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Response of young *Tsuga heterophylla* to deer browsing: developing tools to assess deer impact on forest dynamics

Received: 27 June 2002 / Accepted: 30 April 2003 / Published online: 19 July 2003
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Abstract We used dendroecology to describe and understand the consequences of deer browsing on regenerating western hemlock (*Tsuga heterophylla*). We compared tree shape, growth rate, height and age at four different sites in Haida Gwaii (British Columbia, Canada) that had trees representative of the range of deer impact on trees: (1) trees showing no sign of browsing, (2) escaped trees which were still browsed below the browse line and (3) stunted and heavily browsed trees. Repeated and intense browsing resulted in the small size, compact heavily ramified shape of stunted trees and in the short compact and ramified lower branches of escaped trees. These contrasted with the shape of non-browsed trees, a shape that was also found in escaped trees above the browse line. Before release, all browsed trees experienced stagnation in growth characterised by narrow rings (0.3 mm/year) and a small annual height increment (2.5 cm/year). At release, growth rate increased and stabilised: rings were wider (1.3 mm/year) and annual height increments were greater (10.5 cm/year). Non-browsed trees had a mean ring-width of 1.3 mm/year and an annual height increment of 22 cm/year. Delay in tree recruitment caused by deer varied from site to site. It had been about 15 years for the escaped trees and is estimated at 30–40 years for the stunted trees. Spatial variation in deer impact may reflect spatial variation of browsing pressure resulting from local differences in the availabil-

ity of preferred forage or to differences in tree chemical defences/nutritional values.

Keywords *Tsuga heterophylla* (Raf.) Sarg. · Deer browsing · Growth pattern · Diameter and height growth · Age

Introduction

The introduction of large herbivores (De Vos et al. 1956; Petrides 1975) has often resulted in high ungulate densities and significant impacts on native plant and animal populations (Veblen et al. 1989; Mark et al. 1991). The eradication of native predators has produced similar effects and browsing is increasingly becoming a problem in many parts of the world (Motta 1996; Gill 1999).

One way to study interactions between large herbivores and woody plants is to use dendrochronology to infer the influence of past and present factors on tree diameter growth. While dendrochronologists have used the influence of disturbances recorded in tree ring series to reconstruct spatial and temporal fluctuations of several insect species (Swetnam and Lynch 1989; Morin and Laprise 1990; Veblen et al. 1991; Gross 1992; Jardon et al. 1994; Krause and Morin 1995; Krause and Raffa 1996; Weber 1997) few studies have used ring-width analysis to assess the influence of past damage by ungulates on woody plant growth and dynamics (Motta 1996; Morneau and Payette 1998, 2000; Chouinard and Fillion 2001; Vila et al. 2001, 2002).

On Haida Gwaii (Queen Charlotte Islands, British Columbia, Canada), Sitka black-tailed deer [*Odocoileus hemionus sitkensis* Merriam] were introduced in the northern part of Graham Island (Fig. 1) at the end of the nineteenth century and soon settled the whole archipelago. Current density of deer estimates vary between 13 and 30 deer per km² (Engelstoft 2001; Martin and Baltzinger 2002) and deer have a profound effect on the forest (Pojar et al. 1980; Pojar and Banner 1984; Banner et al. 1989). Their impact on the regeneration and

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growth of western red cedar [*Thuja plicata* D. Don ex Lamb.] (Martin and Baltzinger 2002; Vourc'h et al. 2002a) and of Sitka spruce [*Picea sitchensis* (Bong.) Carrière] (Vila et al. 2002) is significant. In this paper we focus on the impact of deer browsing on a third tree species abundant in the coastal rain forests of north-western America, western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], a species that has also been used in Europe to restock forests after harvesting. Deer browsing damage to this species has been reported (Pojar et al. 1980; Coates et al. 1985) but there has been no study on the consequences of browsing on tree growth.

In order to assess consequences of browsing we linked morphological differences observed on browsed trees to tree height, diameter and age. Our objectives were (1) to link tree shape to browsing history, (2) to assess the effect of deer browsing on growth indices and tree height by comparing browsed and non-browsed trees, and (3) to use these results to assess delay in tree recruitment caused by browsing and discuss mechanisms that could explain spatial variation in this delay. Our ultimate goal was to complement the knowledge already acquired on deer impact on western red cedar (Vourc'h 2001; Vourc'h et al. 2002b) and Sitka spruce (Vila et al. 2002, 2003) to be able to assess and quantify deer impact on the main tree species in these forests and understand how deer have modified their dynamics.

Materials and methods

Study area and deer browsing pressure

Situated on the Pacific coast of Canada, the archipelago of Haida Gwaii (53°N, 132°W) includes more than 150 islands (Fig. 1). Forests consist of a mixture of western hemlock, western red cedar and Sitka spruce. Western hemlock is the dominant species at low elevations where it often forms pure dense stands. The understorey was originally composed of numerous shrubs like [*Gaultheria shallon* Pursh] and [*Vaccinium parvifolium* Smith in Rees] (Banner et al. 1989). In many areas deer browsing has reduced the understorey to old isolated and senescent shrubs (personal observation; Pojar et al. 1980; Banner et al. 1989). In these areas the lack of understorey vegetation, the existence of a browse line and of palatable species confined to inaccessible areas indicate, according to Reimoser et al. (1999), a very heavy herbivore pressure. The reduction in understorey is most advanced on the medium-sized islands off the eastern side of the archipelago (Martin and Daufresne 1999) and less pronounced on parts of Moresby Island (Martin et al. 1994). Between 1996 and 2000 deer censuses and deer cull programs on three medium-sized islands (Daufresne and Martin 1997, Sean Sharpe, unpublished data) yielded density estimates of about 30 deer per km² whereas pellet group counts from transects in old-growth forest patches on the large islands Graham Island and north-eastern Moresby Island (Engelstoff 2001) yielded estimates of about 13 deer per km². Browsing impact on western hemlock ranged from no sign of browsing to heavily browsed and stunted trees. Sampling was done on four sites that were selected as being representative of the whole range of impact. A site selected on Graham Island (Yakoun Lake, site 1, Fig. 1) provided a sample of non-browsed trees. The area had been clear-cut 15–20 years before the study. The second site we selected had trees with an apex that had escaped deer but showing significant signs of current and past browsing. It was situated near the southern end of Moresby Island (Koya Bay, Fig. 1) in a clearing along the

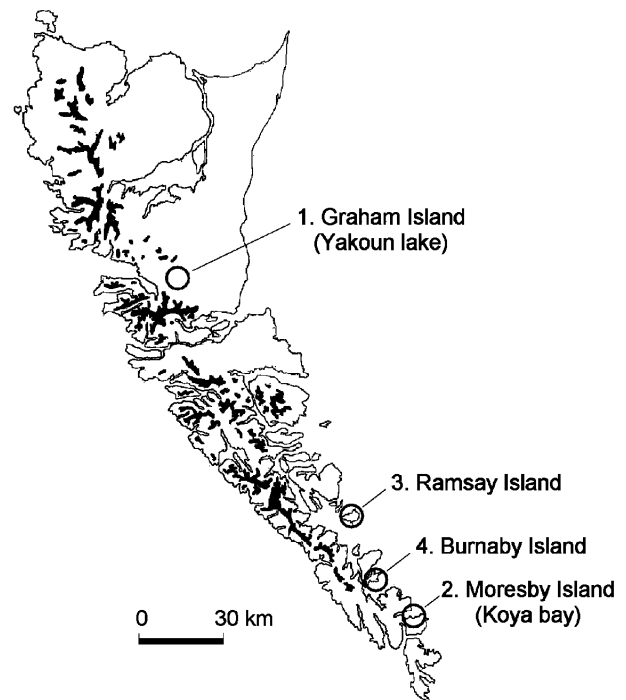


Fig. 1 Map of Haida Gwaii with localisation of sampling sites: 1. Yakoun Lake (Graham Island), 2. Koya Bay (Moresby Island), 3. Ramsay Island, and 4. Burnaby Island

shoreline. The two remaining sites selected were both situated on medium-sized islands along the eastern side of the archipelago (Burnaby and Ramsay Islands, Fig. 1). Their trees were very heavily browsed and had not escaped deer browsing. They were situated in clearings along the shoreline. All these sites were situated on the eastern side of the archipelago which belongs to the Coastal Western Hemlock Zone (Banner et al. 1989). Site characteristics such as aspect, slope, soil type, organic layer, percent of regenerating species and regenerating density of the sampled area were measured in the field and are shown in Table 1.

Sampling protocol

Because the density and availability of regenerating trees varied from site to site, sampling area varied from site to site ranging between 2,500 m² (in the cut block) and 225 m² (clearing along the shoreline on Ramsay Island). The number of trees that could be sampled per site varied between 8 and 25, with a minimum of 12 trees sampled for a single browsing category. We sampled a total of 60 trees: 25 non-browsed trees at site 1 (Graham Island), 12 escaped trees at site 2 (Koya Bay), 23 stunted trees (8 at site 3, Ramsay Island; 15 at site 4, Burnaby Island) (Table 1).

For each tree we measured total height and height of the first branches without visible browsing damage. In escaped trees we also measured crown diameter materialised by the maximal extension of branches under and above the browse line (see Fig. 2) in order to assess changes to tree shape caused by deer browsing.

Ring series and growth pattern

For each tree sampled, we collected a stem-section at the base of the tree, just above the collar, in order to obtain the longest ring series and assess tree age. Tissue structure was made visible by polishing the stem-sections with sand paper of different grades. We cross-dated tree ring series by identifying similar ring sequences

Table 1 Ecological data of the study sites

	Site 1, Yakoun Lake Graham Island	Site 2, Koya Bay Moresby Island	Site 3, Ramsay Island	Site 4, Burnaby Island
Biogeoclimatic zone and sub-zones	Coastal Western Hemlock zone, wet Hypermaritime sub-zone	Coastal Western Hemlock zone, wet Hypermaritime sub-zone	Coastal Western Hemlock zone, wet Hypermaritime sub-zone	Coastal Western Hemlock zone, very wet Hypermaritime sub-zone
Area (m)	50×50	50×12	15×15	34×18
Aspect (°)	230	330	30	165
Slope (°)	21	2	4	4
Context	Regeneration after clear-cut	Coastal, open, natural forest	Coastal, open, natural forest	Coastal, open, natural forest
Light conditions	No canopy, full light conditions	Neighbouring canopy, full light conditions	Neighbouring canopy, full light conditions	Neighbouring canopy, full light conditions
Soil type	Debris of clear-cut, organic and mineral	Organic and mineral	Organic and mineral	Organic and mineral
Organic layer	>30 cm	50 cm	35 cm	45 cm
Regenerating species	60% <i>Tsuga</i> , 20% <i>Picea</i> , 20% <i>Thuja</i>	100% <i>Tsuga</i>	80% <i>Tsuga</i> , 20% <i>Picea</i>	85% <i>Tsuga</i> , 15% <i>Picea</i>
Regeneration density	2/m ²	15/m ²	32/m ²	25/m ²
Tree categories	Non-browsed	Browsed and escaped	Browsed and stunted	Browsed and stunted
Number of trees collected	25	12	8	15

with characteristic features on different samples in order to accurately date each ring (Fritts 1976). Then, we selected two or three suitable radii to measure ring-widths, avoiding irregularities. Stem-sections were measured along these radii using an Eklund measuring device (with a precision of 0.01 mm).

The average width of each ring was calculated in order to obtain individual chronology for each tree (Fritts 1976; Cook and Kairiukstis 1990) and to identify the radial growth pattern.

Individual chronologies of stunted and non-browsed western hemlocks were cross-dated on the basis of calendar years according to classical methods in dendrochronology (Schweingruber 1988). Individual chronologies of escaped western hemlock were cross-dated on the basis of positive abrupt growth changes observed on their radial growth pattern. Finally, we built four mean chronologies corresponding to the four categories of trees sampled at the four sites. In order to compare radial growth pattern between non-browsed trees, stunted and escaped trees and between sites, each mean chronology was plotted with a 99% confidence interval.

Statistical analyses

For each tree, we determined age by counting rings on basal stem-sections. On the basis of the radial growth pattern, we estimated the age at which trees escaped deer (age at release) as well as the number of years that had elapsed since release at the time of sampling. Vila et al. (2003) have shown a direct relation between radial growth increase and the reach of the browse line by the apical bud. This allows age at release to be assessed by counting the number of rings in the sequence of narrow rings (Vila et al. 2003). Because trees were sampled in 1999 (site 1), 2000 (sites 3 and 4) and 2001 (site 2), ages were determined for year 2000. We used ANOVA to test differences in age and height between stunted trees, escaped trees (total age and age at release) and non-browsed trees.

We calculated radial growth indices (which correspond to mean ring-width) for the stunted, escaped and non-browsed trees. For escaped trees, we calculated two radial growth indices, one corresponding to the period of growth under the browse line and the other one to the period above the browse line. We used ANOVA to test differences in tree radial growth with category (stunted, escaped before release, escaped after release and non-

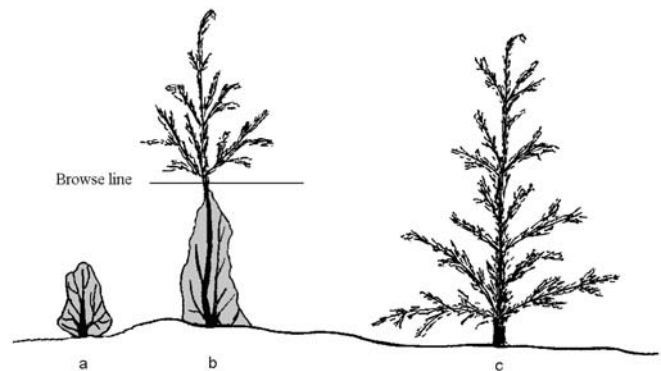


Fig. 2 The three categories based on tree growth shape: **a** browsed “stunted” tree with a very compact shape due to the intense ramification caused by repeated annual browsing of all buds; **b** browsed “escaped” tree which has grown above the browse line. It displays a shrubby stunted shape under the browse line and a normal shape above it; **c** non-browsed tree displaying a normal growth shape with large branches all along the trunk

browsed trees) as the qualitative explanatory variable. The length of ring series used to calculate radial growth indices and for ANOVA was dependent on tree age. The longest available series were used whenever possible.

Height growth indices were calculated for stunted, escaped and non-browsed trees. For stunted and non-browsed trees this index is equal to the height of the tree divided by its age. For escaped trees, we calculated one index under the browse line and one above the browse line. The index under the browse line is equal to the height of the browse line divided by the age of the tree when it did reach the browse line (that is age at release). Above the browse line, the index is equal to [total tree height minus height of the browse line] divided by [total tree age minus tree age when it reached the browse line]. We used an ANOVA to analyse variation in height growth between categories (stunted, escaped before release, escaped after release, and non-browsed trees).

We used the “least-significant differences” (LSD) post hoc test to compare individual levels of the factors.

In the case of stunted trees, where two sites were available (replication) we also tested differences within the category to separate browse effect and site effects. We used a Mann-Whitney test to compare radial growth, height growth tree age and height between the two sites.

Results

Tree shape and browse line

Non-browsed trees had large sized branches all along the trunk (Fig. 2). Escaped trees had a shrubby stunted shape under the browse line and a normal shape above it. There was a significant difference in crown diameter under and above the browse line (mean ± SE; under =0.68±0.20, *n*=12; above =1.03±0.18, *n*=12; *P*<0.05). The very compact shape of “stunted” trees was the result of intense ramification caused by repeated browsing of all buds. The height at which trees were able to resume a normal shape (browse line) was equal to 1.03±0.05 m (*n*=12).

Radial growth pattern and indices

Ring-width of non-browsed trees fluctuated between 1.0 and 2.0 mm and showed high variation between years (Fig. 3). Ring-width of escaped trees varied from less than 0.5 mm during an initial period of growth stagnation (phase 1, relative years -29 to -1) to 2.5 mm after they had escaped (phase 3, relative years 7–19). In the transition period (phase 2, relative years 0–6) there is a progressive increase (0.5–2.5 mm) in ring-width (Fig. 3). Year-to-year variation in ring-width is higher after release than before release. In stunted trees ring-width is less than 0.5 mm and shows little variation between years.

Radial growth varies significantly between the three categories (ANOVA, *P*<0.001). The post hoc tests showed significant (*P*<0.001) differences in radial growth: (1) between non-browsed and stunted trees; (2) under and above the browse line in escaped trees, (3) under the browse line of escaped trees and non-browsed trees. Radial growth is similar (*P*<0.001) between non-browsed trees and escaped trees above the browse line, between stunted and escaped trees under the browse line (Fig. 3). The radial growth of trees exposed to intense browsing is 5–6 times lower than radial growth in the absence of browsing (Table 2). In the category of stunted trees where a replication is available, radial growth indices are similar (Mann-Whitney, *N*₁=236, *N*₂=440, *P*>0.05) at both sites.

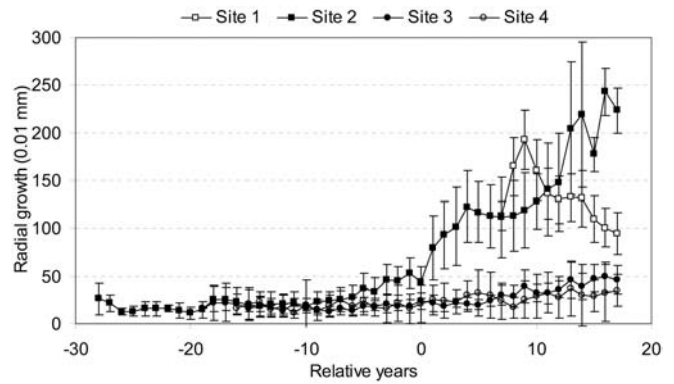


Fig. 3 Comparison of ring-width series between non-browsed (*site 1*), escaped (*site 2*) and stunted (*sites 3 and 4*) western hemlock samples

Height growth index

There is a significant effect of browsing category on height growth (ANOVA, *P*<0.001). Height growth indices are significantly higher for non-browsed trees than for escaped trees under the browse line or for stunted trees (Post hoc test, *P*<0.001, Table 2). Indices of height growth in escaped trees above the browse line were statistically higher than those under the browse line (*P*<0.001). Height growth indices were similar (*P*<0.001) between escaped trees under the browse line and stunted trees and between escaped trees above the browse line and non-browsed trees (Fig. 3, Table 2).

Mean annual height growth was 4- to 10-fold higher in non-browsed trees than in stunted trees or in escaped trees under the browse line (Table 2). In escaped trees mean annual height growth was twice as high above than under the browse line.

In the category of stunted trees height growth indices were similar (Mann-Whitney, *N*₁=7, *N*₂=15, *P*>0.05) at the two sites sampled.

Height and age

There is a significant effect of browsing category on tree height (ANOVA, *P*<0.001) and age (ANOVA, *P*<0.001). non-browsed trees are significantly younger (Post hoc test, *P*<0.001) and taller (*P*<0.001) than escaped and stunted trees (Table 3). The age of escaped and stunted trees is similar (*P*<0.001) but escaped trees are significantly taller than stunted trees (*P*<0.001). In the category of stunted trees tree height (*N*₁=7, *N*₂=15) and age (*N*₁=8,

Table 2 Annual indices of radial and height growth (mean±SE and *n*) for each site and according to tree category

Site	Tree category	Radial growth (mm)	Height growth (cm)
1	Non-browsed	1.323±0.068, <i>n</i> =254	21.86±1.36, <i>n</i> =25
2	Escaped below browse line	0.266±0.022, <i>n</i> =274	5.77±1.05, <i>n</i> =12
2	Escaped above browse line	1.365±0.137, <i>n</i> =102	10.59±3.79, <i>n</i> =12
3	Stunted	0.243±0.021, <i>n</i> =236	2.47±1.06, <i>n</i> =7
4	Stunted	0.263±0.015, <i>n</i> =440	2.03±0.32, <i>n</i> =15

Table 3 Age (in 2000) and height (mean±SE and *n*) of each site according to tree category

Site	Tree category	Age	Height (m)
1	Non-browsed	12.88±0.56, <i>n</i> =25	2.58±0.15, <i>n</i> =25
2	Escaped at release	19.50±3.43, <i>n</i> =12	1.03±0.05, <i>n</i> =12
2	Escaped	33.33±2.92, <i>n</i> =12	2.44±0.03, <i>n</i> =12
3	Stunted	32.14±4.42, <i>n</i> =8	0.74±0.30, <i>n</i> =7
4	Stunted	30.33±3.47, <i>n</i> =15	0.59±0.06, <i>n</i> =15

$N_2=15$) were similar at both sites (Mann-Whitney, $P>0.05$).

Non-browsed trees are also significantly younger ($P<0.001$) than the age of escaped trees at the time of release 15 years ago. The age at release of escaped trees was also significantly younger than the age of stunted trees examined in this study ($P<0.001$); the average height of these stunted trees is still significantly ($P<0.001$) shorter (by about 0.30–0.40 m) than the height estimated for escaped trees at the time of their release (Table 3).

Discussion

Growth response to deer browsing

Browsing has been widely reported to reduce growth rate whatever the species (Gill 1992a). Negative effects of browsing on tree metabolism, radial growth, height growth and tree shape were documented by Gill (1992a, 1992b), Schweingruber (1996) and Peinetti et al. (2001). Such negative effects stem from a reduction in transpiration and nutrient absorption (Schweingruber 1996) and have also been documented when, for example, carbon input is reduced by self-shading (Peinetti et al. 2001).

In the case of deer browsing on evergreen trees, as in the present study, browsing impact on growth results in very narrow rings and small height increments, a pattern differing from that documented in studies on deciduous trees. Krause and Raffa (1996) as well as Bergström and Danell (1995) have shown that browsing caused a reduction of height growth but had no effect on radial growth of the deciduous trees they studied. However these results are not consistent with those of Schweingruber (1996), who observed severe height and radial growth reduction in deciduous trees. Differences between evergreen and deciduous species in radial and height growth in response to deer browsing seem in fact to be strongly dependent on browsing pressure and season of browsing (growing season or dormant period; see Gill 1992a, 1992b). In particular, deciduous trees seem to be less affected than coniferous trees when damage occurs in the winter when the tree is dormant and has its reserves stored in stems and roots (Gill 1992a, 1992b; Peinetti et al. 2001), and is more resilient because of the presence of dormant buds (Gill 1992a; Tuomi et al. 1994).

Our results on height and radial growth indices are consistent with those obtained for other conifers by Vila

et al. (2003) on Sitka spruce and by Chouinard and Filion (2001) on balsam fir [*Abies balsamea* (L.) Mill.]. However, in western hemlock, the first phase of reduced growth is almost twice as long as in Sitka spruce (Vila et al. 2003) even though Sitka spruce seems exposed to similar or often higher browsing pressure than western hemlock. Sitka spruce is able to start escaping deer faster (13 years for Sitka spruce against 19 years for western hemlock). We suggest that this difference, assuming comparable browsing pressure, reflects differences in physical defences rather than differences in the frequency and intensity of browsing, spruce being preferred to western hemlock (Pojar et al. 1980). In Sitka spruce, deer feed exclusively on the soft needles of the spring-flush growth and avoid the thorny ligneous older needles. In addition, when the trees gain in height their apical bud is increasingly protected by the sharp needles of the surrounding branches and by the rigidity of the stem, factors that are all likely to reduce the time until release. In western hemlock browsing can occur over the whole year and can affect needles of any age. In addition, the soft needles and flexible stem of western hemlock provide poor physical protection of the apical bud, even when the tree has exceeded the height deer can normally reach. This may explain the more progressive release observed in the growth pattern of western hemlock in comparison to the abrupt release observed for Sitka spruce (Vila et al. 2002).

Age at release and spatial variation in browsing impact

At our study site at Koya Bay it takes about 19 years for a young western hemlock to reach the height of about 1.2 m necessary to isolate the apical bud from deer reach, instead of 5 years in non-browsed western hemlock on Haida Gwaii (Coates et al. 1985). This suggests that deer cause a delay in sapling recruitment of about 14 years.

However, the stunted trees sampled at sites 3 and 4, which are, on average, 31 years old but have not yet reached the browse line, suggest a projected delay in recruitment of at least 30–40 years. The differences we observe in time lag before release between sites, as well as the occurrence of sites with no signs of browsing, may simply reflect spatial variation in deer pressure on western hemlock. The lack of browsing on site 1 most likely resulted from the higher abundance of preferred forage such as herbaceous plants, red huckleberry shrubs or even regenerating western red cedar available in such clear-cuttings (B. Vila, personal observation; Martin and Baltzinger 2002), western hemlock ranking relatively low in terms of preference by black-tailed deer (Pojar et al. 1980). Higher human pressure (human presence, hunting) in that area and the proximity of alpine summer range may also have played a role (see Martin and Baltzinger 2002 for effect of hunting). All three factors have been shown to influence deer impact on least preferred plant species (e.g. Wallamo and Schoen 1980; Hanley 1984, 1995; Hanley et al. 1989; Gill 1992b;

Reimoser and Gossow 1996; Martin and Baltzinger 2002). The difference observed in age at release between site 2 and sites 3 and 4 could also be explained by site location. Site 2, although it is situated in an old growth forest, is close to forests that have retained, until now, a more lush understorey and are close to alpine summer range (Martin et al. 1994, S. Sharpe, personal communication). Sites 3 and 4, in contrast, are situated on low elevation islands characterised by some of the most severe levels of deer impact recorded on the archipelago (Martin et al. 1994). The replication in the case of the stunted trees suggests the absence of marked site effects within a category and that tree age and height differences between stunted and escaped trees are likely to be linked to a difference in browsing pressure. This interpretation is consistent with what was observed by Vila et al. (2003) for Sitka spruce.

Variation in constitutive tree chemistry is another factor that has been put forward to explain variation in browsing impact between individual trees or populations (Vourc'h et al. 2002a, 2002b for young western red cedar on Haida Gwaii). Browsing itself can affect the palatability of trees, decreasing it by stimulating induced chemical defences or increasing it by reducing the production of chemical defences (Bryant et al. 1983, 1988, 1991; Gill 1992a; Raffa and Smalley 1995). Browsing can affect the nutritive value of the tree and thus its palatability to herbivores. Löyttyniemi (1985) and Edenius (1993) suggested that browsing induced lush growth in Scots pines [*Pinus sylvestris* L.] increasing the probability of rebrowsing, a probability varying with stand age (Bergqvist et al. 2003). In western hemlock the only indices we have for individual variation in tree palatability is the sporadic presence of heavily browsed and non-browsed saplings side by side in the north of the archipelago. Only a simultaneous study of foliage chemistry and of tree age by dendrochronology, as has been done for western red cedar and Sitka spruce by Vourc'h et al. (2002a) and Vila et al. (2002), could bring insights into the role of tree chemistry in browsing impact.

Acknowledgements This research was part of a long-term project by the Research Group on Introduced Species (RGIS, rgis@qcislands.net). Funding was provided by Canada—British Columbia South Moresby Forest Replacement Account (SMFRA), by Forest Renewal British Columbia (FRBC, Award: PA97335-BRE) and by joint funding from Centre National de la Recherche Scientifique and Ministry of Foreign Affairs of France (PICS 489). The Canadian Wildlife Service, the British Columbia Ministry of Forests (Queen Charlotte District), and the Laskeek Bay Conservation Society provided logistic support. We are thankful to Cory Millard and Brian Koepke for their help in the field and to Barb Roswell and Mark Salzl. We also thank two anonymous reviewers for constructive criticism of this manuscript.

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