Volume 255, issue 12, 30 June 2008
ISSN 0378-1127
ELSEVIER

Forest Ecology and Management

Forest Ecology and Management 255 (2008) 3973–3979

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Deer prevent western redcedar (*Thuya plicata*) regeneration in old-growth forests of Haida Gwaii: Is there a potential for recovery?

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ARTICLE INFO

Article history:
Received 4 December 2007
Received in revised form 14 March 2008
Accepted 20 March 2008

Keywords:
Deer browsing
Enclosures
Forest composition
Tree regeneration

ABSTRACT

The current increase in deer populations in many forests has fostered a growing concern about their impact on forest ecology. Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) were introduced to Haida Gwaii (British Columbia, Canada) in the late 19th century, and they have dramatically affected the regeneration of woody species in both old- and second-growth forests since then. The lack of recruitment in western redcedar (*Thuja plicata*) in old-growth forests has been attributed to deer. The objectives of this study were to (1) experimentally confirm that deer browsing causes a lack of western redcedar recruitment and (2) assess the potential for and speed of recovery after a prolonged exclusion of deer. We installed a set of 20 enclosures and monitored them over a period of 8 years from 1997 to 2005. We compared temporal changes in redcedar cover and in the survival and growth of marked seedlings in plots that were or were not accessible to deer. Redcedar cover in the vegetation layer accessible to deer was generally low (from 3 to 5%) but higher inside the enclosures (an average difference of 2.3%). Protected seedlings survived better, were higher, presented more leafed shoots, and had less stems than unprotected individuals, features that suggest that deer were key to the lack of regeneration. However, growth was very slow (protected marked seedlings grew 2.5 cm on average in 8 years) and, under the current conditions, the time required for a protected seedling to escape deer would probably take over two decades. This very slow growth rate under closed canopy conditions probably reflects a gap-phase regeneration strategy and/or sensitivity to competition with other woody species. The combination of a very slow growth with a high palatability and a lack of physical defences, in contrast to the other dominant conifers in this ecosystem, probably explain why redcedar regeneration can be eliminated from old-growth forest by abundant deer populations.

1. Introduction

Human-induced disturbances such as the eradication of large predators, strict control of large game hunting, dramatic changes in agricultural and forestry practices have led to the considerable expansion of deer populations in many temperate forests. Furthermore, in the absence of control mechanisms other than food availability, deer can reach high densities and profoundly affect plant species composition, in particular the absolute and relative abundance of woody species (Anderson and Katz, 1993). Deer have indeed affected forest vegetation both in North America (McShea et al., 1997; Côté et al., 2004) and Europe (Kuiters et al., 1996; Suominen, 1999). Their effect on the vegetation results from the interplay of diet preferences and differential sensitivity and/or recovery of plant species (Stockton et al., 2005). Therefore, deer browsing can modify competitive relationships among plant species (Sage et al., 2003; Côté et al., 2004). Changes in the abundance of a given species can also trigger a cascade of indirect effects on other components of the ecosystem (Pace et al., 1999). Dense deer populations have been shown to have negative effects on animal species by depleting their resources or by modifying the composition and physical structure of their habitat (Côté et al., 2004; Allombert et al., 2005a,b).

The negative effect on tree regeneration was one of the first effects reported in deer-influenced forest systems (Rooney et al., 2002; Palmer and Truscott, 2003; Tremblay et al., 2007). For instance, in North America, white-tailed deer (*Odocoileus virginianus*) are implicated in the recruitment failure of the northern white cedar (*Thuja occidentalis*) and eastern hemlock (*Tsuga occidentalis*)

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doi:10.1016/j.foreco.2008.03.039

(Rooney, 2001; Rooney and Waller, 2003). This has resulted in high costs to the forest industry. Several studies performed in second-growth forests have suggested that deer browsing was able to modify forest composition by the process of selective browsing on tree species. However, in most places the increase in deer density occurred together with changes in land uses, thus introducing confounding effects in experiments that intended to test the hypothesis that deer were the main drivers in forest dynamics. In addition, little information was available on deer effects on tree regeneration in old-growth forests.

The introduction of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) to Haida Gwaii in the late 19th century has provided a unique context to analyse the effect of uncontrolled deer populations on tree regeneration in otherwise undisturbed natural forests. Black-tailed deer are native to such forests on the mainland. In the absence of native deer and of their natural predators, and in a context of mild winters with little or no snow on the ground, the introduced deer proliferated and colonized most of the archipelago. However, the tree composition of the present mature forests still provides a reference of what normal tree composition would be in the absence of deer. Earlier studies have shown that deer had a strong preference for western redcedar (*Thuja plicata*), one of the three dominant conifers in this type of forest, and suggested that they prevent its regeneration in mature forests both under canopy cover and in small gaps (Martin and Daufresne, 1999). When large gaps were created by clear cutting, regeneration was still severely reduced by browsing (Martin and Baltzinger, 2002) but a few trees with a better genetic potential to produce effective chemical defences managed to persist (Vourc'h et al., 2002).

The recovery of the vegetation from severe browsing may require prolonged periods of reduced deer population densities and/or human intervention favouring vegetation recovery (Scheffer et al., 2001). In addition, Augustine et al. (1998) showed that alternative stable states are not necessarily reversible when browsing pressure is reduced.

Therefore, this study was designed to (1) confirm that deer browsing explained the lack of western redcedar recruitment in the mature forests of Haida Gwaii, and (2) assess the potential for, and speed of recovery after, a prolonged exclusion of deer.

2. Materials and methods

2.1. Study area

Our study area is situated on the largest island, Graham (6361 km^2) in the north of the Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia, Canada). Haida Gwaii is located at about 80 km west of the Canadian mainland and belongs to the same climatic zone as the adjacent mainland (Maritime temperate climates; Köppen climate classification) and is in the Coastal Western Hemlock biogeoclimatic zone (Banner et al., 1989). The archipelago is covered with coastal temperate rain forests and still contains over 540 000 ha of mature natural forest of which 203 000 ha are protected. The flora and fauna are similar to those found in Southeastern Alaska, but species richness is lower compared to the mainland (655 vascular plant species on the archipelago versus 2300 on the mainland). The temperate rain forest canopy is dominated by three tall, long-lived conifers: western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*) and western redcedar. Western redcedar (Cupressaceae) is a native evergreen tree from southern Alaska to northern California. Although mainly a coastal species, it is also found as far inland as western Montana. It is a shade-tolerant species, able to grow and reproduce under dense shade. It can reach 50–60 m in height (Pojar and MacKinnon, 1994) but is heavily browsed by Sitka black-tailed deer. Western redcedar is also an important commercial species for the forest industry and old mature trees are an essential cultural component for most First Nations along the western coast of Canada.

Deer were introduced to the archipelago in the North of Graham Island (Masset area) in the late 19th century as a source of game for the settlers of European descent. The mild climate, lush vegetation, absence of wolves and cougars, low hunting pressure and a lack of large competing herbivores allowed the population to increase rapidly; the current estimated population ranges between 113 000 and 250 000 individuals on 8500 km^2 of available habitat (Martin and Baltzinger, 2002). Average population density on the larger islands has been estimated at about 13 deer per km^2 (Engelstoft, 2001). However, on smaller islands covered by old-growth forest density estimates reached 33 deer per km^2 (Daufresne and Martin, 1997). These densities are higher than those found on the mainland, where the presence of natural predators and more severe winters are likely to keep deer populations in check (M.D. Kirchhoff, pers. com.). In our study area, the forest vegetation has already been strongly affected by the long-term presence of deer. In particular, deer have removed most of the understorey vegetation (Stockton et al., 2005) which has become sparse and offers little physical protection to young seedlings.

2.2. Design of the experiment

Our experiment was designed to characterize the impact of deer on forest understorey vegetation and to monitor the changes following deer exclusion. The cover percentage of all species present in the study area was surveyed using the same methodology as for redcedar (see below). However, in the present paper we have chosen to focus on redcedar cover and its regeneration dynamics because of growing concerns about its ability to persist in the forest composition (Wiggins, 1999).

The experiment consisted of 10 pairs of square enclosures (25 m^2) set up in 1997 in 10 sites (two enclosures per site) situated in remnant old-growth forest patches on Graham Island. Each enclosure was paired with an unfenced area (25 m^2). These 10 study sites were initially chosen so that they had an abundance of redcedar seedlings. All sites were situated under mature canopy which limited the amount of light reaching the ground.

We estimated (to the nearest percentage, using a 0.25 m^2 frame) and monitored the cover percentage of redcedar and of the other dominant tree (Sitka spruce and western hemlock) and shrub species (salal, *Gaultheria shallon*), inside the enclosures and in the unfenced reference areas within two distinct height strata: up to 1.5 m above the ground and from 1.5 to 4 m, hereafter referred to as the lower and upper stratum, respectively. The lower stratum is situated below the browse line (1.5 m) corresponding to the maximum height a deer can reach (Martin and Daufresne, 1999): the upper stratum is above the line.

In addition, we marked off sixteen 50-by-50-centimetre square plots per site. We placed four plots inside each enclosure and four outside each enclosure. In each of these plots, we marked 10 redcedar seedlings with numbered darvik bands and regularly monitored them between 1997 and 2005. We thus monitored 800 seedlings in 80 plots protected by the enclosure and 800 seedlings in 80 plots accessible to deer. At each visit, we measured the height of each marked tree, its number of leafed shoots, its number of stems and, in 2005, we estimated the average shoot leaf area by measuring their length and width. We used these morphological measurements to compare the growth and shape of redcedar seedlings in the absence and presence of deer. We always collected the data in late summer or early autumn.

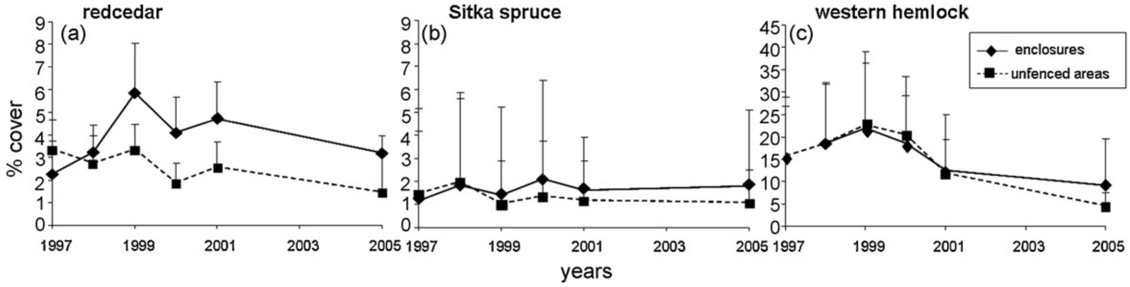

Fig. 1. Change in average cover percentage (+S.E.) per site in the first height stratum (1.5 m above the ground) of the three dominant tree species redcedar (a) Sitka spruce (b) and western hemlock (c) inside and outside enclosures from 1997 to 2005.

2.3. *Statistical analysis*

2.3.1. *Changes in tree cover*

Given that the assumptions of Gaussian distribution, homogeneity of variance and independence could not be verified with our structured data, we conducted non-parametric analyses. We used two-sided non-parametric Wilcoxon signed-rank tests to compare paired cover percentage data sampled inside and outside each enclosure at the same study site at three dates (1997, 2001 and 2005). If a significant difference existed between enclosures and unfenced areas at any given date, we ran a second Wilcoxon signed-rank test to check if the amount of difference was changing over time. For this, we analysed the variation in the difference in cover percentage between the inside and the outside of each enclosure for two periods: first between 1997 and 2001 and then between 2001 and 2005. Since we expected a positive effect of the enclosures, we conducted one-sided tests.

Finally, to document possible effects of interspecific competition in the enclosures, we used a simple linear regression to check if, between 1997 and 2005, there was a correlation between the variation in cover percentage of redcedar, and the variation in cover percentage of western hemlock and of salal (these data show a Gaussian distribution).

2.3.2. *Survival and growth of redcedar seedlings*

We analysed the survival of the marked redcedar seedlings with a Wilcoxon signed-rank test comparing the number of seedlings alive inside and outside the enclosures. As the initial number of seedlings (in 1997) was, by design, similar inside and outside each enclosure (40 seedlings inside and 40 outside), we ran the test on the data collected in 1998, 2001 and 2005, considering the sample size of live seedlings inside the protected plots and the paired unfenced plots as the statistical individual ($n = 20$). Data on seedling height (measured in 1997, 2001 and 2005) were analysed with a Chi-squared test of independence. We defined three classes for seedling height ($\leq$5 cm; (5–10 cm); and $>$10 cm), four classes for the number of leafed shoots (0; 1; (2–5); $>$5 leafed shoots) and two classes for the number of stems (a single stem versus more than one stem). We then calculated the sample sizes in each class inside and outside the enclosures and compared treatments with Chi-squared tests (each class must have a theoretical sample size larger or equal to 5, Cochran, 1954). The average area of leafed shoots measured in 2005 was analysed with a Wilcoxon rank sum test to check if the protection from deer browsing also influenced this trait. We then checked the potential correlation between morphological traits by using simple linear regressions. We conducted the test on the data available for surviving individuals in the enclosures in 2005 (these data show a Gaussian distribution).

We used the S-PLUS 7.0 software for all statistical analyses and the significance threshold was set to $P = 0.05$.

3. Results

3.1. *Tree cover*

Western hemlock had the highest initial cover of all three conifers studied with an average value for the upper and lower strata combined of about 20% per site in 1997, compared to 4% for redcedar and 2% for Sitka Spruce.

Initial redcedar cover was low in both the enclosures and unfenced areas. In the unfenced plots redcedar cover decreased over time (Fig. 1a). We observed significant differences in redcedar cover percentage inside and outside of the enclosures in the lower stratum at the three dates tested (1997, $z = 3.27$, $P < 0.001$; 2001, $z = 3.10$, $P = 0.002$ and 2005, $z = 3.14$, $P = 0.002$). Redcedar cover peaked 2 years after protection. The amount of difference in cover percentage between enclosures and unfenced areas increased between 1997 and 2001 ($z = 3.42$, $P < 0.001$) but remained constant between 2001 and 2005 ($z = -0.72$, $P = 0.76$). In the upper stratum, we observed no significant difference in redcedar cover inside and outside of the enclosures (1997, $z = -0.81$, $P = 0.42$; 2001, $z = -0.61$, $P = 0.54$ and 2005, $z = -0.70$, $P = 0.49$).

Although the cover of Sitka spruce in the lower stratum follows a temporal pattern of response to deer exclusion similar to the one observed for redcedar (Fig. 1b), we detected no significant differences in cover percentage between treatments (1997, $z = 1.78$, $P = 0.08$; 2001, $z = -0.29$, $P = 0.61$ and 2005, $z = 0.27$, $P = 0.39$). Sitka spruce was virtually missing from the upper stratum.

Although the mean cover of western hemlock varied over time (Fig. 1c), we found no difference in mean cover between fenced and unfenced areas at any date, neither in the lower stratum (1997, $z = 0.24$, $P = 0.81$; 2001, $z = 0.06$, $P = 0.95$ and 2005, $z = 0.32$, $P = 0.36$), nor in the upper one (1997, $z = 0.3867$, $P = 0.7$; 2001, $z = -1.4123$, $P = 0.16$ and 2005, $z = -1.22$, $P = 0.22$).

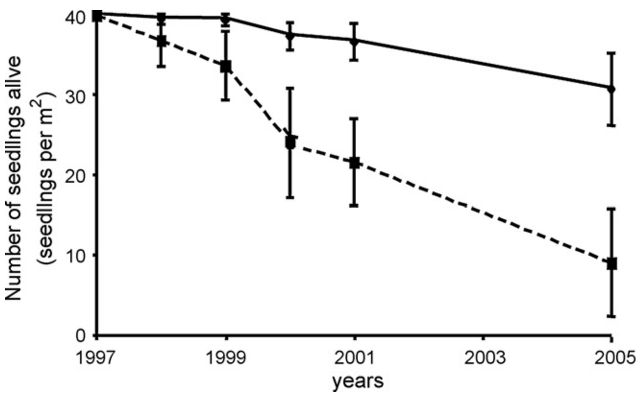

Fig. 2. Change in the number (±S.D.) of redcedar seedlings alive in enclosures and unfenced areas from 1997 to 2005. Dotted line: unprotected individuals; black line: protected individuals.

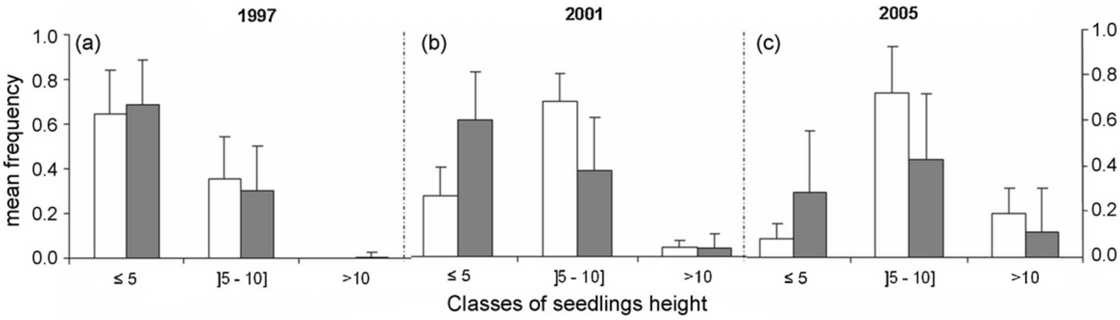

Fig. 3. Mean frequency (+S.E.) of living redcedar seedlings per site, height class (cm) in enclosures and unfenced areas in 1997 (a) 2001 (b) and 2005 (c). Open bars = protected individuals; grey bars = unprotected individuals in each of the 3 years studied.

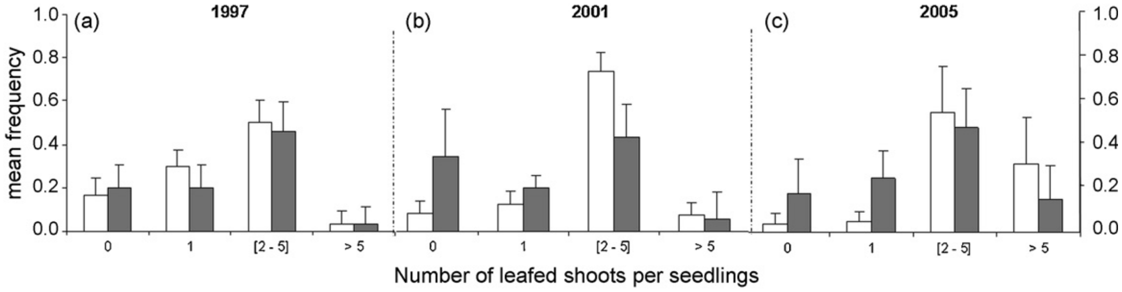

Fig. 4. Mean frequency (+S.E.) of redcedar seedlings per site in the four leafed-shoot classes. Open bars = protected individuals; grey bars = unprotected individuals in each of the 3 years studied.

Finally, we detected a non-significant negative correlation between the variations in redcedar and salal cover percentages ($R^2 = 0.13$, $P = 0.12$) and no correlation between the variations in salal and hemlock cover percentages ($R^2 = 0.003$, $P = 0.83$).

3.2. Regeneration dynamics in redcedar

3.2.1. Seedling survival

The average number of living redcedar seedlings decreased over time in both the fenced and unfenced areas (Fig. 2). Survival was significantly lower outside the fenced area from 1998 ($z = 3.25$, $P < 0.001$), just 1 year after deer exclusion. Of the 80 seedlings marked in 1997, 60 on average were still alive in the fenced areas in 2005 compared to only 19 in the unfenced areas.

3.2.2. Individual height

Surviving individuals grew both inside and outside of the enclosures. In 2005, the average seedling height inside the enclosures was 8.5(±S.D. = 3.1) cm and 6.5(±S.D. = 3.3) cm outside. The tallest individual at this date was 28 cm high inside the enclosures and 21 cm outside.

In 1997, the number of individuals higher than 10 cm was too small to perform a test (theoretical sample size lower than 5), so we pooled them with the individuals of height class (5–10 cm). There was no significant initial difference in seedling height between treatments (Fig. 3a; d.f. = 1, $\chi^2 = 3.01$, $P = 0.08$). Differences between fenced and unfenced areas became significant in 2001 (d.f. = 2, $\chi^2 = 127.9$, $P < 0.001$) and remained so in 2005 (d.f. = 2, $\chi^2 = 140.1$, $P < 0.001$). The relative distribution in height classes diverged between the two treatments with time. In 2001, individuals from the outside belonged mainly to the smallest height class (≤5 cm), whereas individuals from within the enclosures were mostly in the medium height class (5–10 cm) (Fig. 3b). In 2005, only 8% of the protected marked individuals were still in the lowest height class, 72% had grown into the medium height class and 20% were in the highest height class. By contrast, 28% of the unprotected marked individuals were still in the lowest height class (≤5 cm) (Fig. 3c).

3.2.3. Number of leafed shoots

The average number of leafed shoots per seedling increased over time both inside and outside the enclosures. The maximum number of leafed shoots, recorded in 2005, was 19 inside and 18 outside the enclosures.

As for individual height classes, we included individuals with more than 5 leafed shoots in the (2–5) leafed-shoot class because sample sizes were too small both in 1997 and 2001 to carry out the test. There was no significant difference in 1997 between protected and unprotected individuals (d.f. = 3, $\chi^2 = 0.40$, $P = 0.94$). Initially, about 50% of the individuals were mainly in the (2–5) leafed-shoot class (Fig. 4a). In 2001, protected individuals had significantly more leafed shoots than unprotected ones (d.f. = 3, $\chi^2 = 134.2$, $P < 0.001$): about half the unprotected individuals had at most one leafed shoot, whereas 70% of the protected individuals had 2–5 leafed shoots (Fig. 4b). These differences were confirmed in 2005 (Fig. 4c; d.f. = 4, $\chi^2 = 127.2$, $P < 0.001$). Protected individuals had

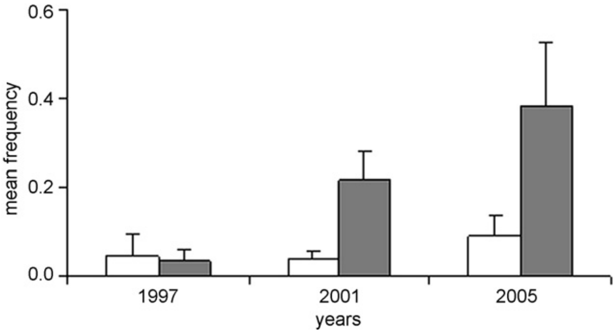

Fig. 5. Mean frequency (+S.E.) of multiple-stemmed redcedar seedlings per site in enclosures and unfenced areas in 1997, 2001 and 2005. Open bars = protected individuals; grey bars = unprotected individuals in each of the 3 years studied.

gained an average of 3 additional leafed shoots from 1997 to 2005, whereas unprotected individuals produced only one.

In addition, the leafed shoots on unprotected plants had a significantly lower area than the ones on protected individuals ($z = 5.3$, $P < 0.001$). This is no surprise as the number of leafed shoots was strongly, positively correlated to the mean area of the shoots (Pearson's coefficient of regression in 2005, $R^2 = 0.37$, $P < 0.001$). Seedlings height and the number of leafed shoots were slightly positively correlated ($R^2 = 0.16$, $P < 0.001$).

3.2.4. Number of stems

In 1997, most of the marked redcedar seedlings were single-stemmed (Fig. 5) and there was no significant initial difference between protected and unprotected individuals (95 and 94% respectively; d.f. = 1, $\chi^2 = 0.77$, $P = 0.38$). With time, the proportion of multiple-stemmed individuals increased strongly in the unfenced areas (Fig. 5), and only very slightly in the enclosures (less than 10% of living seedlings), so that the proportion of seedlings with several stems was significantly higher outside the enclosures than inside, both in 2001 (d.f. = 1, $\chi^2 = 104.2$, $P < 0.001$) and in 2005 (d.f. = 1, $\chi^2 = 115.4$, $P < 0.001$).

4. Discussion

4.1. The impact of deer browsing

We have shown that deer browsing has a direct negative effect on redcedar cover percentage in the lower height stratum. However, this positive effect of deer exclusion results from a decrease in cover in unprotected plots rather than from a gain in cover inside the enclosures. Redcedar cover increased temporarily in the enclosures but the gain fell back to only 2% on average by the end of the study. This can be explained by the progressive loss of individuals after the initial establishment stage and a lack of new individuals getting established during the period considered. The cover of redcedar in the upper stratum in our survey was not affected by the exclusion of deer. This suggests that deer exclusion has not yet lasted long enough to allow a recovery of the lower stratum that is sufficient to affect vegetation cover above 1.5 m. This is confirmed by the slow growth we observed for most of the vegetation in the enclosures and in particular for redcedar where the tallest protected individual had only reached 28 cm in 8 years.

On the other hand, deer browsing has had a dramatic and negative effect on both redcedar survival and the number of leafed shoots per individual. We also showed that the exposure to deer browsing greatly increased the occurrence of multiple-stemmed individuals. This probably mainly resulted from the loss of the apical bud because of deer browsing (Welch et al., 1992), a loss that can directly affect height growth (Gill and Beardall, 2001; Rossell et al., 2005; Forester et al., 2006). However, we also noticed an overall decrease of live seedlings and a small increase in the frequency of multiple-stemmed individuals inside the enclosures, which we interpret as a consequence of a natural withering of the apical bud or due to the consumption by small herbivores (mice or invertebrates). Our results are consistent with the existing literature. Indeed, evergreen conifers can be especially browse-intolerant because of their strong investment in leaf production and because they become target species for deer in winter (Côté et al., 2004). Such an impact is currently exacerbated on Haida Gwaii where decades of deer browsing have severely depleted forage availability in the forest understorey. Martin and Baltzinger (2002) have shown, in their study of redcedar regeneration in cutblocks situated in the same general area than the current study, that it takes the presence of abundant alternative forage (and good access to light) to allow some redcedar regeneration under the current level of deer pressure on Haida Gwaii.

4.2. Recovery after deer exclusion

Among the conifers present, redcedar is the most palatable species, and remains palatable all year round. Sitka spruce comes next in palatability followed by western hemlock. Sitka spruce may become an alternative food source where redcedar and other deer palatable species have become missing or reduced in abundance (Pojar et al., 1980; Martin and Baltzinger, 2002). Although Sitka spruce has been shown a year round component in Roe deer (*Capreolus capreolus*) diet (De Jong et al., 1995), it seems to be mostly, if not exclusively, used in spring on Haida Gwaii where black-tailed deer feed on the new soft shoots that lack the sharp needles characteristic of older stems (JL Martin pers. obs.). In this study, we did record Sitka spruce in the understorey but not in the upper stratum. We found no bonsai-shaped Sitka spruce that would suggest the species has had difficulties to emerge from the lower stratum. The lack of Sitka spruce in the upper stratum most likely resulted from its rarity. Its initial average percentage cover per site in the lower stratum was very low (less than 1.5% in 1997) and the species was entirely missing from some of our sites.

The lack of significant gain in redcedar cover after 2001 could partly be the consequence of competition with other woody species that recover in response to protection from deer or with species less affected by deer browsing such as salal (*Gaultheria shallon*) whose cover remained relatively stable (12%) both inside and outside the enclosures from 1997 to 2005. Sensitivity of redcedar to competition has been demonstrated in coastal forests of British Columbia (Daniels, 2003; Weber et al., 2003). In particular, belowground competition from salal had a negative impact on redcedar (Mallik and Prescott, 2001). This is consistent with the negative correlation we found between the increases in cover percentages of redcedar and salal. However, in a current experiment of long-term reduction in deer numbers on two islands on Haida Gwaii, the recovery of young redcedar was most significant for seedlings that did grow inside dense thickets of regenerating Sitka spruce found in small forest gaps. The young spruce protected the young cedar from browsing but did not seem to prevent their growth despite severe shading (RGIS unpublished results, see Gaston, 2002). The protection of a palatable conifer species by an unpalatable one has already been observed. For instance, patches of Balsam Fir (*Abies balsamea*) have been shown to facilitate Eastern hemlock (*Tsuga Canadensis*) establishment by creating a physical or visual barrier to deer (Borgmann et al., 1999).

Although redcedar is classified as a shade-tolerant species, it seems to need some level of disturbance to get established, and seems to behave as a shade-intolerant species in early seedling establishment, that is before the scale-like foliage stage (Weber et al., 2003). The ability of redcedar to survive in the shade would be more linked to its height than in other shade-tolerant species such as western hemlock (Weber et al., 2003). The population dynamics of redcedar is a combination of a continuous mode of recruitment with a gap-phase establishment (Daniels, 2003). In addition, species with this type of regeneration strategy can establish themselves, survive and grow very slowly for many years under the low light available in mature forests and create an advance regeneration bank of seedlings able to re establish canopy dominance (Tremblay et al., 2007). This could explain the slow growth of our marked seedlings. Slow growth of seedlings and a regeneration strategy based on seedling banks has been observed in northern white cedar, a species closely related to western redcedar (Rooney et al., 2002). This type of regeneration strategy can make forests susceptible to composition changes in situations of severe selective browsing as deer suppress seedlings from the regeneration bank preventing the replacement of older trees when favourable conditions occur. This is generally true for conifers which often lack compensatory growth after browsing events (Cornett et al., 2000). Regeneration of white cedar was shown to be in need of significant and sustained reductions in deer density (Cornett et al., 2000; Rooney et al., 2002).

The positive responses of redcedar to deer exclusion and the pattern of mortality and lack of growth in seedlings exposed to deer browsing clearly suggest that deer browsing explains the current lack of young redcedars in the mature forests of Haida Gwaii. This impact has led to an increased scarcity of this species in the studied strata and could lead to a modification of the canopy composition. The slow growth of protected seedling under closed canopy suggests that young redcedars remain vulnerable to deer browsing for several decades. In the related northern white cedar, seedlings typically required 10 years to grow up to 30 cm and 30 years to reach 3 m (Rooney et al., 2002). In our study, some protected redcedar seedlings had reached 28.5 cm in 2005 from an initial height of 5 cm in 1997. Thus, under current conditions, protection against deer could be required for more than 50 years to allow seedlings to reach the height needed to escape deer browsing. This rate of growth would be significantly increased in case of a major local disturbances (e.g. a wind throw) (Tremblay et al., 2007). Under such improved light conditions redcedar seedlings can present high rates of growth and reach 1.5 m high in less than 10 years (Martin and Baltzinger, 2002).

The likelihood that young, year round palatable, redcedars can escape deer browsing in an understorey already severely depleted in resources for deer is understandably very limited. Our results indicate that any effort to restore redcedar regeneration in old-growth forest patches will need to achieve a significant reduction in deer abundance and maintain this reduction over a long period of time.

Acknowledgements

Funding for this research was provided by the Canada, British Columbia South Moresby Forest Replacement Account (SMFRA); contract # SMFRA99DQC-002, SMFRA Project 24.2, “Pattern of Western Red Cedar Regeneration,” and 2005 contract “*Impacts of introduced deer on cedar regeneration, plant pollination and experimental vegetation restoration in Haida Gwaii*”. The project was also funded by Forest Renewal British Columbia (FRBC); a partnership of forest companies, workers, environmental groups, First Nations, communities and government of British Columbia, research award: PA97335-BRE. Funding assistance by Forest Renewal BC does not imply endorsement of any statements or information contained herein. The Research Group on Introduced Species (RGIS), The Canadian Wildlife Service (CWS) and the Laskeek Bay Conservation Society (LBCS) provided logistical support. Special thanks to Rob Kelly, Isabel Buttler, Janet Gray, Lisa Blant, Carolyn Hesseltine, Steeve Stockton, Julie Gresser and Barb Rowsell for their invaluable assistance. We would like also to thank Frédéric Archaux for helpful comments on earlier drafts of this manuscript.

References

Allombert, S., Gaston, A.J., Martin, J.L., 2005a. A natural experiment on the impact of overabundant deer on songbird populations. Biol. Conserv. 126, 1–13.

Allombert, S., Stockton, S., Martin, J.L., 2005b. A natural experiment on the impact of overabundant deer on forest invertebrates. Conserv. Biol. 19, 1917–1929.

Anderson, R.C., Katz, A.J., 1993. Recovery of browse-sensitive tree species following release from White-tailed deer (*Odocoileus virginianus*) Zimmerman browsing pressure. Biol. Conserv. 63, 203–208.

Augustine, D.J., Frelich, L.E., Jordan, P.A., 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecol. Appl. 8, 1260–1269.

Banner, A., Pojar, J., Schwab, J.W., Trowbridge, R., 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. In: Scudder, G.G.E., Gessler, N. (Eds.), The Outer Shores. Queen Charlotte Islands Museum Press, Skidegate, Haida Gwaii, BC, Canada, pp. 261–279.

Borgmann, K.L., Waller, D.M., Rooney, T.P., 1999. Does balsam fir (*Abies balsamea*) facilitate the recruitment of eastern hemlock (*Tsuga canadensis*)? Am. Midl. Nat. 141, 391–397.

Cochran, W.G., 1954. Some methods for strengthening the common Chi-square tests. Biometrics 10, 417–451.

Cornett, M.W., Frelich, L.E., Puettmann, K.J., Reich, P.B., 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. Biol. Conserv. 93, 359–369.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance: annual review of ecology. Evol. Syst. 35, 113–147.

Daniels, L.D., 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree rings. For. Chron. 79, 517–530.

Daufresne, T., Martin, J.L., 1997. Changes in vegetation structure and diversity as a result of browsing by a large herbivore: the impact of introduced black-tailed deer in the primary forest of Haida Gwaii, British Columbia. In: Gaston, A.J. (Ed.), Laskeek Bay Research, vol. 7. Laskeek Bay Conservation Society, Queen Charlotte City, BC, pp. 2–26.

De Jong, C.B., Gill, R.M.A., van Wieren, S.E., Burlton, F.W.E., 1995. Diet selection by roe deer Capreolus in Kielder forest in relation to plant cover. Forest Ecol. Manage. 79, 91–97.

Engelstoft, C., 2001. Effects of Sitka Black-tailed Deer (*Odocoileus hemionus sitkensis*) on Understorey in Old-growth forest on Haida Gwaii (Queen Charlotte Islands). Master of Science, University of Victoria, British Columbia, Canada.

Forester, J.A., Leopold, D.J., 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, 136–150.

Gaston, A.J., 2002. Vegetation changes on Reef Island following a reduction in deer numbers. In: Conference Summary Lessons from the Islands: Introduced Species and What They Tell us About How Ecosystems Work, Queen Charlotte City and Skidegate, October. Research Group on Introduced Species (RGIS), pp. 20–21.

Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 209–218.

Kuiters, A.T., Mohren, G.M.J., Van Wieren, S.E., 1996. Ungulates in temperate forest ecosystems. Forest Ecol. Manage. 88, 1–5.

Mallik, A.U., Prescott, C.E., 2001. Growth inhibitory effects of salal on western hemlock and western red cedar. Agron. J. 93, 85–92.

Martin, J.L., Daufresne, T., 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. In: Proceedings of the Cedar Symposium: Growing Western Redcedar and Yellow-Cypress on the Queen Charlotte Islands/Haida Gwaii. Edited by G. Wiggins. Canada, British Columbia South Moresby Forest Replacement Account, BC, Ministry of Forests, Victoria, BC, pp. 69–83.

Martin, J.-L., Baltzinger, C., 2002. Interaction among deer browsing, hunting and tree regeneration. Can. J. Forest Res. 32, 1254–1264.

McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), 1997. The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institute Press, Washington.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol. Evol. 14, 483–488.

Palmer, S.C.F., Truscott, A.M., 2003. Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. Forest Ecol. Manage. 182, 31–47.

Pojar, J., Lewis, T., Roemer, H., Wilford, D.J., 1980. Relationship between introduced black-tailed deer and the plant life of the Queen Charlotte islands, British Columbia. Unpublished report, BC Ministry of Forests, Smithers, BC

Pojar, J., MacKinnon, A., 1994. Plants of Coastal British Columbia. Ministry of Forests & Lone Pine Publishing, 528 p.

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

Rooney, T.P., Solheim, S.L., Waller, D.M., 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. Forest Ecol. Manage. 163, 119–130.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecol. Manage. 181, 165–176.

Rossell, C.R., Gorsira, B., Patch, S., 2005. Effects of white-tailed deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. Forest Ecol. Manage. 210, 415–424.

Sage Jr., R.W., Porter, W.F., Underwood, H.B., 2003. Windows of opportunity: white-tailed deer and the dynamics of northern hardwood forests of the Northeastern US. J. Nat. Conserv. 10, 213–220.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413 (6856), 591–596.

Suominen, O., 1999. Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. Ecography 22, 651–658.

Stockton, S.A., Allombert, S., Gaston, A.J., 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, 118–128.

Tremblay, J.-P., Huot, J., Potvin, F., 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. J. Appl. Ecol. 44, 552–562.

Vourc'h, G., Vila, B., Gillon, D., Escarré, J., Guibal, F., Fritz, H., Clausen, T.P., Martin, J.-L., 2002. Disentangling the causes of damage variation by deer browsing on long-lived tree saplings: a chemical and dendrochronological approach. Oikos 98, 271–283.

Weber, A., Gilbert, B., Kimmins, J.P., Prescott, C.E., 2003. Factors limiting the early survivorship of *Thuja plicata* on northern Vancouver Island, British Columbia. Can. J. Forest Res. 33, 854–861.

Welch, D., Staines, B.W., Scott, D., French, D.D., 1992. Leader browsing by Red and Roe deer on Young Sitka Spruce Trees in Western Scotland. II. Effects on growth and tree form. Forestry 65, 309–330.

Wiggins, G.G. (Ed.), 1999. Proceedings of the Cedar Symposium: Growing Western Redcedar and Yellow-Cypress on the Queen Charlotte Islands/Haida Gwaii, Queen Charlotte Islands, Haida Gwaii, British Columbia.