



Assessing spatial variation in browsing history by means of fraying scars

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ABSTRACT

Aim We used fraying scars to understand spatial variation in browsing history. Information on browsing history is an essential background in studies on the long-term effect of deer browsing on the flora and fauna and of its variation in space.

Location We focused on two small neighbouring islands of Haida Gwaii (British Columbia, Canada), Reef Island and South-Skedans Island, colonized by introduced black-tailed deer (*Odocoileus hemionus sitkensis*).

Methods We searched for sites where trees with fraying scars were clustered. We studied the trees that deer selected (species, size) and the characteristics of scars (number, position, size). Using a cross-dating procedure, we dated fraying scars with dendrochronology, obtaining an accurate estimate of the year the scar was formed.

Results On Reef Island, *Thuja plicata* was the tree species chosen for fraying. On South-Skedans Island, where *Thuja plicata* is missing, deer chose *Salix* sp. and *Alnus rubra*. Deer chose only trees with a circumference of less than 50 cm. About two to three fraying scars were recorded per tree. All of them extended between 30–40 and 70–80 cm from the ground and were between 5 and 6 cm in width. On Reef Island, 95% of the scars were formed during the last 50 years. On South-Skedans Island, 95% were formed over the last 10 years. Age distribution of scars showed a constant increase of the number of scars over time. It indicated that deer had colonized Reef Island 53 years prior to this study but were absent or rare on South-Skedans Island until 13 years prior to this study.

Main conclusions These results indicate different colonization dates and thus different length of browsing histories for the islands studied and provide the historical background necessary to analyse the involvement of deer in the current differences in the flora and fauna observed between islands.

Keywords

Deer colonization, dendrochronology, fraying scars, scar characteristics, damaged trees, browsing history, island flora and fauna.

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INTRODUCTION

Forest ecosystems consist of populations of plants and animals that can periodically undergo explosion (Banks, 1991). Sometimes the explosion is caused by a disturbance triggered by natural processes or results from human actions such as species introduction. Whatever its origin, it has the potential to stress the long-lived forest plants and to leave signatures recorded in

tree-ring series (Schweingruber, 1988). When the disturbance caused by animals, such as herbivores, is easy to single out, the external signatures left on the long-lived woody plants can be correlated with the internal signatures left in ring series. These signatures can be used to assess how a disturbance has affected vegetation and ecosystem dynamics. To do so, assessing the history of the disturbance itself (when, where and for how long) can be of crucial importance, especially in the absence of

written records (hunting statistics, published accounts of explorers) or when records are incomplete or discontinuous in time and space.

The introduction, in 1878 of the black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) to Haida Gwaii (British Columbia, Canada), an archipelago with no native large herbivore, provided an opportunity to evaluate our ability to document the history of herbivore colonization and impact by studying the record of the signatures they leave on woody plants. In the absence of detailed written sources about the history of deer colonization after they have been introduced, signatures such as changes in wood anatomical characteristics, abrupt changes in growth, changes in age, the number of stems and sprouts per individual and fraying scars, will be the most reliable historical documents (Vila, 2002, Vila *et al.*, 2002, 2003a,b). Such an approach can be particularly useful to provide an accurate background on browsing history to studies interested in the impact of ungulates on the flora and fauna of islands (Pojar *et al.*, unpubl. rep.; Pojar & Banner, 1984; Banner *et al.*, 1989; Stockton *et al.*, 2001; Stockton, 2003, 2004; Allombert & Martin, 2004; Gaston *et al.*, 2004; Martin *et al.*, 2004).

Fraying scars are among the most conspicuous of the signatures left by deer. They result from rubbing and trashing antlers up and down the stem when removing the velvet and/or during rut (Cemagref, 1981). Fraying causes local debarking and the local death of cambium. The scars remain visible on the trees for several decades and persist inside the wood for the

entire life of the tree. The initial scaring can be dated by means of dendrochronology because radial growth stopped at the lesion point but continued around it. We focused, as an example, on two islands of Laskeek Bay (Reef Island and South-Skedans Island). Both these islands were colonized by the introduced black-tailed deer, but show major differences in the impact of deer on their flora and fauna today (Stockton *et al.*, 2001; Stockton, 2003; Stockton, 2004; Allombert & Martin, 2004; Gaston *et al.*, 2004; Martin *et al.*, 2004). As habitat type and current deer densities were similar in both islands (Martin & Baltzinger, 2002; Stockton, 2003), differences in browsing histories were considered as the first hypothesis to test.

MATERIALS AND METHODS

Haida Gwaii and deer

Haida Gwaii (53°N, 132°W) is situated off the Pacific coast of Canada and includes more than 150 islands (Fig. 1). Our study sites are situated on the eastern side of the archipelago, which belongs to the Coastal Western Hemlock Zone, wet Hyper-maritime sub-zone. Forests consist mostly of a mixture of *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* D. Don ex Lamb. and *Picea sitchensis* (Bong.) Carrière. Early foresters and visitors (Gregg, 1923; Hopkinson, 1931; Hall, 1937) noted that the understorey originally included numerous shrubs such as *Gaultheria shallon* Pursh and *Vaccinium parvifolium* Smith in

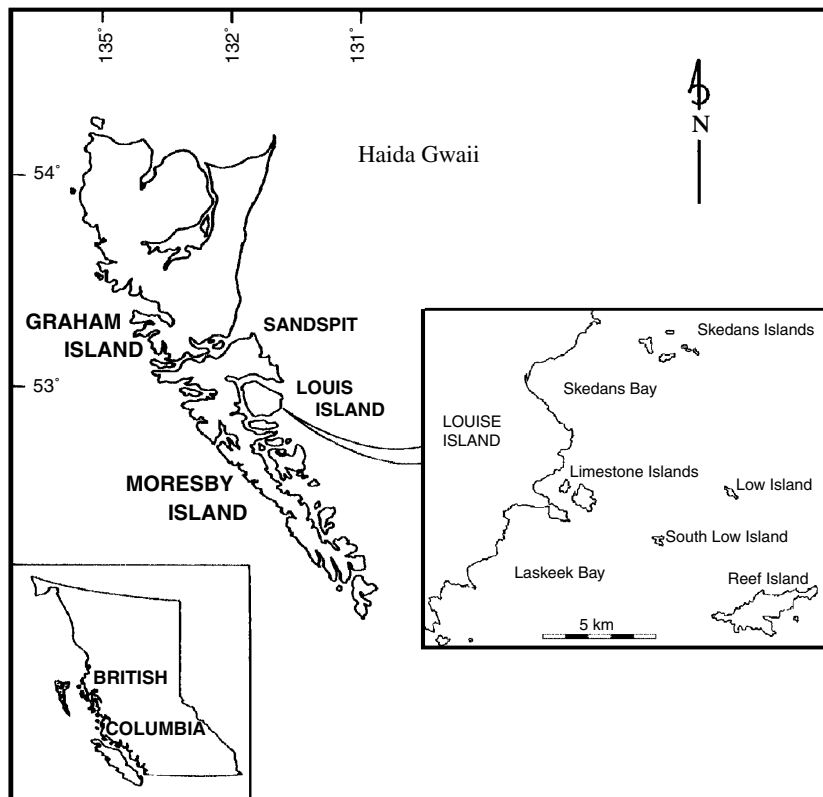


Figure 1 Haida Gwaii archipelago (British Columbia, Canada) with location of Skedans Islands and Reef Island.

Rees (see also Banner *et al.*, 1989). In many areas, deer browsing has reduced shrub cover to isolated old senescent shrubs (Pojar *et al.*, unpubl. rep.; Pojar & Banner, 1984; Stockton, 2003; pers. obs.). In these areas, the absence of ground vegetation, the existence of a browse line and palatable species confined to inaccessible areas such as steep cliffs, the top of rock stacks, stump and suspended logs indicate a very heavy browsing pressure (Reimoser *et al.*, 1999). All authors agree that major changes to the vegetation of the archipelago have resulted from the spread of deer (Pojar *et al.*, unpubl. rep.; Pojar & Banner, 1984; Martin & Daufresne, 1999; Martin & Baltzinger, 2002; Stockton, 2003; Pojar, 2004; Stockton, 2004).

Between 1996 and 2000, deer censuses and deer cull programmes on three medium-sized islands, including Reef Island (Daufresne & Martin, 1997; Martin & Daufresne, 1999; Sharpe, 2004), yielded density estimates that ranged around 30 deer per square kilometre. On South-Skedans, deer density estimated by pellet groups' counts also ranged around 30 deer per square kilometre (Stockton, unpubl. data). These black-tailed deer densities are considered to be higher than elsewhere in British Columbia and Alaska, their natural range (Sharpe, 1999). Across British Columbia and Alaska, black-tailed deer populations are affected by inter-dependent factors such as weather, predation, habitat alteration and energy limitation. Black-tailed deer can achieve rapid population increase due to their early age of first reproduction, annual breeding and capacity for twinning. In Haida Gwaii, these biological attributes, combined with the absence of significant predation, the abundance of food at colonization and a mild climate have resulted in a rapid and dramatic population increase, hence their effects on the ecosystems (Gillingham, 2004).

The islands

The two islands selected, Reef Island and South-Skedans Island (Fig. 1) are both covered by mature old growth forests. They differ markedly in size (249 and 5.6 ha, respectively). Reef Island is an isolated island while South-Skedans Island is part of a cluster of four islands separated by narrow channels allowing deer an easy access to a cumulated forested area of about 13 ha. The Skedans Islands are situated at 1350 m from Louise Island, the closest source of colonization. The distance from Reef Island to Louise Island is about 6500 m. The only type of human activities that ever occurred in these two islands was their traditional use by the population of the nearby Haida villages present until the last quarter of the nineteenth century. Neither commercial logging nor other commercial activity has been documented for these islands. However, at the time of study, the understorey of Reef Island differed from the one of the Skedans Islands (Stockton, 2001, 2003, 2004). On Reef Island, the understorey vegetation had been eliminated by deer in most areas (Daufresne & Martin, 1997; Martin & Daufresne, 1999; Gaston *et al.*, 2004). On South-Skedans Island, the understorey was patchy with areas with a dense understorey, including deer-sensitive species, next to areas with little

vegetation left (Stockton *et al.*, 2001; Stockton, 2003, 2004, pers. obs.).

Sampling sites

We searched fraying scars on both islands. On each of them, we found one site where fraying scars were clustered. A few additional isolated scars were found on Reef Island, whereas none were observed on South-Skedans Island. As a consequence, our samples should be representative of deer fraying on these islands. The site where trees with scars were sampled on Reef Island was characterized by a stand of about 1650 stems per hectare, consisting of *c.* 48% of *Tsuga heterophylla*, 35% of *Thuja plicata* and 17% of *P. sitchensis*. The canopy was dominated by *P. sitchensis* and *Tsuga heterophylla*. *Thuja plicata* was less abundant. The scars were grouped within a site, 25 × 100 m in size, situated on a small hill, well drained with a slope of *c.* 10–14° and with an aspect of 80°. Organic soil was 20–45 cm thick. The site where scars occurred on South-Skedans Island was a more open forest of *P. sitchensis* typical of the smaller islands. *Tsuga heterophylla* was poorly represented. The few *Thuja plicata* present were young and branched from their base to their top. They were growing in the middle of large thickets of shrubs. Broad-leaved trees such as *Salix* sp., *Alnus rubra* Bong. and *Pyrus fusca* Raf. were present. The site where scars were concentrated was 10 × 20 m in size. It was badly drained with a slope of less than 5°, its aspect was 210°, and it had mineral soil 40 cm thick.

Characteristics and position of fraying scars

Fraying scars were characterized by a strong contrast between the light yellow colour of the denuded xylem and the grey or brown colour of the bark. This contrast makes trees with fraying scars conspicuous. Scars were also easily recognizable by their shape and their position on the trunk. When trees are used repeatedly over the years, scars are superposed. Growth at the periphery of the lesion gradually overgrows the scar. However, xylem remains exposed for several decades depending on species and scar superposition. We recorded the species identity and the circumference class for each tree damaged by deer. We measured the tree circumferences at a height of 50–60 cm above the ground for all the trees present within a 5 m radii around each frayed tree. For each scar, we also recorded the height above the ground of its base and of its top. We measured scar-width at the middle between its base and top, but only for scars for which the healing callous tissue could be dated on both sides of the scar.

Sampling

Within each sampling area, we looked for the presence of scars on each tree. All trunks exhibiting growth anomalies that could correspond to overgrown wounds were checked allowing us to sample old scars only revealed by the presence of irregularities

on the trunks. Because coring is not an efficient method for trees with probable decaying wood, all trees with fraying scars were cut down, trunk sectioned and a section at the medium level of the scar collected for aging.

Estimation of scar age

Sections were finely sanded using successively finer grits of sand paper (80–120–180–320). Scars were dated under the binocular microscope by cross-dating ring-width series of damaged trees using as reference ring-width chronologies (Schweingruber, 1988). Cross-dating is a procedure based on the variability of ring structure (width, density, anatomical characteristics), which makes it possible to correctly estimate the year of scar formation by looking for possible missing or double rings (Schweingruber, 1988). In our case, we established, for each species, patterns of narrow rings that were diagnostic and used them to date visually each ring of the sample series. We obtained the reference chronology for *Thuja plicata* by averaging five mean chronologies of dominant trees that had not been damaged by fraying. Each mean chronology corresponded to a sample of non-wounded trees collected in the Laskeek Bay area. They were built according to classical dendrochronological methods (Schweingruber, 1988). In the absence of similar data for *A. rubra* and *Salix* sp. we cross-dated these trees by using exclusively their own tree-ring series mean chronologies. When cross-dating was unsuccessful, we counted the rings situated between the lesion and the bark to estimate a date. The exact year of scar formation was determined only when the wounding occurred during the xylem growth. When scars were formed when the cambium was dormant, there may be a ± 1 -year error inherent in the dating assuming that all rings were cross-dated. Hence, dating spans 2 calendar years, the fall of year t and the spring of year $t + 1$. In the present paper, we used the oldest estimate as the year of scar formation.

Finally, to document the consequences that fraying scars can have on tree health, we recorded the presence/absence of wood alteration among the rings formed after the scar was inflicted, the presence of compartmentalization and healing speed. We estimated healing speed (cm year^{-1}) for each species by dividing the width of the callous tissue covering the scar by the number of years since the scar was inflicted.

Data analysis

We used chi-squared tests to analyse tree selection by deer. We plotted circumference classes for trees with and without fraying scars and compared mean circumferences of trees with and without fraying with a t -test. Because once a fraying scar occurs on a tree it can become a signal influencing deer choice (CEMAGREF, 1981), we used the circumference that the tree had when the first fraying occurred as tree circumference. We constructed age-frequency distributions of scars for the two islands using only scars for which dating was sure.

RESULTS

Trees selected for fraying

On Reef Island, we examined 34 *Thuja plicata* with fraying scars and measured circumferences of 254 trees around them (49 *Thuja plicata* without fraying scars, 130 *Tsuga heterophylla* and 75 *P. sitchensis*). Neither *P. sitchensis* nor *Tsuga heterophylla* were frayed whatever their circumference (Fig. 2a). Deer only frayed *Thuja plicata* trees ($\chi^2 = 82.8$, $\text{ddl} = 2$, $P < 0.001$). These frayed *Thuja plicata* were always characterized by circumferences of less than 50 cm ($P < 0.001$; Fig. 2b).

On South-Skedans Island, we examined nine *A. rubra* and 21 *Salix* sp. with fraying scars and measured the circumferences of 25 trees around them (two *Salix* sp. and eight supplementary *A. rubra* without fraying scars, five *Tsuga heterophylla* and 10 *P. sitchensis*). Neither *P. sitchensis* nor *Tsuga heterophylla* (poorly represented) were frayed (Fig. 3a). Deer only selected *A. rubra* and *Salix* sp. ($\chi^2 = 25.4$, $\text{ddl} = 2$, $P < 0.001$). Frayed *A. rubra* and *Salix* sp. were always characterized by circumferences of less than 50 cm (Fig. 3b).

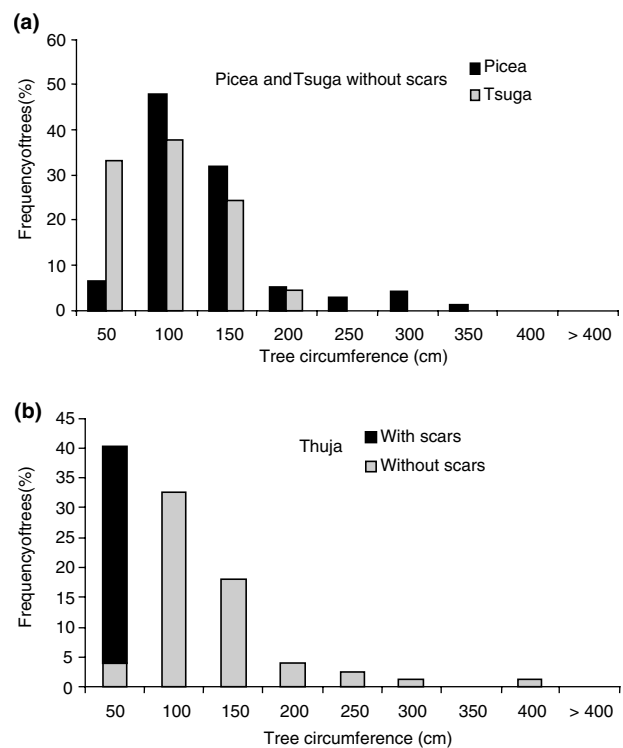


Figure 2 Frequencies of trees (%) according to their circumference at a height of 50–60 cm in Reef Island. (a) Circumferences of neighbouring *Picea sitchensis* (black) and *Tsuga heterophylla* (grey) without fraying scars. (b) *Thuja plicata* with fraying scars (black) and without fraying scars (grey).

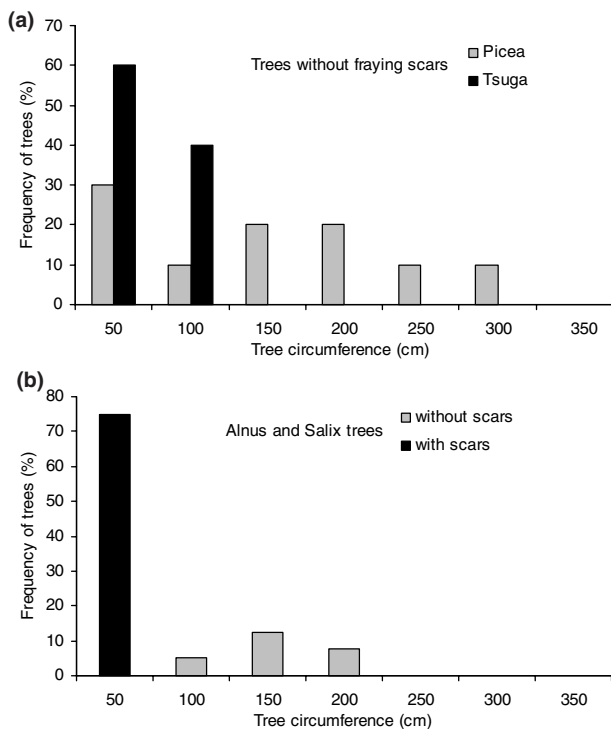


Figure 3 Frequencies of trees (%) according to their circumference at a height of 50–60 cm in South-Skedans Island. (a) Circumferences of neighbouring *Picea sitchensis* (black) and *Tsuga heterophylla* (grey) without fraying scars. (b) *Salix* sp. and *Alnus rubra* with fraying scars (black) and without fraying scars (grey).

Position and characteristics of fraying scars

Two to three scars occurred on average on each tree with scars (mean \pm SE; 2.9 ± 0.3 for *Thuja plicata*; 2.0 ± 0.2 for *A. rubra* and 2.2 ± 0.3 for *Salix* sp.). On *Thuja plicata*, fraying scars were between 29.4 ± 1.4 and 64.3 ± 1.9 cm high. In the presence of a slope, fraying scars were preferentially oriented downslope. On South-Skedans Island, scars ranged from 35.7 ± 3.0 to 72.9 ± 3.7 cm from the ground for *A. rubra* and from 40.7 ± 2.7 to 74.0 ± 2.9 cm from the ground for *Salix* sp. Accordingly, trunk length impacted by fraying was c. 30–40 cm. Scar-width at fraying measured between 5 and 6 cm (5.9 ± 0.5 cm on *Thuja plicata*; 5.1 ± 0.6 cm on *A. rubra* and 4.6 ± 0.4 cm on *Salix* sp.). Scar-width showed no relation with stem circumference at fraying ($R^2 = 0.004$ for *Thuja plicata*, 0.00002 for *Salix* sp. and 0.2 for *A. rubra*).

Age–frequency distributions of scars

Seventy-seven percent of the 96 scars collected on Reef Island and 100% of the 65 scars (47 on *Salix* sp. and 18 on *A. rubra*) collected in South-Skedans Island were dated with certainty by visual cross-dating of narrow rings (see Fig. 4 for an example with each species). On Reef Island, we frequently observed narrow rings on *Thuja plicata* in 1905, 1911, 1922, 1929, 1931, 1941, 1948, 1951, 1958, 1963, 1967, 1972, 1975, 1990 and 1993

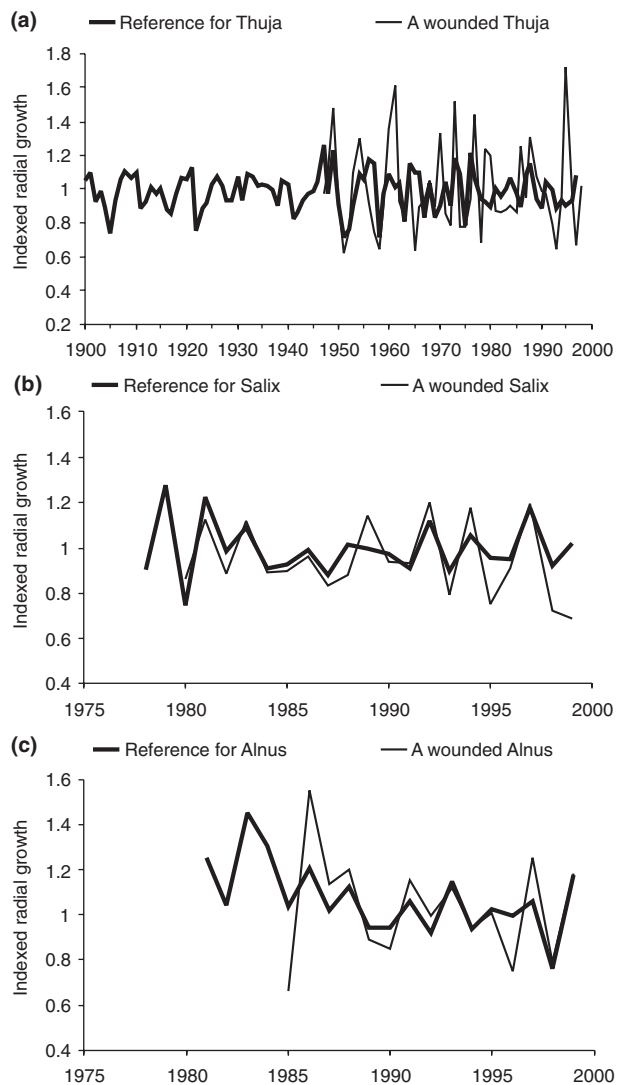


Figure 4 Example of visual cross-dating of chronology reference with wounded trees for (a) *Thuja plicata*, (b) *Salix* sp. and (c) *Alnus rubra*.

(Fig. 4a). On South-Skedans Island, we observed narrow rings for *Salix* sp. in 1980, 1983, 1987, 1991, 1993 and 1998 (Fig. 4b) and for *A. rubra* in 1985, 1987, 1992, 1994 and 1998 (Fig. 4c). The grouping of scars into 5-year age classes showed that their age distribution spanned over the 50–60 years before the study on Reef Island (Fig. 5) and over the 10–15 years before the study on South-Skedans Island (Fig. 6). Only two scars were formed before 1950 on Reef Island and only three before 1987 on South-Skedans Island. On Reef Island, most scars were formed in the course of the 20 years (61.6%) before the study and on South-Skedans Island, 95% of the scars were formed during the 10 years before the study. Age distributions of scars show a constant increase with time of the number of scars inflicted during a 5-year period (Figs 5 & 6).

Healing speed was equal to 0.20 ± 0.03 cm year⁻¹ for *Thuja plicata*, 0.40 ± 0.07 cm year⁻¹ for *A. rubra* and 0.30 ± 0.03 cm year⁻¹ for *Salix* sp. In theory, the mean

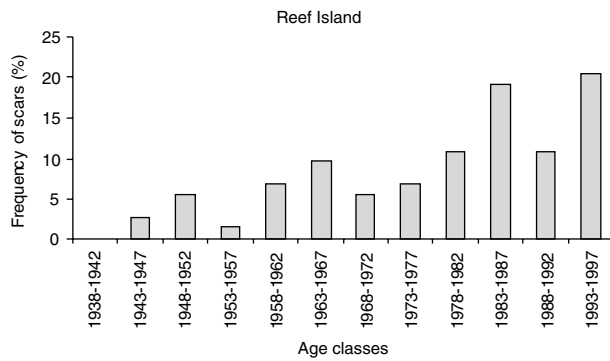


Figure 5 Age structure of fraying scars of *Thuja plicata* on Reef Island.

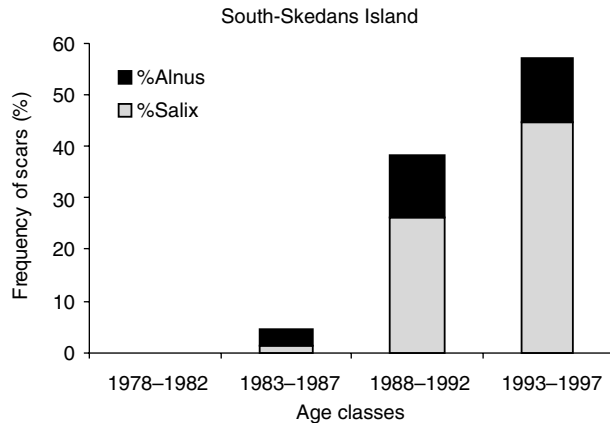


Figure 6 Age structure of fraying scars of *Alnus rubra* (black) and *Salix* sp. (grey) on South-Skedans Island.

number of years necessary to close a scar of average size would be *c.* 13 years for *A. rubra*, 15 years for *Salix* sp. and 29 years for *Thuja plicata*. However, the speed of healing is often slowed down by wood decay. Once healing is completed, typical shape irregularities continue to make frayed trees conspicuous to the observer for decades.

On Reef Island, 14.7% of *Thuja plicata* with frayed scars had insect galleries; 67.7% had decayed wood tissue in rings formed after the scar, 8.8% had both decayed wood and insect galleries. Only 8.8% of the trees are not altered. When the wood did decay, cavities did form in the trunk. There were no signs of compartmentalization on the *Thuja plicata* trees sampled (Fig. 7a). On South-Skedans Island, 100% of trees with fraying scars had discoloured wood tissue in rings formed after the scar, but we did not observe decaying wood or cavities. All frayed trees sampled on this island showed signs of compartmentalization (confinement of discoloured wood, Fig. 7b).

DISCUSSION

Trees selected and consequences of fraying

Several studies have analysed the way deer selected trees for fraying (see Gill, 1992). According to Gill (1992), physical

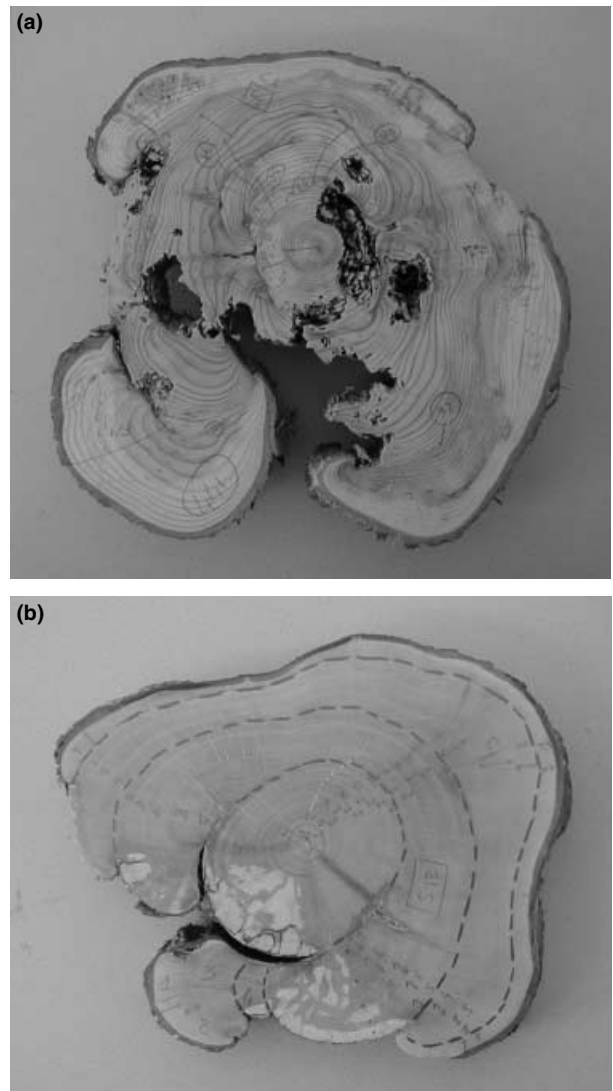


Figure 7 Fraying scars on cross-section collected on (a) on *Thuja plicata* showing decayed wood and cavities formed in the trunk without sign of compartmentalization and (b) *Salix* sp. showing discoloured wood tissue compartmentalized but no decaying wood or cavities.

characteristics appear more important than tree species. In the present study, deer seem to prefer trees that are less than 50 cm in circumference and *Thuja plicata* or *Salix* sp. and *A. rubra* over *Tsuga heterophylla* or *P. sitchensis*. Thompson (1969, cited in Gill, 1992) had already identified *Thuja plicata* as a preferred tree species in a comparison involving 17 different species, a preference probably related to the soft texture of its bark. Our study confirmed earlier findings (CEMAGREF, 1981) that fraying scars occur all around the trunk at a height of less than 0.80 m. Although some authors (Morneau & Payette, 1998; Girompaire & Ballon, 1992) have shown that there was a relation between the size of the scar and the actual size of the stem used for fraying, we failed to find such a relationship.

The long-term survival of a tree after injury depends on its ability to insulate itself from pathogens by closing wounds on the outside and compartmentalizing them on the inside. This process starts with a chemical reaction that delays the spread of pathogens and proceeds with the formation of a barrier to isolate infested tissue (Shigo, 1984) from healthy tissue. In our case, *Salix* sp. and *A. rubra* were able to compartmentalize wounds consecutive to all fraying scars and were able to close them. On the contrary, *Thuja plicata* trees were not able to compartmentalize their wounds. This absence of compartmentalization associated with a slow process of healing favours wood decay. In the case of *Thuja plicata*, this lack of compartmentalization may lead to the loss of the scarred trees from the future population of mature trees. The colonization of an island by deer can, therefore, have a retroactive effect on *Thuja plicata* abundance by inhibiting proper growth of trees established before deer colonization. This occurs in a context where *Thuja plicata* regeneration is already inhibited by deer browsing (Pojar *et al.*, unpubl. rep.; Pojar & Banner, 1984; Martin & Baltzinger, 2002).

This also raises the question of the premature loss of scarred trees from the early period of deer colonization on Reef Island. To estimate this potential bias, we searched for stumps and remains of such dead trees on the study site. Such remains should still be easy to identify given the time span considered and the rate of wood decay in these forests (pers. obs.). We observed only one dead tree that was probably frayed and we were not able to cross-date, suggesting that, over the time period considered since deer colonization, the loss of frayed trees is highly unlikely. In addition, the 21 scars that could not be dated with certainty in Reef Island were distributed across all age classes, further suggesting the absence of time-related biases in our age distribution of scars.

Scars and deer colonization

Age of the oldest scars and scar age distribution suggest different colonization histories for the two islands we studied as an example. While fraying scars suggest that deer were established on Reef Island during the mid-1940s (at least 53 years on Reef Island at the time of this study, 2000 being the year of reference), they suggest that deer did not take a stronghold on South-Skedans Island before the mid-1980s. Vila (2002), by coupling dendrochronology to analyses of modifications of plant shape and shrub stem age structures by deer browsing, show that deer had become the main factor shaping the understorey on Reef Island about 40 years before the time of this study (that is in the early 1960s). This suggests a delay of 10–15 years between the time deer presence can be detected by fraying scars and the time age structures of long-lived shrubs are strongly affected.

Gill (1992) indicated that the incidence of fraying by roe deer was expected to increase with increasing deer density. Positive relationships between the number of scars and deer population density have also been reported for bark stripping.

But differences between sites in scar densities can be wrongly interpreted as deer density differences (Gill, 1992). In the present study, however, the pattern of increasing number of fraying scars over time on a given site is in agreement with the expected increase in deer density on both islands after the initial colonization in the course of the twentieth century. Our results are also consistent with the occurrence on South-Skedans Island, but not on Reef Island, of 20–25 years old (22.58 ± 0.36 years old) *Thuja plicata* trees. As pointed out in other studies (Pojar *et al.*, unpubl. rep.; Pojar & Banner, 1984; Martin & Baltzinger, 2002), regeneration of *Thuja plicata* in the old growth forests of Haida Gwaii stops soon after deer colonization. The young trees occurring today in South-Skedans were likely to have their apical leaves out of the reach of deer during the mid-1980s at the time the oldest scars were formed (Vila, unpubl. data).

The reasons for such a delayed colonization of the Skedans remain unclear. These islands are closer to the source of colonization (1350 m) than is Reef Island (6500 m), even taking into account the fact that the channel separating the Skedans from Louise has strong tidal currents. An alternative would be that the Skedans were colonized at the same time as Reef Island, but that it took deer longer to have a visible impact. Such a delay would be hard to understand. First, because of the similitude in the understorey on the two islands, second because if we use deer densities measured on Reef and other nearby islands (see Martin & Baltzinger, 2002) it would take only a population of four to five deer to significantly impact the understorey over the years. Another scenario would be that an early colonization was followed by extinction allowing the island to recover before recolonization. But the lack, so far, of fraying scars older than 13 years is not in favour of the latter scenarios.

The results we obtained from fraying scars and shrub stem structures (this study and Vila, 2002) do allow the grouping of the islands in Laskeek Bay according to the length of their browsing history. Stockton *et al.* (2001), Allombert & Martin (2004), and Martin *et al.* (2004) and Stockton (2004) used this grouping to show that the longer the browsing history the lower the abundance and diversity of the vegetation, insects and birds in the forest understorey, demonstrating how retrieving the information stored by ligneous plants can be essential in our efforts to understand how forest ecosystems work.

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