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Forest Ecology and Management 180 (2003) 413–424
Forest Ecology and Management
www.elsevier.com/locate/foreco

# Growth change of young *Picea sitchensis* in response to deer browsing

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Received 28 March 2002; received in revised form 9 September 2002; accepted 11 November 2002

**Abstract**

Taking advantage of the introduction of the black-tailed deer to the Queen Charlotte Islands (British Columbia, Canada), we used dendrochronological analyses to understand the consequences of deer browsing on Sitka spruce growth. We compared shape, radial growth, height growth and age of young spruce in three sites. We identified two types of trees growing side by side: (1) stunted and heavily browsed spruce, smaller than the browsing limit and (2) escaped spruce that were taller than the browsing limit but still browsed in their lower part. The compact and heavily ramified shape in stunted spruce was the result of repeated and intense browsing. In escaped spruce this was also the case below the browsing limit ($1.16\,\mathrm{m} \pm 0.07$ m), in sharp contrast with the normal shape that escaped spruce resumed above the browsing limit. We show that the release of browsing pressure, once the tree reaches the browsing limit, is characterised by an abrupt increase in radial growth. Before release, trees show a growth stagnation characterized by narrow rings (0.5 mm per year) and small annual height increments (<5 cm per year). After release, trees show a growth stabilisation characterised by wider rings (3 mm per year) and larger annual height increments (20 cm per year). We use this pattern to estimate frequency and age at release and their possible variation over time. Age differences between stunted and escaped spruce are highly significant and indicate that, despite of browsing, most if not all trees will ultimately reach the browsing limit and escape. Heavy deer pressure (30 deer per km$^2$) delays spruce sapling recruitment by about 8 years. This delay varies in relation to site quality and seems to have increased over time, suggesting an increase in browsing pressure.


*Keywords:* *Picea sitchensis* (Bong.) Carrière; Deer browsing; Growth pattern; Growth indices; Age; Temporal variations

## 1. Introduction

The introduction of large herbivores to many parts of the world (de Vos et al., 1956; Petrides, 1975) has often resulted in high ungulate densities and in significant impacts on native plant populations (Veblen et al., 1989; Mark et al., 1991). The elimination of predators from areas where large herbivores are native has produced similar effects. As a consequence, browsing is becoming increasingly a problem in many parts of the world (Gill, 1999; Motta, 1996). These changes however also provide "quasi-experimental" situations to better understand plant–herbivore interactions and the possible role large herbivores have in shaping ecosystem structure and diversity (Schmitz et al., 2000; Terborgh et al., 2001).

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0378-1127/03/$ – see front matter 
doi:10.1016/S0378-1127(02)00655-2

In long-lived plants, especially trees of the temperate regions, the early stage of the plant's life is the time when the crucial interaction with large herbivores occurs. One way to study how large herbivores interact with woody plants is to use an historical inductive approach such as dendrochronology to get an annual estimation of the impact of past and present factors influencing growth. While dendrochronologists have used the records left by disturbances on tree ring series to reconstruct spatial and temporal abundance and variation of several animal species (Krause and Raffa, 1996; Morin et al., 1993) only a limited number of studies have used ring-width analyses to assess the influence of damage by vertebrate herbivores to the growth and dynamics of woody plants (Motta, 1995, 1996, 1997; Morneau and Payette, 1998; Chouinard and Filion, 2001).

In this paper, we take advantage of the introduction of the Sitka black-tailed deer (*Odocoileus hemionus sitchensis* Merriam) to the Queen Charlotte Islands (British Columbia, Canada) to analyse the effect of deer browsing on the regeneration of one of the dominant tree species in North American temperate coastal rain forests, the Sitka spruce (*Picea sitchensis* (Bong.) Carrière). This species has also been extensively used in Europe to restock forests after harvesting. Damages to Sitka spruce by different deer species have been reported but few studies (Staines and Welch, 1984; Mitchell and McCowan, 1986) have actually focused on the consequences of browsing on its growth and regeneration. Our objective was to assess how browsing by Sitka black-tailed affects early growth of Sitka spruce by linking morphological differences observed on browsed Sitka spruce with its growth patterns, growth indices and age in order: (1) to identify growth shapes that would be characteristic of browsed spruce; (2) to link observed radial and height growth indices to these shapes; (3) to use these results to estimate frequency and age at release and delays in recruitment. Finally we compared tree response to browsing between different sites under similar browsing pressure.

## 2. Material and methods

### 2.1. Queen Charlotte Islands and sampling sites

Situated on the west coast of Canada, the Queen Charlotte Islands (53N, 132W) (also known as Haida Gwaii) include more than 150 islands. We selected adjacent islands (East Limestone and Reef Islands) situated in Laskeek Bay within the Coastal Western Hemlock Zone, wet Hypermaritime subzone (Fig. 1). Native old-growth forests consist of a mixture of Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Western redcedar (*Thuja plicata* D. Don ex Lamb.) and Sitka spruce (Banner et al., 1989) in stands that have some of the highest growth rates in North America (Peterson et al., 1997).

The islands we studied were colonized by the Sitka black-tailed, originally absent from the archipelago, after they were introduced to Graham Island at the end of the 19th century. There were no large herbivores native to the islands except for the rare and endemic caribou (*Rangifer tarandus dawsonii* Seton) that became extinct in the 1920s. Today black-tailed deer exert a profound effect on the forests of the Queen Charlotte Islands (Pojar et al., 1980; Pojar and Banner, 1984; Martin et al., 1993; Engelstoft, 2001). They are the only deer that ever occurred on the islands of Laskeek Bay and their densities are estimated at 30 deer per km$^2$ on the study sites (Martin and Daufresne, 1999). On these islands deer often feed along the shorelines and in windthrows because of the higher nutritive value of the vegetation (Shimoda et al., 1994) and the higher plant availability.

In the three sites we selected the absence of ground vegetation, the existence of a browsing limit and the confinement of palatable species to inaccessible areas indicate a very heavy browsing pressure (Reimoser et al., 1999). Site 1 was situated on Reef Island (249 ha). Sites 2 and 3 were both situated on East Limestone Island (Fig. 1). Ecological data are presented in Table 1. Sites 1 and 2 are windthrows. Site 3 is the result of a fire that occurred at the beginning of the century; dominant trees are alders (*Alnus rubra* (Bong.)) and regenerating spruce grow under their canopy. There are no major ecological differences between sites 1 and 2 (Table 1) and they are considered as replicates of sites with good light conditions. To the contrary, in site 3 the dense canopy (basal area = 92) causes much poorer light conditions, at least in summer, and lower spruce density. This latter site was sampled to document the influence of browsing pressure in shade conditions.

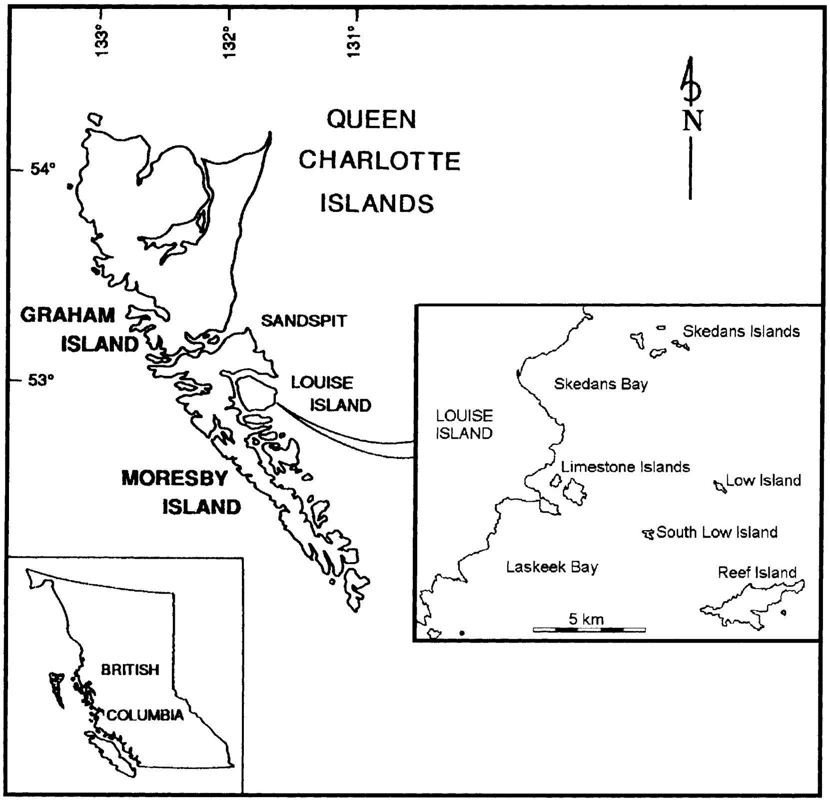


Fig. 1. Queen Charlotte Islands in British Columbia (Canada) with East Limestone Island and Reef Island where spruces were sampled.

### 2.2. Sampling protocol

At each site, we sampled: (1) "stunted" spruce that had a shrubby, bonsai-like shape and were smaller than the browsing limit; (2) "escaped" spruce which had grown above the browsing limit. The latter have a shrubby stunted shape under the browsing limit and a normal shape above it (Fig. 2). Although there was no evidence of mortality or morbidity that could be caused by browsing we found some small individuals

Table 1
Ecological data of the sampled sites

| | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Sampled area (m) | 20.40 | 35.70 | 20.90 |
| Aspect | 200° | 300° | 165° |
| Slope | 24° | 3° | 10° |
| Moisture | Well drained | Badly drained | Well drained |
| Light conditions | No canopy | No canopy | Alder canopy |
| | Luminous | Luminous | Shady |
| Soil type | Organic | Organic | Organic |
| Soil depth | 60 cm | 50 cm | 30 cm |
| Main species of the canopy | Sitka spruce | Sitka spruce | Alder |
| Regenerating species | Spruce only | Spruce only | Spruce only |
| Regeneration density ($m^{-2}$) | 19 | 12 | 0.8 |

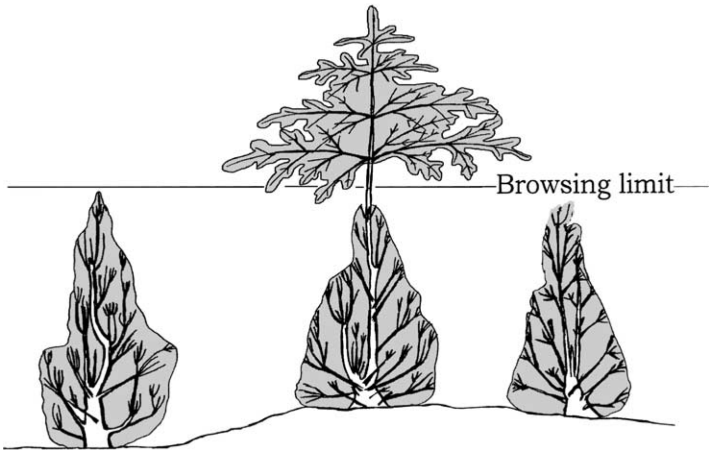


Fig. 2. Schematic representation of stunted spruce that are heavily browsed and smaller than the browsing limit, and escaped spruces that have exceeded the browsing limit. Escaped spruces displayed a stunted shape under the browsing limit and a normal shape above. Stems under the browsing limit are sometimes sinusoidal and multistemmed.

(stunted spruce) which were, in place, suppressed by taller trees (escaped spruce). As a consequence, we did not sample stunted spruce that were growing in the shade of escaped spruce.

We measured height of the first branch without any browsing damage to define the browsing limit. We also measured the total height of each tree. We sampled cross-sections or cores of saplings at the bottom of the stem, just above the collar, in order to get the longest ring series to determine tree age. Finally, at site 2, we cored 10 additional escaped individuals, this time at three different heights (0.20, 0.70 and 1.20 m), to perform a stem analysis linking without ambiguity radial growth, height growth and spruce shape.

### 2.3. Ring series and growth pattern

To analyze ring series, we made tissue structure visible by polishing the cross-sections or cores with sand paper. We cross-dated tree rings by identifying similar ring sequences with characteristic features on different individuals (Fritts, 1976). Then we measured each ring from 2 to 3 radii selected to avoid irregularities using an Eklund measuring device (1/100 mm). We calculated the average value for each ring width to obtain individual chronology for each tree (Fritts, 1976).

Six mean chronologies corresponding to the six samples (three sites $\times$ two types of trees) were built from this data. Individual chronologies of stunted spruce were cross-dated on the basis of calendar years according to classical dendrochronology methods (Schweingruber, 1988). Individual chronologies of escaped spruces were cross-dated on the basis of changes observed on their radial growth pattern. In order to compare radial growth between escaped and stunted trees within a site and between the sites, each mean chronology was plotted with a 95% confidence interval.

### 2.4. Age and growth indices

Potential factors explaining age, radial and height growth indices were investigated. Analyses of variance with a two-way nested experimental design were conducted. This kind of analysis allows to test the significance of the effect of a given factor once the effect of another one has been removed. Least-significant differences (LSD) were used to test the significance of differences between individual levels of the factors.

We estimated the age of each tree by counting rings on basal cross-sections or on cores. Age differences between stunted and escaped saplings were assessed by the ANOVA with site (sites 1–3) and category (stunted versus escaped) as the qualitative explanatory variables. On the basis of growth pattern and spruce shape, it was possible to estimate the age at which spruce escaped browsing (age at release) as well as the number of years that had passed since release at the time of sampling. We used the same ANOVA model to test differences between age at release of escaped trees and current age of stunted spruce.

We calculated radial growth indices (which correspond to ring-width mean) for samples of escaped and stunted spruce at each site. For escaped spruce, we calculated two radial growth indices, one corresponding to the period of growth under the browsing limit and one to the period above the browsing limit. ANOVA were used to test differences in tree radial growth with site (sites 1–3) and category (stunted, escaped before release and escaped after release) as the qualitative explanatory variables. The length of ring series used to calculate radial growth indices and for the ANOVA depended on tree age. We used the longest available series whenever possible. We calculated indices of height growth for stunted and escaped spruce. For the latter, we calculated one index under the browsing limit and one above the browsing limit. For stunted trees this index is equal to the height of the tree divided by its age. For escaped trees, the index under the browsing limit is equal to the height of the browsing limit divided by tree age when it had reached browsing limit (that is age at release). Above the browsing limit, the index = (total tree height − height of the browsing limit)/(total tree age − tree age when it reached the browsing limit). ANOVA were used to test differences in trees height growth with site (sites 1 and 3) and category (stunted, escaped before release and escaped after release) as the qualitative explanatory variables.

## 3. Results

A total of 190 trees were sampled in the three sites in July 1999 (31 stunted and 34 escaped on the site 1; 35 stunted and 34 escaped on the site 2; 14 stunted and 42 escaped on the site 3).

### 3.1. Spruce shape and browsing limit

Only the emerging current year's growth was browsed, older thorny leaves being physically defended. A small section of current growth of about 1 mm was usually left on the tree, from which new ramifications grew (and were browsed) the following spring. This intense process of ramification results in the very compact shape observed in stunted trees. When the apex of such stunted trees reaches the browsing limit, the tree resumes a normal development of stem and branches that contrasts with the short branched and compacted lower part. Stems under the browsing limit are often sinusoidal as a result of a loss of apical dominance (Fig. 2). Some spruces are multistemmed, browsing of terminal stem inducing reiteration processes. The height at which spruce resumed a normal shape, i.e. the browsing limit, was equal to about 1.20 m (1.16 m ± 0.07 m).

### 3.2. Radial growth pattern in stunted and escaped trees

Average ring width of stunted trees was <0.8 mm and showed little variation between years. Escaped trees were characterized by a particular radial growth pattern with: (1) a period of growth stagnation with ring width <0.8 mm, comparable to the pattern observed in stunted trees; (2) a period of abrupt growth increase from 0.8 to 2.5 mm; (3) a period during which growth stabilizes and fluctuates (2.5–3 mm, Fig. 3).

In the 10 escaped trees cored at three different heights, the basal cores taken at 0.20 m from the ground show the typical growth pattern characterizing these three phases. The intermediate core (0.70 m) is characterized by a shorter sequence of rings typical of the first phase, and the terminal core (at 1.20 m) only shows ring patterns typical of the third phase (wide rings, Fig. 4).

There is an overall significant effect of site on radial growth ($P < 0.001$). In stunted trees radial growth is similar in all sites ($P < 0.01$; Fig. 5). In site 1 radial growth of stunted trees is similar to radial growth of escaped trees before they escaped (phase 1, Fig. 6a). In sites 2 and 3 current growth of stunted trees is significantly lower than growth observed for escaped trees before they reached the browsing limit ($P < 0.001$; Fig. 6b and c). In escaped trees, radial growth is, in all sites, six to seven times larger above the browsing limit than under the browsing limit ($P < 0.001$; Table 2). Below the browsing limit radial growth is significantly lower in site 1 than in sites 2 and 3 ($P < 0.01$; Fig. 7). Above the browsing limit

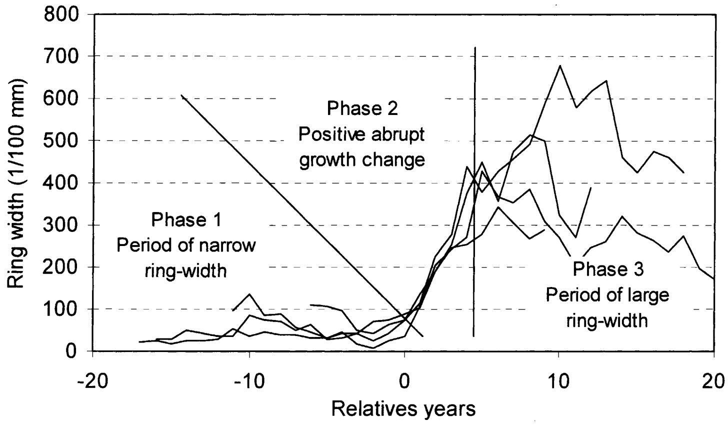


Fig. 3. Radial growth pattern showing the typical variation in ring widths with time in four escaped spruces sampled on Limestone Island.

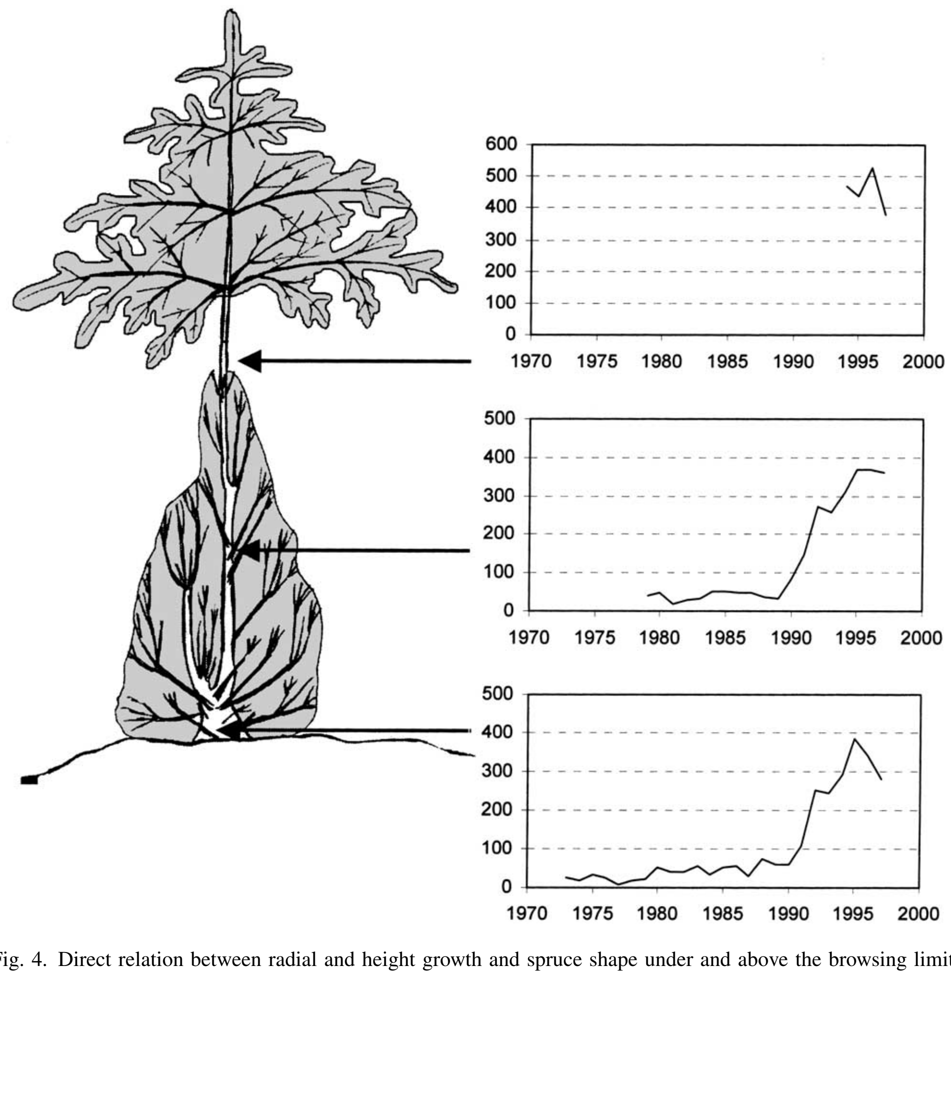

Fig. 4. Direct relation between radial and height growth and spruce shape under and above the browsing limit.

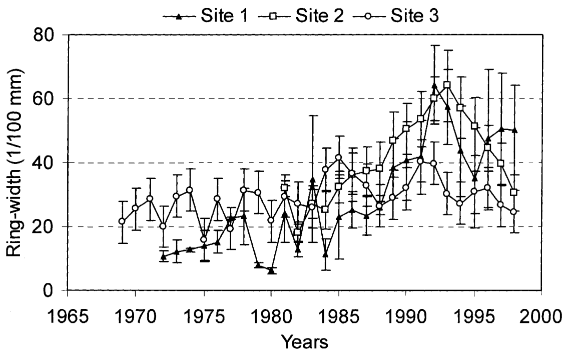


Fig. 5. Comparison of ring-width sequences between the three samples of stunted spruces.

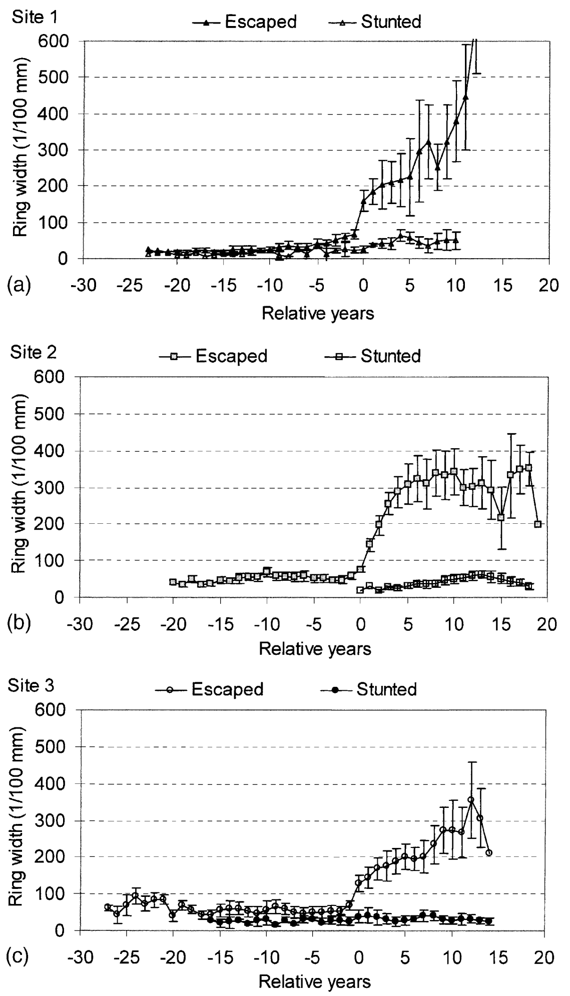


Fig. 6. Comparison between stunted and escaped spruces: (a) of the site 1; (b) of the site 2; (c) of the site 3.

radial growth is lower in site 3 than in sites 1 and 2. During the period just after escaping radial growth of escaped trees in site 1 is significantly higher than radial growth in site 2 and 3 ($P < 0.001$; Fig. 7). Later on, radial growth in sites 2 and 3 become similar while radial growth in site 1 becomes significantly higher than in sites 2 and 3 (Fig. 7).

### 3.3. Height growth indices

For site 2, we have no data on height growth above the browsing limit. The ANOVA on indices of height growth did not reveal a site effect ($P = 0.49$). Height growth is similar between stunted and escaped trees before the latter escape browsing ($P < 0.001$, Table 3). Height growth is similar in sites 1 and 3 both under and above the browsing limit ($P < 0.001$). Above the browsing limit height growth of escaped trees was two to four times larger than under the browsing limit ($P < 0.001$; Table 3).

### 3.4. Age comparison between stunted and escaped spruces

In each site stunted saplings were significantly younger than saplings which had escaped browsing ($P < 0.001$, Table 4). Age of stunted trees, age of escaped trees and age at escaping were significantly higher in site 3 than in sites 1 and 2 (significant site effect, $P < 0.001$). When age at release (Table 5) was compared with age (Table 4) and height (Table 6) of the stunted spruce sampled on the sites, the age range observed in stunted spruce at the time of study (Table 4) was not different of the age range estimated for escaped spruce at the time of release (9–12 years ago, Table 5). However the average height of stunted spruce at the time of study was significantly ($P < 0.001$) smaller by about 0.20–0.30 m than the height we estimated for escaped spruce at the time of release (Table 6).

## 4. Discussion

### 4.1. Growth response to deer browsing

Deer impact on growth is characterised by very narrow rings and by small height increments, both on

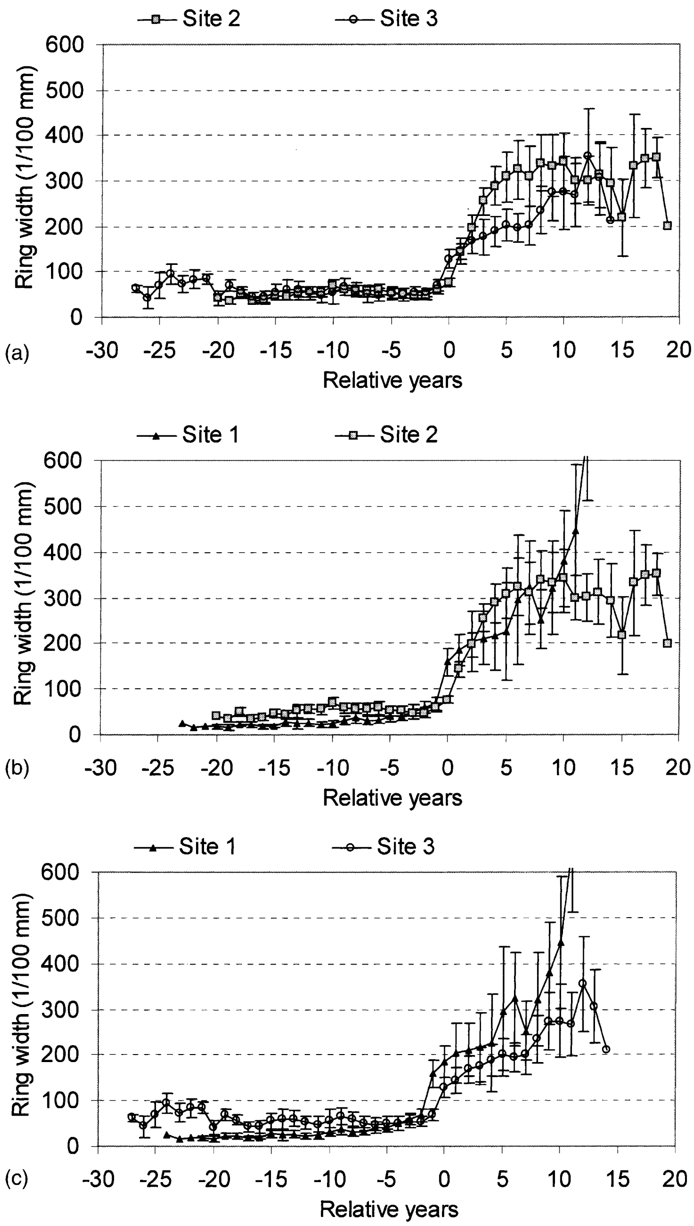


Fig. 7. (a) Comparison between samples of escaped spruces of sites 2 and 3; (b) comparison between samples of escaped spruces of sites 1 and 2; (c) comparison between samples of escaped spruces of sites 1 and 3.

stunted and escaped spruce before release. Our results on height and radial growth indices are consistent with those of Chouinard and Filion (2001) on balsam fir (*Abies balsamea* (L.) Mill.). The removal of new shoots reduces the amount of meristem and limits gain in foliage area (Schweingruber, 1996). However our results show that in spruce the impact of browsing is a temporary phenomenon. By coupling radial and height growth analyses we show that young spruce suffer severe browsing which results in a stunted sapling stage (Gill, 1992). Once the apex of the tree exceeds about 1.20 m in height, the tree can escape

Table 2
Radial growth indices of each category according to site and extreme values observed

| Radial growth indices and S.D. (mm per year) | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Average radial growth | | | |
| Stunted | 0.393 ± 0.260 | 0.461 ± 0.0.248 | 0.308 ± 0.160 |
| Escaped under browsing limit | 0.386 ± 0.219 | 0.574 ± 0.270 | 0.547 ± 0.354 |
| Escaped above browsing limit | 2.717 ± 1.576 | 3.167 ± 1.569 | 2.094 ± 0.963 |
| Maximal radial growth | | | |
| Stunted | 0.615 ± 0.040 | 0.813 ± 0.239 | 0.420 ± 0.190 |
| Escaped under browsing limit | 0.554 ± 0.273 | 0.910 ± 0.161 | 0.813 ± 0.773 |
| Escaped above browsing limit | 5.628 ± 1.770 | 5.342 ± 0.969 | 3.493 ± 1.351 |
| Minimal radial growth | | | |
| Stunted | 0.237 ± 0.183 | 0.245 ± 0.098 | 0.226 ± 0.085 |
| Escaped under browsing limit | 0.260 ± 0.230 | 0.289 ± 0.112 | 0.236 ± 0.159 |
| Escaped above browsing limit | 1.145 ± 0.089 | 0.813 ± 0.338 | 1.112 ± 0.542 |

Table 3
Height growth indices of each category according to site and extreme values observed

| Height growth indices and S.D. (cm per year) | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Average height growth | | | |
| Stunted | 8.14 ± 2.30 | 6.42 ± 1.80 | 4.59 ± 1.49 |
| Escaped under browsing limit | 10.11 ± 4.23 | 8.97 ± 2.07 | 6.68 ± 1.52 |
| Escaped above browsing limit | 17.89 ± 10.16 | No data | 20.70 ± 9.75 |
| Maximal height growth | | | |
| Stunted | 10.89 | 10.80 | 5.88 |
| Escaped under browsing limit | 20.00 | 15.00 | 8.77 |
| Escaped above browsing limit | 38.57 | No data | 49.25 |
| Minimal height growth | | | |
| Stunted | 3.14 | 3.62 | 2.43 |
| Escaped under browsing limit | 6.11 | 5.09 | 4.48 |
| Escaped above browsing limit | 6.25 | No data | 6.55 |

Table 4
Characteristics of tree age (mean and S.D. in years) with respect to sampling site and spruce type

| | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Stunted | 13.2 ± 7.6 | 12.7 ± 2.7 | 19.1 ± 5.5 |
| Escaped | 21.9 ± 6.6 | 25.5 ± 3.7 | 26.1 ± 4.9 |
| Youngest stunted spruce | 9 | 8 | 11 |
| Oldest stunted spruce | 35 | 18 | 31 |
| Youngest escaped spruce | 13 | 16 | 16 |
| Oldest escaped spruce | 32 | 32 | 36 |

Table 5
Characteristics of spruce age at release (mean and S.D. in years) with respect to sampling site

| | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Escaped at release | 12.8 ± 5.0 | 13.9 ± 3.4 | 17.8 ± 4.8 |
| Youngest at release | 8 | 8 | 10 |
| Oldest at release | 21 | 23 | 25 |
| Years since escaped (in 1999) | 9.7 ± 2.8 | 12.1 ± 3.8 | 8.8 ± 3.4 |

Table 6
Comparison of height (m) of 13 (sites 1 and 2) and 18 (site 3) year old spruce 9–12 before 1999 with height of 13 (site 1 and 2) and 19 (site 3) year old spruce in 1999

| | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Stunted | 0.92 ± 0.11 | 0.79 ± 0.19 | 0.80 ± 0.10 |
| Escaped at time of release | 1.16 ± 0.07 | 1.16 ± 0.07 | 1.16 ± 0.07 |

deer, a stage characterised by a positive change in radial growth and large annual height increments. This change in growth rate provides a signature allowing to reconstruct spatial and temporal dynamics of deer impact on Sitka spruce.

### 4.2. Individual and spatial variations in deer impact

Height and radial growth rate are variable among trees within a tree category (Tables 2 and 3). Genetic differences in growth rate, tolerance to browsing as well as micro-site characteristics may explain this variability. Variations in tree palatability, visibility or shape have been shown to influence sensitivity to browsing (Chouinard and Filion, 2001; Vourc'h et al., 2001, 2002). However, in the case of Sitka spruce Vila et al. (2002) showed that there was no evidence for chemical nor nutritive variation coupled with variation in browsing impact. Although height and radial growth were essentially a function of tree height with respect to the browsing limit they were nevertheless influenced by site conditions. Because of shallow soils and poorer light conditions growth indices after release are lower in site 3 than in sites 1 and 2. The reverse is observed before release possibly in connection with lower incidence of browsing in sites with poorer soils and/or light conditions and consequently their effects on plant quality for deer. Using carbon/nutrient balance, Iason et al. (1996) showed that high soil nutrient levels increased the growth but that growth was depressed by shade.

### 4.3. Age and release

Tree age varies greatly within our categories. Stunted spruce were between 8 and 35 years old. Age at release varied between 8 and 25 years. Vila et al. (2002) by sampling equally accessible spruce in the sites 1 and 2 showed that accessibility, nutritive values and chemical compounds were not correlated to escaping browsing. This study shows that tree age is. Overall, stunted spruce, smaller than the browsing limit are younger than spruce taller than the browsing limit. Thus although their growth is severely reduced by browsing, spruce tree will eventually reach the browsing limit and escape deer. These results are consistent with those of Duncan et al. (1994) and of Vila et al. (2002) but are species dependant. Indeed, under high browsing pressure, the escaping of western redcedar on the Queen Charlotte Islands, is essentially a function of a better potential in some individuals to produce chemical defenses (Vourc'h et al., 2002) and of ecological context (e.g. hunting pressure, Martin and Baltzinger, 2002).

### 4.4. Delays in recruitment as indicator of browsing pressure

At our study sites it took approximately 13 (sites 1 and 2) to 18 years (site 3) for a young spruce to reach the height of about 1.20 m necessary to isolate the apical bud from deer reach. On the basis of the work of Coates et al. (1985) on the Queen Charlotte Islands showing that non-browsed spruce need only 5 years to reach a height of 1.10 m, we conclude that browsing by deer delays sapling recruitment by at least 8–13 years under the deer densities and site conditions we sampled.

As sites 1 and 2 are ecologically similar and with comparable deer densities, these results suggest a direct relationship between deer density and deer impact on tree growth and age at release. The positive association of deer population density and intensity of browsing is widely accepted (Eiberle, 1985; Eiberle and Zehender, 1985; Gill, 1992). As was expected the more constraining environmental conditions in site 3 (similar deer densities but poorer light and soil) increase the age at which spruce reach the browsing limit.

The fact that: (1) radial growth currently observed in stunted trees is lower than past radial growth observed for escaped trees before they reached the browsing limit and (2) escaped spruce reached the browsing limit 9–12 years ago at about 13 years of age on sites 1 and 2 and 18 years on site 3, whereas, today, stunted spruce of the same age at these sites are still 0.20–0.30 m shorter than the browsing limit, suggest that browsing pressure has increased over the 15 years before our study. This could be caused by an increasing deer density or by a higher browsing pressure on these sites in a context of decreasing forage availability.

## 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 for his help in the field.

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