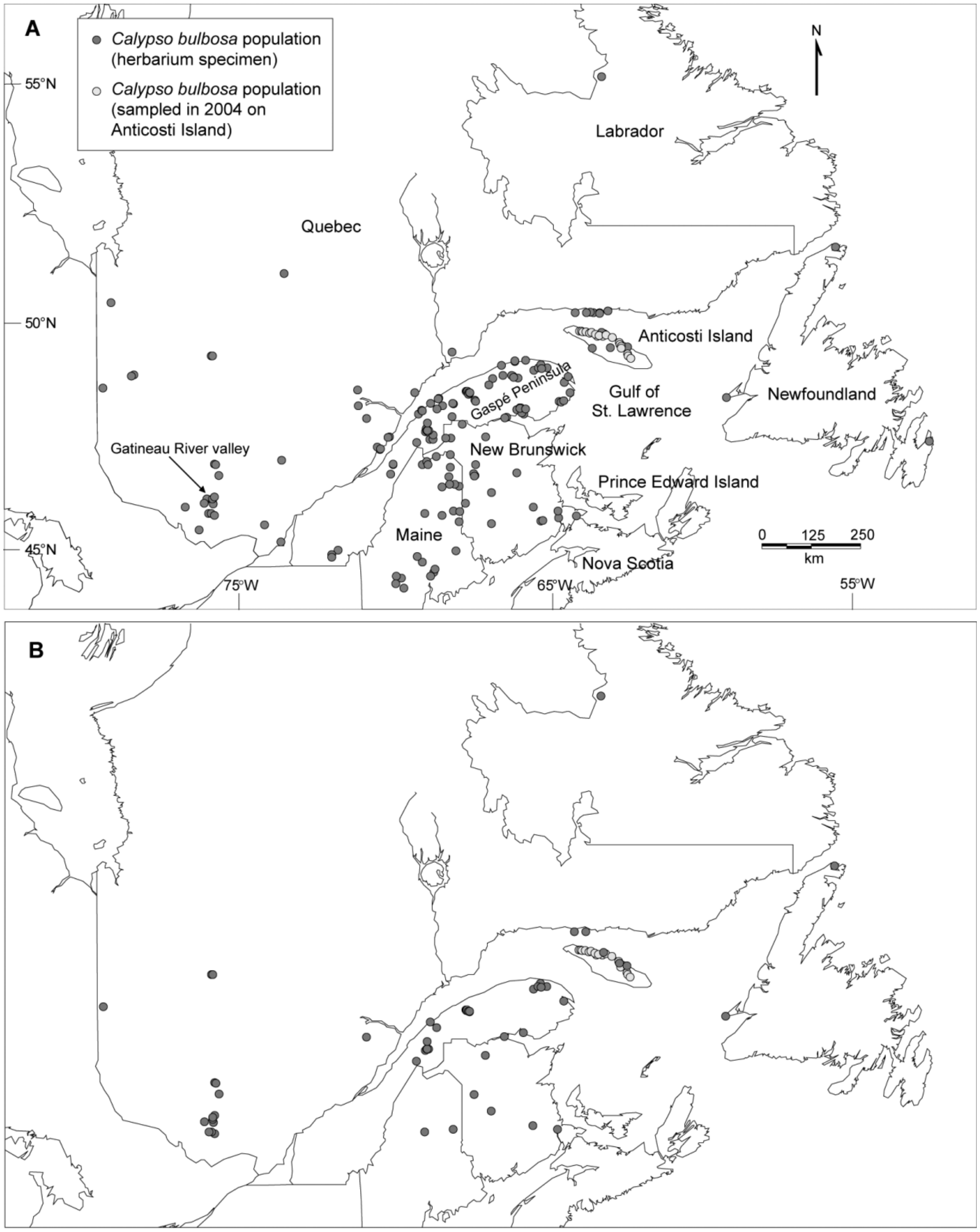
Spatial distribution of fairy slipper populations on Anticosti Island

A survey of fairy slipper populations was undertaken on Anticosti Island from 8–21 June 2004, i.e., during the blooming period of the orchid. Without flowers, a population of this species is inconspicuous and almost impossible to detect. Considering the very short flowering period and the limited accessibility of most parts of the islands (very few roads), the survey was concentrated along three transects (Fig. 1). A sampling station was established every 5 km along the Transanticostienne Road, which crosses the island along its longest axis (northwest to southeast), over a distance of 255 km. Sampling stations were also established along two other roads crossing the island on the opposite axis, one in the western part of the island (Rivière Jupiter – Rivière-à-l'Huile; 60 km long), and the other in the eastern part (Pourvoirie Cerfsau; 25 km long).

Field sampling stations were identified using the kilometre markers positioned along the roads. Only one side of the road (randomly selected) was surveyed. Two or three observers searched on foot for fairy slipper individuals, during a maximum period of 90 min divided by the number of observers. The search was interrupted after the discovery of the first individual; its exact location was then taken with a global positioning system. A 10 m × 10 m quadrat was delineated around the orchid, and the total number of fairy slipper individuals in the quadrat, with and without flowers, was counted. A close examination of each individual was done to detect any evidence of deer browsing. At stations where no fairy slipper was found, a 10 m × 10 m quadrat was delineated 100 m from the road kilometre marker.

In each quadrat, dead and live tree stems (>1 m) were identified to the species and counted, and the diameter at breast height (DBH) was measured. DBH data were used to calculate the basal area occupied by each species (Brack 2001). The tree cover density was measured with a spherical densitometer. Facing each direction (north, south, east, west), an observer took four measurements of the tree cover density at the center of the quadrat. The cover of the moss, herbaceous, shrub, and tree layers < 1 m high was also visually estimated using the following classes: 0%, <1%, 1%–

Fig. 2. Spatial distribution of fairy slipper (*Calypso bulbosa*) populations sampled in northeastern North America. (A) all populations, (B) only populations sampled since 1980.



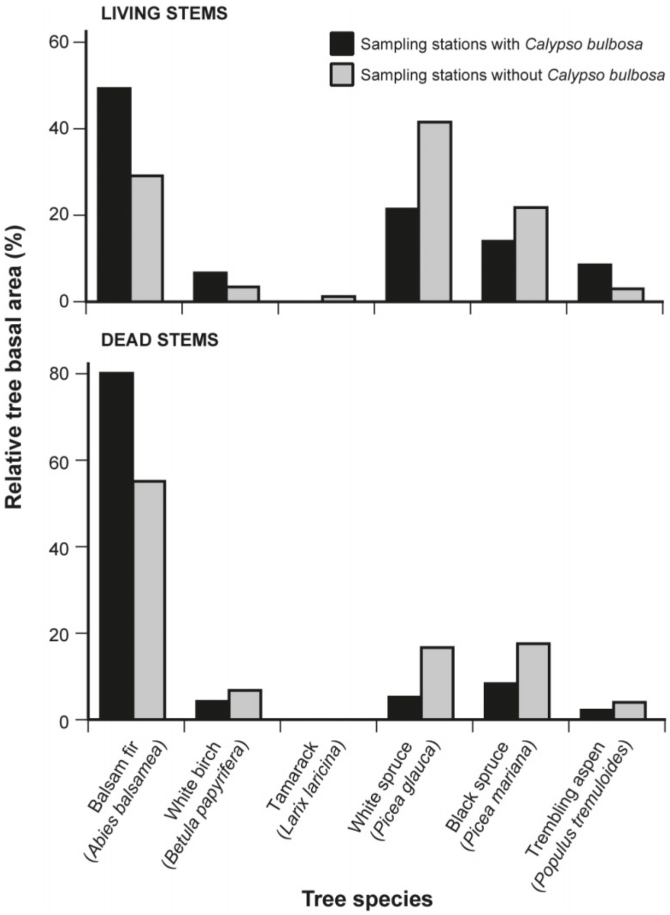
5%, 6%–10%, 11%–25%, 26%–50%, 51%–75%, and 76%–100%.

The drainage of the sampling site was visually evaluated using the following scale: (1) excessive, (2) fast, (3) good, (4) moderate, (5) imperfect, (6) poor, and (7) very poor (Brais et al. 1996). In each quadrat, a Dutch Auger soil sampler was used to take 10 random measurements of the thickness of the organic horizons (O, L, F, and H combined; Soil Classification Working Group 1998). Additional soil samples were also collected to gather data on their physicochemical properties. These samples were collected at the centre of the quadrat. The pH and the concentration of chemical elements (Ca, K, Mg, and Na) of the organic (O) and mineral (B) horizons (Soil Classification Working Group 1998) were measured using the Mehlich extraction method (Mehlich 1984). A particle size analysis was also done on mineral soil samples (Bouyoucos 1962).

Data analysis

T-tests were used to differentiate between sampling stations with or without fairy slipper, based on tree cover density or the basal area of living or dead tree stems (Scherrer 1984). A Hotelling's T^2 test was also used to differentiate between sampling stations with or without fairy slipper

Fig. 3. Relative tree basal area (by species) for living or dead stems in sampling stations of Anticosti Island (Quebec) with or without fairy slipper (*Calypso bulbosa*).



based on physicochemical soil characteristics (Hair et al. 1987). To predict the presence or the absence of the fairy slipper at a particular site, the multicollinearity between the variables was first verified using Pearson's correlation coefficients. Because some variables were significantly correlated, a factor analysis with a VARIMAX rotation (Hair et al. 1987) was used to create a set of new uncorrelated variables (factors). Several binary logistic regression models (Zar 1999) integrating different variables and factors (groups of several variables) were then constructed using the ENTER method (Menard 2002). Each model was evaluated with the Hosmer and Lemeshow likelihood-ratio test for the goodness-of-fit, to determine whether the data were well adjusted to the model, and with the Nagelkerke R^2, which provides an estimation of the level of variance explained by the model (Menard 2002). The Akaike's information criterion (AIC) value was also calculated for each model. A lower AIC score indicates a better model fit (Bollen 1989; Burnham and Anderson 2002). SPSS software (SPSS Inc. 2003) was used for all statistical analyses.

Results

Spatial distribution of the fairy slipper in northeastern North America

Data from herbarium specimens and scientific literature indicated the presence of a minimum of 237 distinct fairy slipper populations in the provinces or states surrounding the Gulf of St. Lawrence, i.e., 190 in Quebec, 26 in Maine, 17 in New Brunswick, and four in Newfoundland-and-Labrador (Fig. 2). However, most reports on the fairy slipper were not recent. Only 87 (37%) of fairy slipper records have been catalogued since 1980, most of them on Anticosti Island, in the Gaspé Peninsula and in western Quebec (Gatineau River valley). A total of 188 herbarium specimens provided information about the habitat colonized by the orchid. About 88% of specimens were collected in a forest stand, mainly in white cedar (71% of specimens sampled in a forest) stands. Fir forests were rarely mentioned (5% of specimens) on herbarium specimen labels as a habitat for the species.

Spatial distribution of the fairy slipper on Anticosti Island

A total of 69 sampling stations were surveyed along the roads of Anticosti Island (Fig. 1). About 38% of these stations had a tree cover dominated by black spruce, 30% by balsam fir, and 29% by white spruce, respectively. One station was located in a peatland, and another in a trembling aspen (*Populus tremuloides* Michx.) stand. The fairy slipper was present in 19 of the 69 stations. Most fairy slipper populations were found in the northeastern part of the island, along the Transanticostienne Road, between kilometres 30 and 120, and between kilometres 145 and 205.

Characteristics of sampling stations with or without fairy slipper on Anticosti Island

The sampling stations with fairy slipper on Anticosti Island were, in general, dominated by fir, based either on the living or dead tree basal areas (Fig. 3). On the other hand, white spruce and black spruce were important components of sites without fairy slipper. However, although most populations of the orchid (12) were found under fir-dominated tree cover, some were also found in black spruce (5) and white spruce (2) stands. There was no significant difference between sampling stations with or without fairy slipper based on either tree cover density or the basal area of living tree stems. However, the basal area of dead tree stems was significantly higher in sampling stations with fairy slipper than in the stations without the orchid ($p = 0.032$). No significant difference was found between sampling stations with or without fairy slipper for physicochemical soil characteristics ($p = 0.127$).

A total of 396 fairy slipper individuals were found in the 19 quadrats that were delineated at the stations where the orchid was present. About 19% of the individuals were in bloom. Approximately half the individuals were found under a tree cover dominated by fir (51%). The others were present in white spruce (28%) or black spruce (21%) stands. At least two flowers had been browsed, but it was impossible to identify the animal responsible for browsing.

Model predicting the presence or the absence of the fairy slipper on Anticosti Island

The variables that were strongly correlated with each other were introduced in a factor analysis. These variables were fir basal area (living stems only), basal area of dead

Table 1. Correlation coefficients between environmental variables sampled on Anticosti Island (Quebec) and three factors resulting from a factor analysis.

Variable	Factor 1	Factor 2	Factor 3
Basal area of living stems of balsam fir (*Abies balsamea*)	0.941	0.122	–0.099
Basal area of dead stems (all tree species included)	0.861	–0.136	0.158
Tree cover	0.261	0.779	0.275
Moss cover	–0.312	0.753	–0.234
Mg concentration in the soil (organic horizon: O)	0.103	0.250	0.746
Mg concentration in the soil (mineral horizon: B)	–0.046	–0.205	0.850

Table 2. Results of a binary logistic regression model predicting the presence or the absence of the fairy slipper (*Calypso bulbosa*) on Anticosti Island (Quebec).

Significant variable	Coefficient (β)	SE	Wald	*p*
Factor 1: basal area of living stems of balsam fir (*Abies balsamea*) and of dead stems (all tree species included)	1.161	0.387	8.981	0.003
Factor 2: plant cover (trees and mosses)	–0.858	0.341	6.323	0.012
Ca concentration in the organic horizon (O) of the soil	0.001	0.001	3.817	0.050
Factor 3: Mg concentration in the organic (O) and mineral (B) horizons of the soil	–0.870	0.450	3.738	0.050

trees (all species included), tree and moss cover, and Mg concentration of the organic and mineral horizons. Three factors were extracted from these six variables. These three factors explained 76% of the total variance observed. Factor 1 is correlated (Table 1) with the basal areas of fir and dead trees, which are the variables with the highest correlation coefficient for this factor (0.941 and 0.861, respectively), Factor 2 with tree cover (0.779) and moss cover (0.753), and Factor 3 with Mg concentration in the organic (0.746) and mineral (0.850) horizons.

The best binomial logistic regression model (based on AIC scores) predicting the presence (or absence) of the fairy slipper at a particular site on Anticosti Island (one of the 69 sampling stations surveyed) included seven variables, i.e., the Ca concentration of the organic horizon, and the six variables that were grouped into three factors by the factor analysis. Globally, the model correctly predicted 86% of the presence or absence of the fairy slipper, with a better prediction of absence (92% correctly predicted) than of presence (68%). The Hosmer and Lemeshow likelihood-ratio test for the goodness-of-fit was significant (p = 0.337; the p value must be > 0.05 for this particular test), and the Nagelkerke R^2 was 0.442. The best predictor of fairy slipper presence (Table 2) was the basal area of fir and of dead trees (Factor 1). The second, third, and fourth best predictors were the vegetation cover (Factor 2), and the concentration of Ca and Mg (Factor 3) in the soil. According to this model, a fir stand, with a large quantity of dead logs and low levels of tree and moss cover, is more likely to harbour a fairy slipper population than any other forest stand on Anticosti Island. A high concentration of Ca and a low concentration of Mg in the soil will also favour the presence of the orchid.

Discussion

The historical data on the spatial distribution of the fairy slipper suggest that Anticosti Island is one of the few sites in northeastern North America where numerous populations of the orchid are still present. The fairy slipper is usually associated with calcareous soils and old-growth forest stands (Case 1987; Higman and Penskar 1996; Reddoch and Reddoch 1997; this study). Anticosti Island is one of the rare sites around the Gulf of St. Lawrence with large areas of calcareous soils (Avramtchev 1985). Moreover, the island still harbours old fir forests, essentially because large-scale logging activities have only been initiated since 1995 (Beaupré et al. 2004). Likewise, the Gaspé Peninsula — another region with several fairy slipper populations — also has large tracts of old-growth fir forests harbouring numerous rare plant species (Desponts et al. 2004); these two regions apparently provide high-quality habitats for the species.

The fairy slipper is now considered a rare species in several provinces or states (Maine, Michigan, New Brunswick, Newfoundland-and-Labrador, Vermont, Wisconsin), and has probably disappeared from the states of New Hampshire and New York, and from the District of Ottawa (Reddoch and Reddoch 1997; Dignard and Pouliot 2004). The apparent recent decline of fairy slipper populations in most regions of northeastern North America can be attributed, in part, to a low sampling effort of herbarium specimens during recent decades (MacDougall et al. 1998; Delisle et al. 2003), but it is more likely the result of an increasing scarcity of habitat. Land reclamation for agriculture or residential development and the extension of large-scale logging activities are probably responsible for the decline of the fairy slipper in several parts of its range (Caljouw 1981; Higman and Penskar 1996; Reddoch and Reddoch 1997). For instance, only 15% of the boreal forest of Quebec that is economically suitable for logging has never been harvested (Commission d'étude sur la gestion de la forêt publique québécoise 2004), which suggests that the area occupied by old-growth forests in the province is very low. The proportion occupied by old forest stands is also decreasing in the Atlantic provinces (Stewart et al. 2003), owing to the expansion of logging activities during recent decades (Hurley et al. 2004).

On Anticosti Island, a forest site dominated by fir, with a large quantity of dead logs and low levels of tree and moss cover, is more likely to harbour a fairy slipper population. These characteristics are typical of the old-growth fir forests of eastern Quebec (Desponts et al. 2004). On the island, the fir stands are particularly old, i.e., 90 to 120 years (Doucet et al. 1996; Potvin et al. 1999). Blowdowns represent the main disturbances in these stands. Gaps are progressively created by small groups of falling trees (Potvin et al. 2003; Thompson et al. 2003). These gaps (more light) are beneficial for the fairy slipper (Case 1987; Reddoch and Reddoch 1997). Normally, they are rapidly filled by fast-growing shrub species, fir seedlings and saplings (Desponts et al. 2004), but this phenomenon is absent on Anticosti Island because of the intense browsing activity of the deer (Tremblay et al. 2006, 2007; Casabon and Pothier 2007). For instance, the biomass of fir and birch (*Betula papyrifera* Marsh.) seedlings < 30 cm-tall in fir forest stands is extremely low ($<1\ g{\cdot}m^{-2}$) on Anticosti Island because of deer browsing, even in sites where seedlings have been released from growth suppression by timber harvesting (Tremblay et al. 2006). Furthermore, almost all deciduous shrub species or tree saplings that were very common before the introduction of deer (*Amelanchier* spp., *Diervilla lonicera* P. Mill., *Populus balsamifera* L., *Populus tremuloides* Michx., *Prunus pensylvanica* L., *P. virginiana* L., *Sorbus americana* Marsh., *Viburnum edule* (Michx.) Raf.) are now rarely found in sites accessible to the animals (Tremblay et al. 2005). It is thus likely that deer maintain favourable light conditions for the fairy slipper for long periods, as long as the fir stand has not been replaced by a dense spruce population.

Dead trees represent an important component of fairy slipper habitat (Mousley 1924; Dignard and Pouliot 2004). The coarse woody debris laying on the soil provides a good substrate for fungus development (Sippola and Renvall 1999; Desponts et al. 2004; Storaunet et al. 2005). Fungi are essential for seed germination and seedling development of orchids (Currah et al. 1988; Zettler 1996). It is also possible that coarse woody debris protect the fairy slipper from deer browsing: a phenomenon observed for other herbaceous species (Rooney 1997; Webster and Parker 2000; Webster et al. 2001), although there is little evidence that the fairy slipper is browsed by deer.

A high concentration of Ca and a low concentration of Mg in the soil could favour the presence of the orchid on Anticosti Island. It is not surprising to find a positive link between the fairy slipper and Ca, since the species is clearly associated with calcareous soils (Reddoch and Reddoch 1997). Mg is essential for plant growth (Shaul 2002), but a high Mg/Ca ratio usually decreases the capacity of a plant to absorb Ca, thereby inhibiting plant growth (Proctor 1971; Fageria 2001). This may explain why the fairy slipper is not likely to be found where Mg concentrations are elevated, but this hypothesis remains to be tested.

On Anticosti Island, the fairy slipper has not been restricted to fir forests. In fact, almost half the individuals were found in spruce stands. It is possible that on Anticosti Island, the presence of the fairy slipper is associated with forest age and structure (the latter being strongly influenced by deer) rather than with fir per se. Elsewhere in northeastern North America, the fairy slipper rarely grows under a fir cover; the understory is usually too dense for the species. On the other hand, the orchid is very often collected in old cedar stands, which share many characteristics with the fir forests of Anticosti Island: open tree cover, several dead trees, and sparse understory (Scott and Murphy 1987; Heigh et al. 2003; Hannah 2004; Park et al. 2005). Old cedar stands are also frequently and heavily browsed by deer (Cornett et al. 2000; Rooney et al. 2002).

Conclusion

On Anticosti Island, the white-tailed deer has apparently had a positive impact on the fairy slipper by eliminating the competition between the orchid and other understory plants (browsing of shrubs, fir seedlings, and saplings). There is no evidence that the animal browses on the orchid, probably because the plant is too rare and ephemeral to be attractive for deer. On the other hand, deer have hampered the regeneration of fir forests; old fir stands that are eliminated by blowdowns, insect outbreaks, fires, or logging are replaced by spruce stands, which may have an impact on the long term survival of the fairy slipper. According to the forest dynamics models that have been constructed for Anticosti Island (Potvin et al. 2003), fairy slipper populations should survive during the next 50 years in the few old fir stands that will remain on the island, especially if the populations of the orchid that have been identified in this study are protected from logging (which is now the case). Meanwhile, as they mature, white and black spruce stands should develop structural characteristics (openings, dead logs) similar to old fir forests, which may offer a good quality habitat for the orchid. This hypothesis could be tested by long-term monitoring of the fairy slipper populations present in fir and spruce stands. In conclusion, this study showed that the interactions between a rare plant and a herbivore are in some cases complex, and are not limited to a simple relationship where the plant progressively disappears due to browsing.

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References

Anderson, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecol. Appl. **4**(1): 104–109. doi:10.2307/1942119.

Augustine, D.J., and Frelich, L.E. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. **12**(5): 995–1004. doi:10.1046/j.1523-1739.1998.97248.x.

Avramtchev, L. 1985. Carte géologique du Québec. Ministère de l’Énergie et des Ressources du Québec, Direction générale de l’exploration géologique et minérale, Québec, Que.

Beaupré, P., Bédard, C., Dufour, C., Gingras, A., Malenfant, C., and Potvin, F. 2004. Plan général d'aménagement intégré des ressources du milieu forestier de l'île d'Anticosti. Parties 1 à 7. Ministère des Ressources naturelles, de la Faune et des Parcs du Québec, Société de la faune et des parcs du Québec et Produits forestiers Anticosti Inc., Québec, Que.

Bollen, K.A. 1989. Structural equations with latent variables. Wiley, New York, N.Y.

Bouchard, A., Hay, S., Brouillet, L., Jean, M., and Saucier, I. 1991. Les plantes vasculaires rares de l'île de Terre-Neuve. Musée canadien de la nature, Ottawa, Ont.

Bouyoucos, G.J. 1962. Hydrometer method improved for making particle size analyses of soils. Agron. J. **54**: 464–465.

Boyden, T.C. 1982. The pollination biology of *Calypso bulbosa* var. *americana* (Orchidaceae): initial deception of bumblebee visitors. Oecologia (Berl.), **55**(2): 178–184. doi:10.1007/BF00384485.

Brack, C. 2001. Forest measurement and modeling. Measuring trees, stands and forests for effective forest management. Australian National University, Canberra [online]. Available from fennerschool-associated.anu.edu.au//mensuration/home.htm [cited 1 December 2008].

Brais, S., Brazeau, M., Brown, J.-L., Camiré, C., Paré, D., and Robitaille, A. 1996. Géologie, dépôts de surface et sols forestiers. *In* Manuel de foresterie. *Edited by* J.A. Bérard and M. Côté. Presses de l'Université Laval et Ordre des ingénieurs forestiers du Québec, Québec, Que. pp. 3–95.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Spinger, New York, N.Y.

Caljouw, C. 1981. Life history and management recommendations for Calypso, *Calypso bulbosa*, in Scraggly Lake Public Lot. T7 R8 WELS. Report to the Bureau of Public Lands, Augusta, Maine.

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

Casabon, C., and Pothier, D. 2007. Browsing of tree regeneration by white-tailed deer in large clearcuts on Anticosti Island, Quebec. For. Ecol. Manage. **253**(1–3): 112–119. doi:10.1016/j.foreco.2007.07.009.

Case, F.W. 1987. Orchids of the western Great Lakes region. Cranbrook Institute of Science, Bloomfield Hills, Mich.

Centre de données sur le patrimoine naturel du Québec. 2004. *Calypso bulbosa*. Ministère du Développement durable, de l'Environnement et des Parcs du Québec, Centre de données sur le patrimoine naturel du Québec, Québec, Que.

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

Commission d'étude sur la gestion de la forêt publique québécoise. 2004. Rapport de la Commission d'étude sur la gestion de la forêt publique québécoise. Gouvernement du Québec, Québec, Que.

Commission de toponymie du Québec. 2008. TOPOS sur le web. Commission de toponymie du Québec, Québec, Que. [Online]. Available from www.toponymie.gouv.qc.ca/ct/accueil.html [cited 1 December 2008].

Cornett, M.W., Frelich, L.E., Puettmann, K.J., and Reich, P.B. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. Biol. Conserv. **93**(3): 359–369. doi:10.1016/S0006-3207(99)00129-9.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. **35**(1): 113–147. doi:10.1146/annurev.ecolsys.35.021103.105725.

Currah, R.S., Hambleton, S., and Smreciu, A. 1988. Mycorrhizae and mycorrhizal fungi of *Calypso bulbosa.* Am. J. Bot. **75**(5): 739–752. doi:10.2307/2444206.

Delisle, F., Lavoie, C., Jean, M., and Lachance, D. 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. J. Biogeogr. **30**: 1033–1042.

Desponts, M., Brunet, G., Bélanger, L., and Bouchard, M. 2004. The eastern boreal old-growth balsam fir forest: a distinct ecosystem. Can. J. Bot. **82**(6): 830–849. doi:10.1139/b04-063.

Dignard, N., and Pouliot, D. 2004. Calypso bulbeux variété américaine. Plantes susceptibles d'être désignées menacées ou vulnérables au Québec. Ministère des Ressources naturelles, de la Faune et des Parcs du Québec et Ministère de l'Environnement du Québec, Québec, Que.

Doucet, R., Pineau, M., Ruel, J., and Sheedy, G. 1996. Sylviculture appliquée. *In* Manuel de foresterie. *Edited by* J.A. Bérard and M. Côté. Presses de l'Université Laval et Ordre des ingénieurs forestiers du Québec, Québec, Que. pp. 965–1004.

Environnement Canada. 2005. Normales et moyennes climatiques au Canada 1971–2000. Environnement Canada [online]. Available from www.climate.weatheroffice.ec.gc.ca [cited 5 April 2005].

Fageria, V.D. 2001. Nutrient interactions in crop plants. J. Plant Nutr. **24**(8): 1269–1290. doi:10.1081/PLN-100106981.

Fletcher, J.D., Shipley, L.A., McShea, W.J., and Shumway, D.L. 2001. Wildlife herbivory and rare plants: the effects of white-tailed deer, rodents, and insects on growth and survival of Turk's cap lily. Biol. Conserv. **101**(2): 229–238. doi:10.1016/S0006-3207(01)00070-2.

Forrester, J.A., Leopold, D.J., and Underwood, H.B. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. Am. Midl. Nat. **156**(1): 135–150. doi:10.1674/0003-0031(2006)156[135:ITEOWD]2.0.CO;2.

Hair, J.F., Anderson, R.E., and Tatham, R.L. 1987. Multivariate data analysis with readings. Macmillan, New York, N.Y.

Hannah, P.R. 2004. Stand structures and height growth patterns in northern white cedar stands on wet sites in Vermont. North. J. Appl. For. **21**: 173–179.

Heigh, J., Fox, G., McKenney, D., and Rollins, K. 2003. The economic impact of the 1998 ice storm on eastern Ontario woodlots: case studies of red pine and white cedar. For. Chron. **79**: 31–46.

Higman, P.J., and Penskar, M.R. 1996. Special plant abstract for *Calypso bulbosa* (calypso orchid). Michigan Natural Features Inventory, Lansing, Mich.

Horsley, S.B., Stout, S.L., and deCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. **13**(1): 98–118. doi:10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2.

Hurley, J.E., Loo, J., DesRochers, P., and Hirvonen, H. 2004. L'état de santé des forêts au Canada, écozone de l'Atlantique maritime 2003. Ressources naturelles Canada, Service canadien des forêts, Direction générale des sciences, Ottawa, Ont.

Kraft, L.S., Crow, T.R., Buckley, D.S., Nauertz, E.A., and Zasada, J.C. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. For. Ecol. Manage. **199**: 219–230.

Lefort, S., Tremblay, J.-P., Fournier, F., Potvin, F., and Huot, J. 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of their distribution range. Ecoscience, **14**(1): 109–116. doi:10.2980/1195-6860(2007)14[109:IOBFAW]2.0.CO;2.

Luer, C.A. 1975. The native orchids of the United States and Canada excluding Florida. New York Botanical Garden, New York, N.Y.

MacDougall, A.S., Loo, J.A., Clayden, S.R., Goltz, J.G., and Hinds, H.R. 1998. Defining conservation priorities for plant taxa in southeastern New Brunswick, Canada using herbarium records. Biol. Conserv. **86**(3): 325–338. doi:10.1016/S0006-3207(98)00031-7.

MapInfo Corporation. 2005. MapInfo Professional, version 8.0. MapInfo Corporation, Troy, Ohio.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun. Soil. Sci. Plant Anal. **15**(12): 1409–1416. doi:10.1080/00103628409367568.

Menard, S.W. 2002. Applied logistic regression analysis. Sage Publications, Thousand Oaks, Calif.

Mosquin, T. 1970. The reproductive biology of *Calypso bulbosa* (Orchidaceae). Can. Field Nat. **84**: 291–296.

Mousley, H. 1924. Calypso. J. N Y Bot. Garden, **25**: 25–30.

Natural Resources Canada. 2008. Querying geographical names of Canada. Natural Resources Canada, Ottawa, Ont. [online]. Available from geonames.nrcan.gc.ca/search/search_e.php [cited 1 December 2008].

Park, A., Kneeshaw, D., Bergeron, Y., and Leduc, A. 2005. Spatial relationships and tree species associations across a 236-year boreal mixedwood chronosequence. Can. J. For. Res. **35**(3): 750–761. doi:10.1139/x04-199.

Pellerin, S., Huot, J., and Côté, S.D. 2006. Long term effects of deer browsing and trampling on the vegetation of peatlands. Biol. Conserv. **128**(3): 316–326. doi:10.1016/j.biocon.2005.09.039.

Potvin, F., Beaupré, P., Gingras, A., and Pothier, D. 1999. Le cerf et les sapinières de l'île d'Anticosti. Société de la Faune et des Parcs du Québec, Direction de la faune et des habitats, Québec, Que.

Potvin, F., Beaupré, P., and Laprise, G. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Québec: a 150-year process. Ecoscience, **10**: 487–495.

Proctor, J. 1971. The plant ecology of serpentine: III. The influence of a high magnesium/calcium ratio and high nickel and chromium levels in some British and Swedish serpentine soils. J. Ecol. **59**(3): 827–842. doi:10.2307/2258143.

Proctor, H.C., and Harder, L.D. 1995. Effect of pollination success on floral longevity in the orchid *Calypso bulbosa* (Orchidaceae). Am. J. Bot. **82**(9): 1131–1136. doi:10.2307/2446066.

Reddoch, J.M., and Reddoch, A.H. 1997. The orchids in the Ottawa district: floristics, phytogeography, population studies and historical review. Can. Field Nat. **111**: 1–185.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Ministère des Resources naturelles du Québec, Direction de la gestion des stocks forestiers et Direction des relations publiques, Québec, Que.

Rooney, T.P. 1997. Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. J. Torrey Bot. Soc. **124**(4): 280–285. doi:10.2307/2997262.

Rooney, T.P., Solheim, S.L., and Waller, D.M. 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. For. Ecol. Manage. **163**(1-3): 119–130. doi:10.1016/S0378-1127(01)00532-1.

Russell, F.L., Zippin, D.B., and Fowler, N.L. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. Am. Midl. Nat. **146**(1): 1–26. doi:10.1674/0003-0031(2001)146[0001:EOWTDO]2.0.CO;2.

Sauvé, D.G., and Côté, S.D. 2007. Winter forage selection in white-tailed deer at high density: balsam fir is the best of a bad choice. J. Wildl. Manage. **71**(3): 911–914. doi:10.2193/2006-056.

Scherrer, B. 1984. Biostatistique. Gaëtan Morin, Chicoutimi, Que.

Scott, M.L., and Murphy, P.G. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. Am. Midl. Nat. **117**(1): 10–16. doi:10.2307/2425702.

Shaul, O. 2002. Magnesium transport and function in plants: the tip of the iceberg. Biometals, **15**(3): 309–323. doi:10.1023/A:1016091118585. PMID:12206396.

Sippola, A.-L., and Renvall, P. 1999. Wood-decomposing fungi and seed-tree cutting: a 40-year perspective. For. Ecol. Manage. **115**(2-3): 183–201. doi:10.1016/S0378-1127(98)00398-3.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Agriculture and Agri-Food Canada, Ottawa, Ont.

SPSS Inc. 2003. SPSS version 12.0. SPSS Inc., Chicago, Ill.

Stewart, B.J., Neily, P.D., Quigley, E.J., Duke, A.P., and Benjamin, L.K. 2003. Selected Nova Scotia old-growth forests: age, ecology, structure, scoring. For. Chron. **79**: 632–644.

Stockton, S.A., Allombert, S., Gaston, A.J., and Martin, J.-L. 2005. A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. Biol. Conserv. **126**(1): 118–128. doi:10.1016/j.biocon.2005.06.006.

Storaunet, K.O., Rolstad, J., Gjerde, I., and Gundersen, V.S. 2005. Historical logging, productivity, and structural characteristics of boreal coniferous forests in Norway. Silva Fenn. **39**: 429–442.

Thompson, I.D., Larson, D.J., and Montevecchi, W.A. 2003. Characterization of old 'wet boreal' forests, with an example from balsam fir forests of western Newfounland. Environ. Rev. **11**(S1): S23–S46. doi:10.1139/a03-012.

Tremblay, J.-P., Thibault, I., Dussault, C., Huot, J., and Côté, S.D. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. Can. J. Zool. **83**: 1087–1096.

Tremblay, J.-P., Huot, J., and Potvin, F. 2006. Divergent nonlinear responses of the boreal forest field layer along an experiment gradient of deer densities. Oecologia (Berl.), **150**(1): 78–88. doi:10.1007/s00442-006-0504-2.

Tremblay, J.-P., Huot, J., and Potvin, F. 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. J. Appl. Ecol. **44**(3): 552–562. doi:10.1111/j.1365-2664.2007.01290.x.

United States Board on Geographic Names. 2008. Geographic names information system. United States Geological Survey, Washington DC [online]. Available from geonames.usgs.gov [cited 1 December 2008].

Webster, C.R., and Parker, G.R. 2000. Evaluation of *Osmorhiza claytonii* (Michx.) C.B. Clarke, *Arisaema triphyllum* (L.) Schott, and *Actaea pachypoda* Ell. as potential indicators of white-tailed deer overabundance. Nat. Areas J. **20**: 176–188.

Webster, C.R., Jenkins, M.A., and Parker, G.R. 2001. A field test of herbaceous plant indicators of deer browsing intensity in mesic hardwood forests of Indiana, USA. Nat. Areas J. **21**: 149–158.

Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, N.J.

Zettler, L.W. 1996. Symbiotic seed germination of terrestrial orchids in North America during the last decade. A progress report. *In* Proceedings of the North American native terrestrial orchids propagation and production conference. *Edited by* C. Alen. National Arboretum, Washington DC. pp. 43–54.