



# Can we reconstruct browsing history and how far back? Lessons from *Vaccinium parvifolium* Smith in Rees

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## Abstract

We assessed the impact of browsing by black-tailed deer (*Odocoileus hemionus sitkensis*) on a common long-lived shrub (the red huckleberry, *Vaccinium parvifolium*) on Haida Gwaii (British Columbia, Canada). We studied how deer impact can be used as a marker of deer abundance and fluctuation and a means to reconstruct the recent history of deer browsing over a significant section of the archipelago. We compared islands with and without deer to understand processes involved in these changes. We compared shrub features such as number of stems and regenerating sprouts, age and height of stems and stem age-structures between deer-free and deer-affected islands and analysed their spatial and temporal variation. Deer, by browsing regenerating sprouts, stopped stem replacement. On deer-affected islands the number of stems per individual shrub was 2–4 times lower than on deer-free islands. The number of regenerating sprouts was 8–15 times higher. Stems were, on average, 2–3 times older. There was no variation in these characteristics among deer-free islands. They varied both spatially and temporally among deer-affected islands revealing spatial and temporal variation in deer impact. Deer impact has been prevalent for at least 40–50 years before this study in all sites with deer but one. In the latter, the most distant from the point of introduction, severe impact seemed to date to less than 10 years before this study. On Reef Island, Ramsay Island and Burnaby Island, deer impact was prevalent 10–20 years earlier than on Louise and Haswell Islands, although the two latter were much closer and more easily accessible from the point of introduction. Using independent information, we interpreted this pattern as the result of differences in climate and habitat rather than of a delay in colonisation. Effects of isolation on dispersal, pattern of land use or access to alpine summer range are all likely to affect delay between colonisation and severe impact.

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## 1. Introduction

Ungulate herbivores can have a profound effect on vegetation structure and composition (Allen et al.,

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1995; Anderson and Loucks, 1979; Tilghman, 1989; Woodward et al., 1994). Such effects have been inferred from comparative analyses of current plant diversity, species composition and of vegetation structure and biomass (Hernandez and Silva-Pando, 1996; Peinetti et al., 2001). Long-lived understory plants, which can resist browsing for many years, have the potential to record variation in browsing pressure through changes in biological characteristics and growth pattern. Dendrochronology looks at such biological changes and can provide a temporal reconstruction of the intensity and spatial variation of browsing.

Plant shape is a main feature modified by browsing (CEMAGREF, 1981; ONC, 1994; Vila et al., 2002). However, shape modifications have only been little used (Chouinard and Filion, 2001; Vila et al., 2001, 2002) to analyze and reconstruct the history and variation of deer browsing (Vila et al., 2003a,b). Rubbing and fraying scars have been used to date deer impact (Vila et al., 2004) but are sparsely distributed (see Gill, 1992). There is a need for characteristics of impact that are widely distributed on long-lived understory plants and which provide information on deer presence and impact level. Plant architecture (stem number, number of regenerating sprouts), plant height (Anderson, 1994) and plant age (Roughton, 1972) have the potential to provide such information (Roughton, 1972; Banks, 1991).

In this study we analyzed the variation of such biological characteristics in red huckleberry (*Vaccinium parvifolium* Smith in Rees), a common and long-lived ligneous shrub, in relation to browsing by Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) on Haida Gwaii (British Columbia, Canada). Deer were absent from these islands until they were introduced to the northern island at the end of the 19th century. Today these islands provide a natural laboratory offering, side by side, islands with introduced deer and islands without deer. We selected red huckleberry as an indicator species because it is widespread in the understory of coastal forests of north-western North America (Pojar and MacKinnon, 1994). Red huckleberry is a preferred forage for deer (Daufresne, 1996), but can survive browsing for long periods, even when browsing is intensive. It can, therefore,

record variation in deer impact over long periods of time.

We compared adjacent islands with and without introduced deer (1) to identify how deer modify morphology (sprouts and stems), age structure and height of red huckleberry, and (2) to understand the processes involved in these changes. We used these changes as markers of deer presence and fluctuation and reconstructed browsing history over the southern half of the archipelago.

## 2. Material and methods

### 2.1. Material and sites

#### 2.1.1. Study area and deer density

Situated about 80 km off the Pacific coast of Canada, the archipelago of Haida Gwaii (53°N, 132°W) includes more than 150 islands (Fig. 1). Our sampling sites are situated on the eastern side within the Coastal Western Hemlock Zone, wet Hypermaritime sub-zone (Banner et al., 1989). Forests consist of a mixture of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* D. Don ex Lamb.) and sitka spruce (*Picea sitchensis* (Bong.) Carrière). The western hemlock is the dominant species at low elevation where it often forms pure dense stands. The understory was originally dense and composed of shrubs like salal (*Gaultheria shallon* Pursh) and red huckleberry (*Vaccinium parvifolium* Smith in Rees; Banner et al., 1989). In many areas deer browsing has reduced it to old, isolated and senescent shrubs (personal observation; Pojar et al., 1980). In these areas the absence of ground vegetation, the existence of a browse line and of palatable species confined to inaccessible areas indicate a heavy browsing pressure according to the table completed by Reimoser et al. (1999). This process of understory impoverishment is most advanced on the medium-sized islands situated on the eastern side of the archipelago (Martin and Daufresne, 1999). Between 1996 and 2000 censuses and deer cull programs on three medium-sized islands (Daufresne and Martin, 1997, Sean Sharpe unpublished data) yielded density estimates of around 30 deer per km<sup>2</sup>. Pellet group counts from transects in old-growth forest patches on the large islands of Graham Island and northeastern Moresby

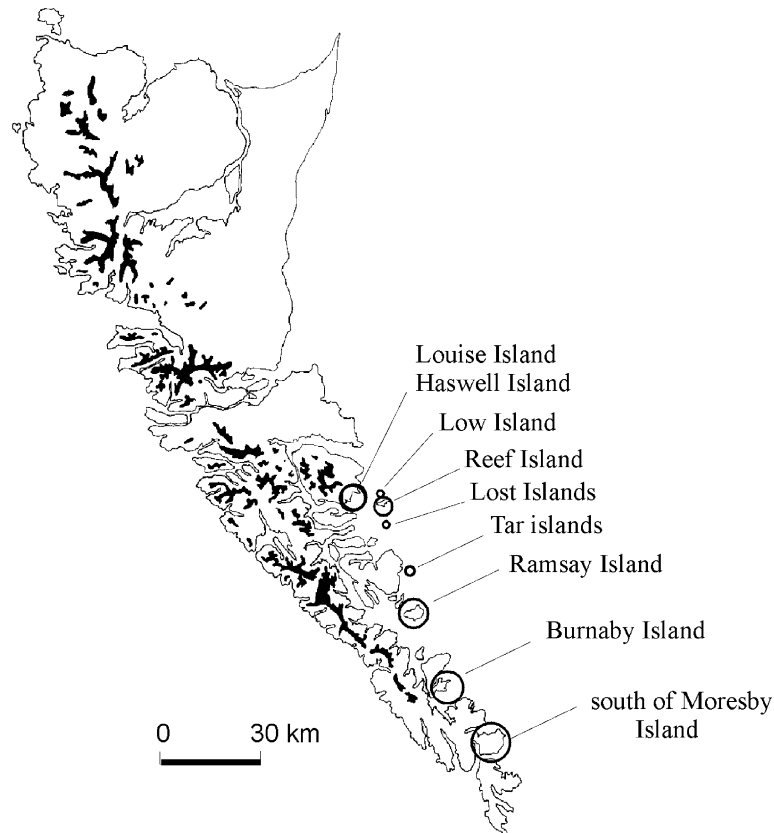


Fig. 1. Sites sampled on Haida Gwaii.

Island (Engelstoft, 2001) yielded estimates of about 13 deer per km<sup>2</sup>.

### 2.1.2. Red huckleberry

Red huckleberry is widely distributed along the Pacific coast, from northern Alaska to California. It can reach up to 4 m, and has many stems per individual. It grows in soils rich in decaying wood, at low to middle elevation (Pojar and MacKinnon, 1994). It is the second dominant shrub after salal and thrives under densely shaded conditions that few other higher plants can tolerate. It often forms dense thickets especially along margins of clearings and in logged-over areas (Calder and Taylor, 1968). New stems are produced by a particular organ situated at the stem base, the lignotuber or burl, an aggregation of short branchlets terminated by dormant buds and fused into a complex, patterned mass of wood (Garland and Marion, 1960). This process of vegetative regenera-

tion by sprouting is the primary means by which red huckleberry plants are maintained for long periods (Haeussler et al., 1990). Its foliage and sprouts are highly palatable to deer. Stems tall enough to be out of reach of deer can survive deer browsing for long periods of time.

### 2.1.3. Vegetation description of the islands sampled

The cover of vegetation on deer-free islands averages 65.0% in the ground layer (0–50 cm), 56.2% in the 50–150 cm layer, and 43.8% between 1.5 and 4 m (Stockton, in press). Red huckleberry represents 9% of the cover in the shrub layer (Martin and Daufresne, 1999). On deer-affected islands vegetation cover averages 26.2, 10.7, and 20.3% in these three layers respectively and red huckleberry occurs as isolated individuals taller than the browse line, which is between 1.1 and 1.5 m. On the islands most severely

affected, the cover of red huckleberry is lower than 1% (Martin and Daufresne, 1999; Stockton, in press), existing shrubs being remnants of plants that have been progressively reduced by introduced deer (Pojar et al., 1980; Pojar and Banner, 1984).

## 2.2. Sampling

### 2.2.1. Sites

We collected samples on islands with and without deer. When island size was large (>15 ha), several sites were sampled to avoid biases caused by local particularities.

We sampled red huckleberry on the three largest of the few deer-free islands found on Haida Gwaii. All three were situated in Laskeek Bay: Low Island (9.6 ha), Lost Island (5.3 ha) and Tar Island (6 ha). On these small islands, the area sampled covered a large proportion of the area favorable to red huckleberry. The islands with deer that we studied were, from north to south: Louise Island, Haswell Island, Reef Island, Ramsay Island, Burnaby Island and the southern tip of Moresby Island (Fig. 1). Louise Island is one of the largest islands of the archipelago (35,000 ha) and is only separated from the main islands (northern part of Moresby) by a narrow dredged channel. It has extensive areas of alpine habitat and has been logged extensively. Logging occurred from the depression years (1920s and 1930s) until ca. 1950 (M. Salzl, Ministry of Forest, personal communication; Dalzell, 1968) and resumed in the last quarter of the 20th century. Haswell Island is a small island (13.3 ha) 150 m off shore from Louise Island. Reef Island is a medium sized (249 ha) island 6 km off shore from Louise. It has some of the most severe deer impact recorded on the archipelago (Martin et al., 1993). All three islands are situated in Laskeek Bay. Further south, Ramsay Island is situated at 5 km off shore from Moresby Island, but can be reached by deer through a chain of stepping stone islands. Burnaby Island (6600 ha) is only separated from Moresby Island at low tide by a narrow water channel. Finally, we sampled huckleberry on a peninsula situated in the south-east of Moresby Island within the CWH vWH forest zone. In each location we sampled between 1 and 3 sites, depending on island size.

To control the reliability of age determination by ring counting we also collected additional plants

inside a 20 ha enclosure established in 1988 by Western Forest Products on its Tree Farm Licence (TFL 24) (Bennet, 1996) on northern Moresby Island.

### 2.2.2. Sampling protocol: definitions and implementation

For each site, defined as an homogeneous area where sampled shrubs were growing, we recorded the size of the sampling area, aspect, slope, soil depth, forest basal area, the number of individuals and the number of stems and sprouts per individual (Table 1). Stems were defined as aerial organs consisting of woody plant tissue supporting buds, leaves and sometimes flowers. Regenerating sprouts were defined as new shoots, less than 20 cm tall, emerging from the litter and connected to a lignotuber. Individual plants were defined as one or more stems and regenerating sprouts growing together, all connected to the same lignotuber. For each individual, we recorded the number of stems and regenerating sprouts, measured the height (at 5 cm accuracy) of all stems, and collected the basal cross-sections, labelling samples by individual.

The objective was to collect at least 15 individuals per site. We could not meet this objective in some of the sites especially on deer-free islands. The limited area of these islands, their difficult access, and, above all, the need to restrain the destructive impact of this sampling technique relative to the total size of the local plant population all played a role in reducing actual sample size. We collected all stems on each of the individuals sampled.

## 2.3. Analyses

### 2.3.1. Specimen preparation

Because cambial activity is not always uniform in time and space over the entire plant (Kolishchuk, 1990), and because of distortions, ring legibility depends on sample preparation. Cross-sections were meticulously sanded using successively finer grits of sand paper (80–120–180–320–400), a procedure described by Stokes and Smiley (1968). After removing the sanding marks left by the preceding grit, each section was polished to further improve the legibility. Cross-section preparation was examined through a binocular ( $\times 40$ ) and further sanded and polished in case of reading difficulty.

Table 1  
Ecological characteristics of sampled sites

Island site	Louise		Haswell		Reef		Ramsay		Burnaby		South Moresby		Low	Lost	Tar
	1	2	1	2	1	2	1	2	1	2	1	2			
Area (m)	25 × 100	20 × 80	20 × 60	20 × 40	20 × 150	20 × 40	20 × 60	30 × 50	25 × 60	30 × 200	20 × 40	25 × 200	15 × 30	15 × 20	5 × 10
Aspect (°)	30	50	340	180	130	280	160	40	170	165	340	110	40	300	290
Slope (°)	7	<5	11	0–12	19	33	9	9–12	10	6	2	13–15	16	3	8
Organic layer (cm)	40–60	>50	15–30	30–40	25–40	40–60	20–55	30–45	15–40	>45	55	>40	15–50	75	>30
Basal area (m <sup>2</sup> /ha)	60	76	92	46	45	38	35	40	30	40	40	55	76	31	20
Individuals	21	25	27	16	13	15	24	18	18	20	11	13	15	14	4
Stems	40	43	42	27	23	29	53	43	47	52	42	56	134	82	40
Individuals/island	46		27		44		42		38		24		15	14	4
Stems/island	83		42		79		96		99		98		134	82	40

The area is the surface where shrubs were sampled and growing in similar and homogeneous conditions.

### 2.3.2. Age determination method

The initial step in age determination was to assess which radius of the cross-section was most legible. Then, for each cross-section, rings were pointed. Rings were counted on two radii from the pith to the bark of each cross-section in order to be sure that no ring was missed.

### 2.3.3. Reliability of age determination

A method to assess age of woody plants is to simply count annual rings. But, because of possible deficiencies of cambial activity (Kolishchuk, 1990), analysis of ring series by dendrochronological methods (Schweingruber, 1988) is often preferred to better control potential errors by cross-dating ring series to reference chronologies. However, Belingard et al. (1997) have shown that it was difficult to use ring series in red huckleberry for inter-individual cross-dating. In order to ensure that shrub age is not over-estimated, the solution consists in using reference plants of known-age or from sites with a well known history (fires, hurricanes, experiments, managements; Roughton, 1972). In the absence of plants with known-age, we used a deer enclosure established after clear cutting to provide a reference. If age estimates are systematically higher than time elapsed since clear cutting then the production of multiple rings is likely and solutions to correct the estimates have to be looked for.

### 2.4. ANOVAs and post-hoc multiple comparison tests

We used parametric or non-parametric ANOVAs to test the significance of “category” and “island-within category” effects. Variances of the non-transformed response variables were not homogeneous.

The log 10 transformed values of variables “age of each stem” and “age of the youngest stem” per individual had homogeneous variances. We analysed their effect using a parametric nested ANOVA test. Satterthwaite’s correction was applied on the degree of freedom to account for unequal sample size (Sokal and Rohlf, 1995). Post hoc multiple comparison Tukey HSD tests were conducted and 95%-confidence intervals for averaged differences were computed.

Variances remained heterogeneous for log 10 transformed values of response variables “number of

stems”, “number of regenerating sprouts” and “height of the shortest stem” per individual. For these we first tested the category effect by using a non parametric Kruskal–Wallis test on the non transformed values. When the category effect was found significant, we tested the effect of “island-within category” using multiple comparisons based on Kruskal–Wallis tests. We applied a Bonferroni correction to significance levels.

ANOVAs were performed in the R environment (<http://www.r-project.org/>). The R-code for Tukey HSD test was provided by Professor P.J. Turk (<http://www.math.montana.edu/~turk/>).

We plotted age structures (percentage per classes) and used a chi-square test of independence to test similitude or difference of age structures between islands within a category and between categories. Age structures were used to estimate a date at which

drastic changes occurred in the understory of the different islands with deer.

### 3. Results

The number of individuals collected per island varied between 4 and 46 and the number of stems per island between 40 and 134 (Table 1).

#### 3.1. Age determination

Stem ages were determined relative to the year 2000. The age of the 96 stems collected in the 12 year old deer enclosure of Western Forest Product varied between 3 and 12 years. No double ring was observed. In absence of overestimated age, no age correction was applied.

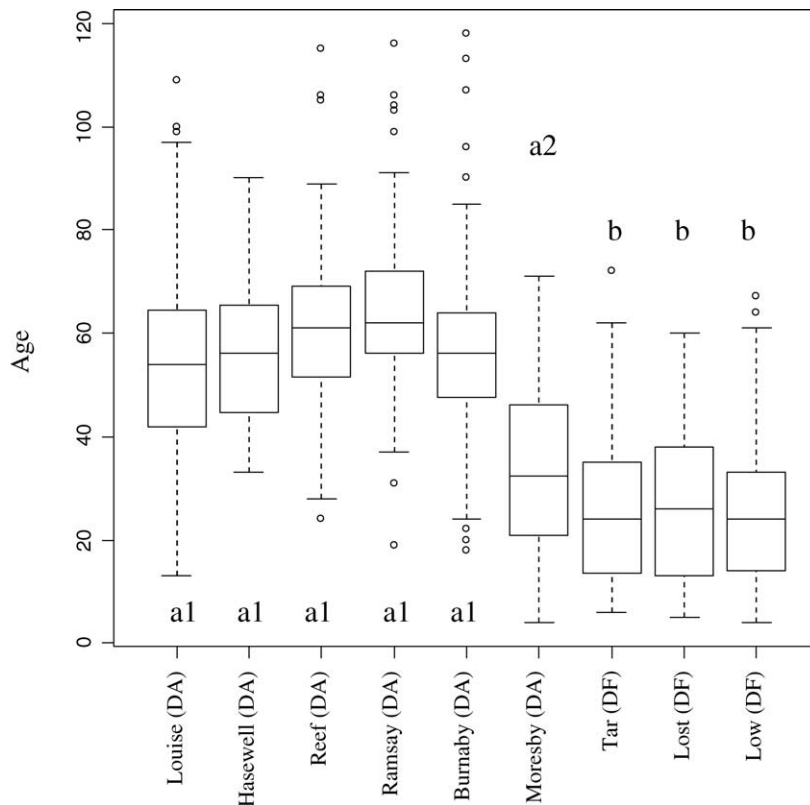


Fig. 2. Age of all stems on deer-affected (DA) and deer-free (DF) islands. Letters indicate  $P$ -values. (a and b)  $P < 0.001$ ; (a1 and a2)  $P < 0.001$ ; (b)  $P > 0.05$ .

### 3.2. Shrub characteristics

#### 3.2.1. Stem age

Stems were significantly older on the deer-affected (54.14 ± 1.70) than on the deer-free islands (25.96 ± 1.81; nested ANOVA,  $F = 443.49$ ,  $P < 0.001$ ; Fig. 2). We detected a significant island effect within the deer effect, ( $F = 30.58$ , d.f. = 1,  $P < 0.001$ ). We recorded no difference between the deer-affected islands of Louise (59.35 ± 4.90), Haswell (56.21 ± 4.12), Reef (61.51 ± 3.67), Ramsay (63.69 ± 3.39) and Burnaby (56.95 ± 3.40), nor between the deer-free islands of Lost (25.95 ± 3.14), Low (25.75 ± 2.47) and Tar (26.67 ± 5.03). Stems were significantly younger in samples from the southern tip of Moresby Island (34.46 ± 3.16) than in the five other deer-affected islands (multiple comparison tests,  $P < 0.001$ ). Stems from the southern tip of Moresby Island were older than stems from the deer-free Low, Lost and Tar Islands ( $P < 0.001$ ; Fig. 2).

#### 3.2.2. Youngest stem per individual

The youngest stem per individual was, on average, older on deer-affected islands (50.87 ± 2.48) than on deer-free islands (10.30 ± 3.08, nested ANOVA,  $P < 0.01$ ; Fig. 3). There was no difference in age of youngest stem between five of the deer-affected islands (Louise island, 51.41 ± 4.42; Haswell Island, 55.74 ± 5.89; Reef Island, 55.41 ± 3.93; Ramsay Island, 58.52 ± 4.86 and Burnaby Island; 52.37 ± 6.05), nor between the deer-free islands (Lost Island, 10.71 ± 3.76; Low Island, 10.33 ± 5.87 and Tar Island, 8.75 ± 3.03). A significant island effect was detected ( $F = 30.90$ , d.f. = 1,  $P < 0.001$ ) within the deer effect; the youngest stems from the southern tip of Moresby Island (20.79 ± 4.86) were younger on average than those from the five other deer-affected islands (multiple comparison tests,  $P < 0.001$ ). The youngest stems from the southern tip of Moresby Island were older than those from deer-free Low and Lost Islands ( $P < 0.001$ ) but did not differ

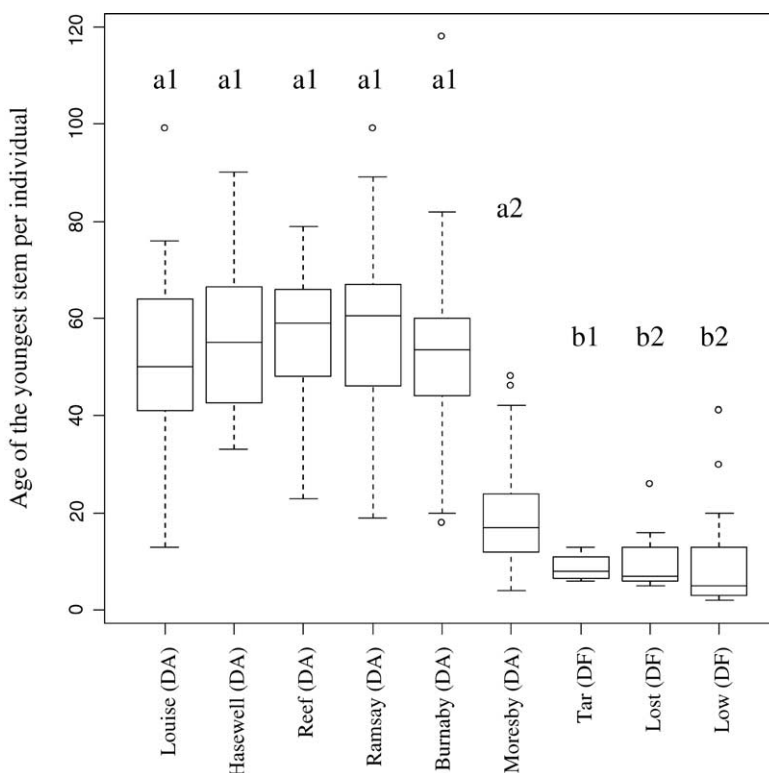


Fig. 3. Age of the younger stem per individual on deer-affected (DA) and deer-free (DF) islands. Letters indicate  $P$ -values. (a and b)  $P < 0.001$ ; (a1 and a2)  $P < 0.001$ ; (a2 and b1)  $P > 0.05$ ; (a2 and b2)  $P < 0.001$ ; (b)  $P > 0.05$ .

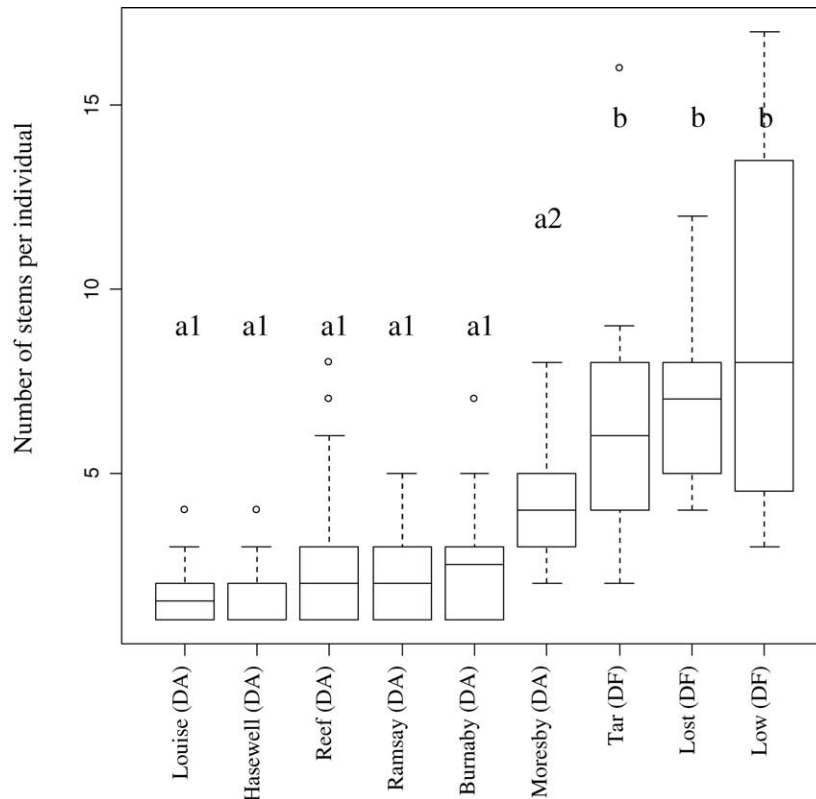


Fig. 4. Number of stems per individual on deer-affected (DA) and deer-free (DF) islands. Letters indicate  $P$ -values. (a and b)  $P < 0.001$ ; (a1 and a2)  $P < 0.001$ ; (a2 and b)  $P < 0.05$ .

significantly in age from those of Tar Island, the third deer-free island ( $P > 0.05$ ; Fig. 3).

### 3.2.3. Number of stems per individual

The mean number of stems per individual differed between deer-free (mean  $\pm$  1.96 standard error =  $7.76 \pm 1.40$ ) and deer-affected ( $2.31 \pm 0.18$ ) islands (ANOVA of Kruskal–Wallis,  $X^2 = 69.57$ , d.f. = 1,  $P < 0.001$ ; Fig. 4). We observed no variation between deer-free islands ( $X^2 = 1.14$ , d.f. = 2,  $P = 0.56$ ) whereas the mean number of stems per individual differed significantly between deer-affected islands ( $1.61 \pm 0.38$  to  $4.08 \pm 0.55$ ,  $X^2 = 47.28$ , d.f. = 5,  $P < 0.001$ ; Fig. 4). Comparing islands by pairs (multiple comparison tests), the plants at the south of Moresby had a significantly higher number of stems than plants from the other samples from deer-affected islands and a significantly smaller number of

stems than plants from deer-free islands ( $P < 0.05$ ; Fig. 4).

### 3.2.4. Number of sprouts per individual

The mean number of regenerating sprouts per individual was significantly lower on deer-free (mean  $\pm$  1.96 standard error =  $0.92 \pm 0.53$ ) than on deer-affected islands ( $9.28 \pm 1.07$ ; ANOVA of Kruskal–Wallis,  $X^2 = 36.55$ , d.f. = 1,  $P < 0.001$ ; Fig. 5). There was no variation within deer-free islands ( $X^2 = 0.16$ , d.f. = 2,  $P = 0.92$ ; Fig. 5). The mean number of regenerating sprouts per individual differed significantly within deer-affected islands ( $3.99 \pm 1.18$  to  $15.12 \pm 2.98$ ,  $X^2 = 66.92$ , d.f. = 5,  $P < 0.001$ ; Fig. 5). The number of regenerating sprouts per individual from Reef Island differed from all other deer-affected islands and the number of regenerating sprouts per individual of the southern tip of Moresby Island differed from two other deer-affected



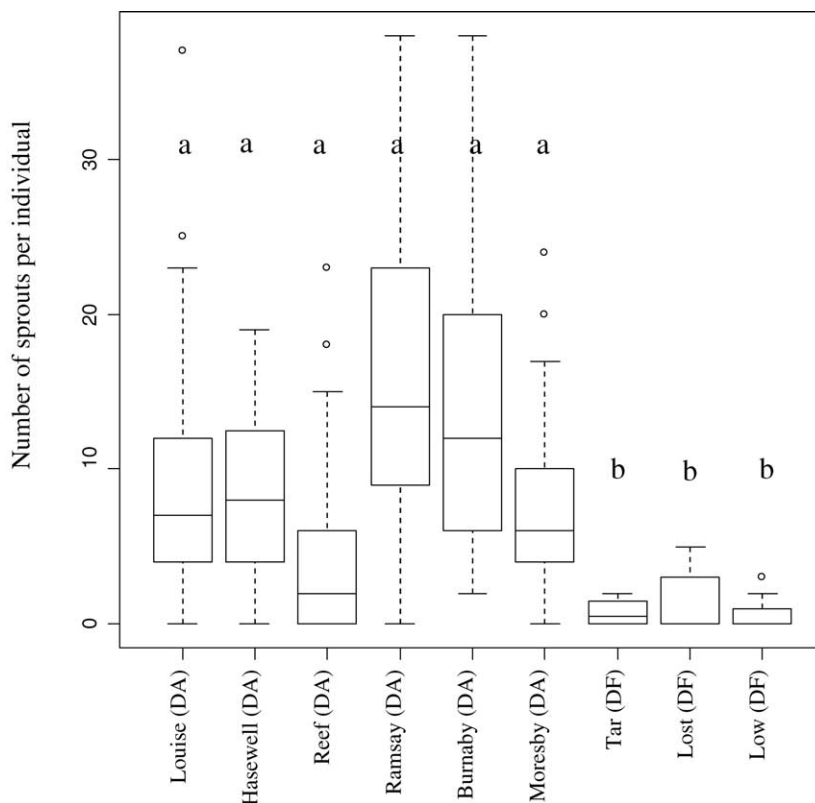


Fig. 5. Number of regenerating sprouts per individual on deer-affected (DA) and deer-free (DF) islands. Letters indicate  $P$ -values. (a and b)  $P < 0.001$ ; (a) island effect is due to Reef and south Moresby islands, for more details see the text.

islands Ramsay and Burnaby islands (Multiple comparison tests,  $P < 0.05$ ). The number of regenerating sprouts per individual differed between Haswell and Ramsay Islands ( $P < 0.05$ ).

### 3.2.5. Shortest stem per individual

The shortest stems per individual were taller on deer-affected islands ( $3.19 \pm 0.10$  m) than on deer-free islands ( $1.42 \pm 0.31$  m; ANOVA of Kruskal–Wallis,  $X^2 = 50.28$ , d.f. = 1,  $P < 0.001$ ; Fig. 6). The size of the shortest stem did not vary within deer-free islands (ANOVA of Kruskal–Wallis,  $X^2 = 5.41$ , d.f. = 2,  $P = 0.067$ ). Height of the shortest stem per individual differed significantly within deer-affected islands (ANOVA of Kruskal–Wallis,  $X^2 = 21.50$ , d.f. = 5,  $P < 0.001$ ). The plants from the southern tip of Moresby Island ( $2.50 \pm 0.36$ ) differed from those from the two other deer-affected islands, Reef ( $3.54 \pm 0.19$ ) and Ramsay ( $3.25 \pm 0.20$ ) islands (Multiple comparison

tests,  $P < 0.05$ ). The plants from the southern tip of Moresby Island did not differ from those of the two deer-free Tar and Lost Islands ( $P > 0.05$ ) but differed from those of Low Island the third deer-free island ( $P < 0.05$ ; Fig. 6).

## 3.3. Stem age structures and time since prevalence of deer impact

### 3.3.1. Age structures

Stem age structures were similar on deer-free islands ( $X^2 = 5.66$ , d.f. = 8,  $P = 0.68$ ). Stem age structures were also similar on the deer-affected islands within Laskeek Bay (Louise, Haswell and Reef islands;  $X^2 = 13.48$ , d.f. = 10,  $P = 0.20$ ) and were similar to those observed on Ramsay Island ( $X^2 = 10.72$ , d.f. = 5,  $P = 0.06$ ). Age structure on Ramsay Island differed from the one on Burnaby Island ( $X^2 = 15.56$ , d.f. = 6,  $P < 0.05$ ) and age structure on Burnaby

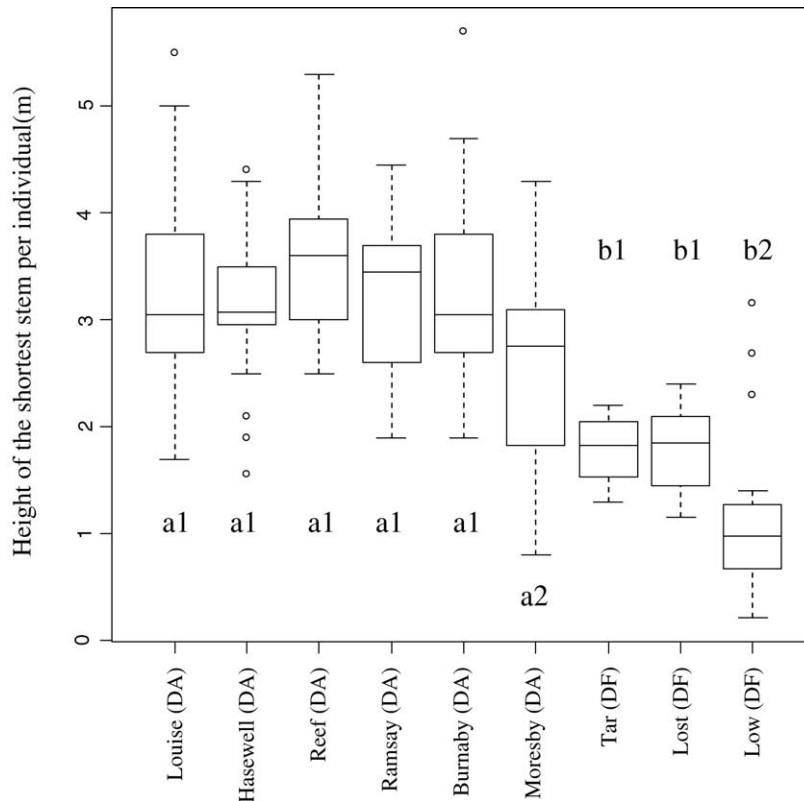


Fig. 6. Height of the shortest stem per individual on deer-affected (DA) and deer-free (DF) islands. Letters indicate  $P$ -values. (a and b)  $P < 0.001$ ; (a1 (Reef and Ramsay islands) and a2)  $P < 0.001$ ; (a1 (other islands) and a2)  $P > 0.05$ ; (a2 and b1)  $P > 0.05$ ; (a2 and b2)  $P < 0.05$ .

Island differed from the age structure on southern Moresby Island ( $X^2 = 73.22$ , d.f. = 6,  $P < 0.001$ ). The latter also differed from the age structure observed on deer-free islands ( $X^2 = 29.59$ , d.f. = 5,  $P < 0.001$ ; Fig. 7).

### 3.3.2. Time since deer prevalence

On deer-free islands, 93.6% of stems were less than 50 years old and the five youngest age classes each contained between 10 and 25% of the stems. The 21–30 years class was the most represented with 25% of the stems. On deer-affected islands in Laskeek Bay only 34.7% of the stems were less than 50 years old. The 60–70 years class was the most represented with 27.3% of stems. On Ramsay Island, even less stems (18.7%) were younger than 50 years. The 60–70 years class was again the most represented with 32.3% of stems. On Burnaby Island, 28.2% of stems were less than 50 years old and the 50–60 years class was the

best represented (39.4% of stems). Finally on the southern tip of Moresby Island, most (85.8%) stems were less than 50 years old with the 40–50 years class being the most represented (25.5% of stems).

Overall, age classes from 0 to 30 years were under represented, or lacking, on deer-affected islands in Laskeek Bay, from 0 to 50 years on Ramsay Island, from 0 to 40 years on Burnaby Island and only from 0 to 10 years on south of Moresby Island (Fig. 7).

## 4. Discussion

### 4.1. Stems and browsing impact

In the absence of deer browsing, individual plants were characterized by a large number of stems ( $7.76 \pm 1.40$  per individual) and a low number of regenerating sprouts ( $0.92 \pm 0.53$  per individual). In presence

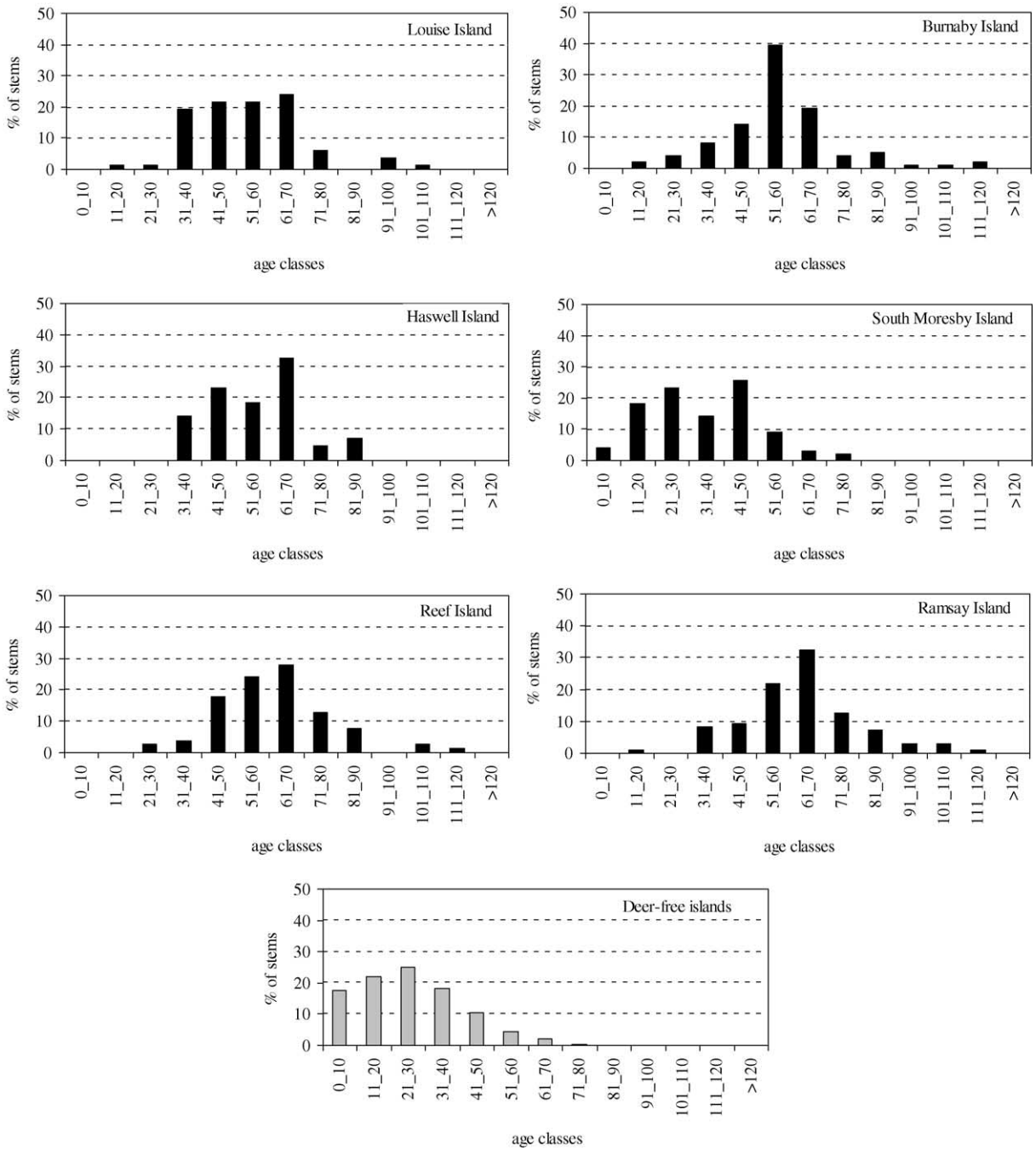


Fig. 7. Age structures (10-years classes) of the different islands or group of islands considered and classed southward.

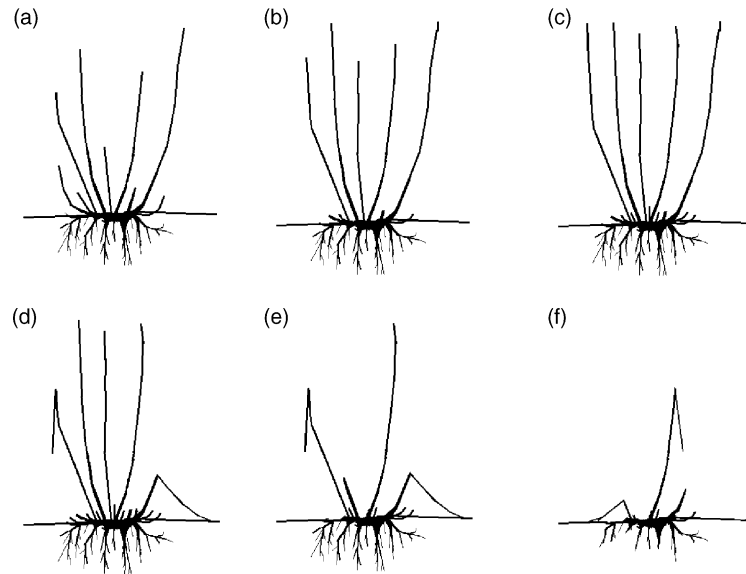


Fig. 8. Mechanisms by which browsing disturbs sprout regeneration. (a) Without disturbance, individual sprouting is low, continuous and compensates the death of older stems. (b) When deer browse regenerating sprouts, the regular process of stem replacement is stopped. (c) Stems tall enough to escape deer continue to grow and age. (d) Heavily browsed regenerating sprouts tend to accumulate at the base of the individual. (e) In parallel, the number of stems per individual plant decreases with time. (f) Stems age and die; because of lack of regeneration, the plant dies.

of deer, stem recruitment was stopped and the youngest stems were indicative of the date when deer pressure became high and stopped stem recruitment. Stems age structure was a good synthetic indicator of when browsing pressure became the dominant factor structuring the understory. The height of the shortest stem had little value as an indicator of deer impact history as height growth integrates also light conditions and soil quality.

In the absence of deer, the rate of sprouting is low but compensates the death of the older stems (Fig. 8a). Under these conditions mature stems die at about  $25.96 \pm 1.80$  years of age. When deer feed intensively on regenerating sprouts, the regular process of stem replacement is stopped (Fig. 8b). Stems tall enough to escape deer continue to grow and age ( $63.69 \pm 3.40$  years, for example, on Ramsay Island). As long as deer pressure is maintained the regeneration of the plant is stopped. But, even on heavily browsed shrubs, regenerating sprouts keep emerging from the lignotuber, a site of carbohydrate storage and of nutrient concentration (James, 1984). Sprouts are produced each spring and are then browsed. Their stumps accumulate

at the base of the surviving stems ( $9.28 \pm 1.07$  sprouts per individual; Fig. 8d). When the nutrient reserves of the lignotuber become exhausted, the emergence of new sprouts slows down while aging stems die off. This process leads to a progressive reduction over time of the number of stems per individual ( $2.31 \pm 0.18$  stems per individual with an average age of  $54.14 \pm 1.70$  years, Fig. 8e) and to the death of the plant (Fig. 8f).

#### 4.2. Consequences on shrub understory

These processes explain the large differences observed in the number of stems per individual and in the number of regenerating sprouts between deer-affected and deer-free islands. They also explain the differences in age structures observed where deer are present. Within the category of the deer-affected islands, spatial and temporal variations are observed whereas none occur among deer-free islands.

The samples from the south of Moresby Island differ significantly from all other samples on deer-affected islands in several features (stem age and

number of stems per individual). All these characteristics suggest that prevalent deer impact is more recent in the south of Moresby Island than on other deer-affected islands. This was confirmed by a deficit in young stems limited to the 10 years before this study whereas this deficit ranged between 40 and 50 years before this study on all other deer-affected islands. We obtained similar results for salal (*Gaultheria shallon* Pursh) (Vila et al., in press). At first sight this could be interpreted as the result of a longer time lag before the colonisation of this southern location as deer had been released in the north of the archipelago (Carl and Guiguet, 1972). However there are written records of deer being present in the south of the archipelago since at least 1946 (Duff and Kew, 1958), giving deer sufficient time for an earlier severe impact on shrubs (Vila et al., in press). The longer delay before severe impact may reflect differences in forest type and/or in climate between southern Moresby where precipitation in late fall and early winter (Calder and Taylor, 1968) are higher than in the other sites we studied. Habitat differences can influence deer population dynamics (Forchhammer et al., 1998; Clutton-Brock and Clouston, 2002; Weisberg et al., 2002) and higher precipitations, in particular, can negatively affect the nutritional quality of forage (Masters, 1999) and deer density (Latham et al., 1997).

The length of time since deer impact became prevalent also varied between the remaining samples. On Reef Island, Ramsay Island and Burnaby Island, deer impact was prevalent 10–20 years earlier than on Louise or Haswell islands, although deer had to colonize Louise Island before they colonized Reef, Ramsay or Burnaby Island. This apparently counter intuitive result could be, at least in part for isolated Reef and Ramsay islands, explained by what Krebs et al. (1969) coined the fence effect. Under restriction to dispersal, animal population would reach higher densities than in situations where dispersal is easier. Isolation could therefore speed up deer density increase after colonisation and shorten the time lag necessary for deer impact to become prevalent. But the isolation argument does not apply to Burnaby Island. Among the other features distinguishing Louise Island from the three other islands are more prevalent clear-cut logging (M. Salzl, personal communication; Dalzell, 1968), which provides temporary but abundant forage to deer (see Wallamo and Schoen, 1980;

Reimoser and Gossow, 1996), and access to alpine summer range, another temporary source of rich forage. Both features are susceptible to influence deer impact (Carlock et al., 1999; Ford et al., 1999; Harstad, 1985) on the understory of adjacent old growth forests.

Variation between sites, localities or regions in these features (number of stems, age of youngest stems, number and fate of sprouts) coupled with the longevity of red huckleberry can provide a useful tool to assess current, and to reconstruct past browsing history at different spatial and temporal scales. In case of colonisation of new localities by deer, as in this study, many of the features described can be used to assess the time when the impact of such a deer population has become prevalent after the initial phase of colonisation. As many of these features are reversible when browsing pressure relaxes and the plants are still alive (deer cull experiments on Reef Island; RGIS, unpublished data) they can also be used for monitoring habitat restoration and management actions planned to reduce browsing pressure on forest habitat.

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