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Can we reconstruct deer browsing history and how? Lessons from *Gaultheria shallon* Pursh

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Abstract – We identified and analysed browsing signatures left by Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Salal (*Gaultheria shallon*) to reconstruct deer browsing history. Radial growth analyses showed negative abrupt growth changes on islands with deer probably linked to defoliation. Deer browsing pressure was best assessed by the incidence of morphological changes caused by browsing in section form, lobes, pith form, pith position or the presence of decaying wood and by changes in stem age structures. Salal stems were twice older (30 years) on islands with deer than on islands without deer (16 years). On islands with deer deficit of stems in the youngest age classes suggested that deer impact has been strong on these shrubs for at least 20 years in the northern sites and for about 10 years in the southern ones.

deer browsing history / negative abrupt growth change / morphological characteristics / age structures / *Gaultheria shallon* Pursh

Résumé – Est-il possible de reconstituer l'histoire de l'abrouissement et comment ? Ce que nous apprend *Gaultheria shallon* Pursh. Nous avons identifié et analysé les signatures relatives à l'abrouissement du cerf à queue noire (*Odocoileus hemionus sitkensis*) sur le salal (*Gaultheria shallon*) et utilisé celles-ci pour reconstituer son histoire. L'analyse de la croissance radiale a révélé des décroissances brutales probablement liées à des défoliations. La pression et l'histoire d'abrouissement sont le mieux appréhendées par l'occurrence des caractères anatomiques tels que la forme de la section, la présence de lobes, la forme et la position de la moelle, la présence de bois altérés ou le déficit en jeunes tiges. L'analyse des âges révèle que les tiges de salal sont deux fois plus âgées en présence de cerfs (30 versus 16 ans). Sur les îles avec cerf, on observe un déficit de jeunes tiges qui suggère un impact fort du cerf depuis 10 ans dans les sites du sud et de 20 ans au moins dans les sites du nord.

histoire de l'abrouissement par le cerf / décroissance brutale / caractères morphologiques / structures d'âge / *Gaultheria shallon* Pursh

1. INTRODUCTION

Ungulate herbivores can have a profound effect on forest structure and plant communities [1, 2, 9, 57]. They affect plant morphology [13, 30], plant growth [8, 51, 52, 55] and plant chemistry [5, 55]. Disturbance of forest ecosystems by herbivory can be analysed by a posteriori approaches based on woody plant morphology [30] and on the analysis of ring-width series [45, 46]. Indeed, records of annual growth and wood density, age structure and morphological characteristics [13, 25, 27, 43, 56] are valuable signatures of past disturbances that have affected woody plants. Growth time series have been successfully used to infer spatial and temporal variations affecting several herbivore populations [31–33, 36].

Documenting and understanding deer impact on forest ecosystems is increasingly needed by forestry and conservation agencies as a result of increasing deer populations in many

regions. This necessitates appropriate and practical tools to be developed in order to document and quantify the signatures deer leave on the vegetation.

The Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia) provides a unique opportunity for such a methodological study. Except for the extinct Dawson caribou (*Rangifer tarandus dawsoni* Seton) there was no other deer native to the islands. Sitka black-tailed deer was introduced on Graham Island at the turn of the 20th century [7] and soon colonised most of the archipelago thereby affecting plant regeneration [10, 11, 15, 38, 39], causing wood depreciation, high seedling mortality and delay in recruitment [49, 50].

Salal (*Gaultheria shallon* Pursh) and Red huckleberry (*Vaccinium parvifolium* Smith in Rees) are the two commonest long-lived woody shrubs in coastal forests of northwestern North America [6, 12, 17, 18] and are well suited for such a study.

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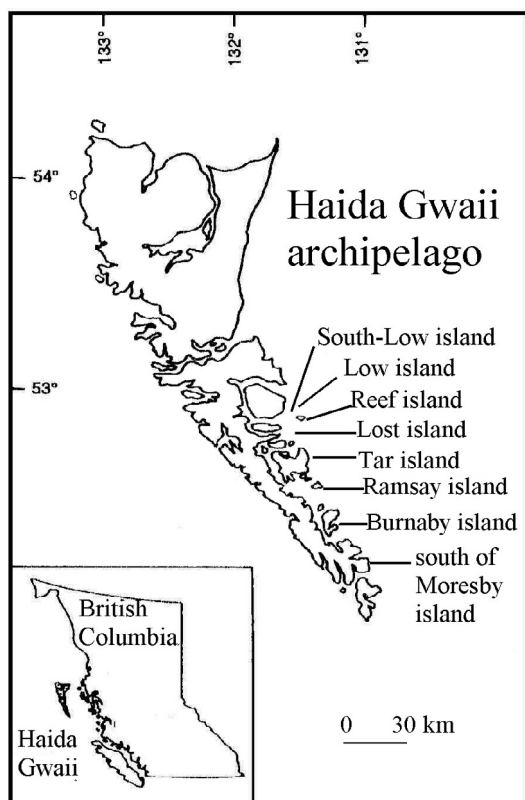


Figure 1. Sites sampled on the Haida Gwaii archipelago (British Columbia, Canada).

Our objective in this paper is to identify and analyse browsing signatures left by Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) on Salal and to investigate how they can be used to reconstruct deer browsing history. Although salal is commonly eaten by deer [17], it is one of the rare ligneous species that is able to remain for several decades even on heavily browsed sites and can, therefore, record variation in deer impact through prolonged periods. Taking advantage of the occurrence, side by side, of islands with and without introduced deer, we compare (1) radial growth of salal, (2) the morphological characteristics of its stems and (3) stem age and height structures between deer-free and deer-affected islands. We then use one of these signatures, stem age structure, to reconstruct deer browsing history on the islands studied.

2. MATERIALS AND METHODS

2.1. Material and sites

2.1.1. Haida Gwaii and deer

Haida Gwaii (53° N, 132° W), has about 300 islands, is 300 km long and lies ca. 80 km off mainland Canada [51] (Fig. 1). Except for the Dawson caribou, extinct since the beginning of the 20th century [7], mammalian herbivores were absent from these islands until black-tailed deer were introduced. The study took place on the eastern side

of the archipelago which, for most parts, belongs to the Coastal Western Hemlock Zone, wet hypermaritime sub-zone and to the very wet hypermaritime sub-zone in the southern end of the archipelago. 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 understory was originally densely covered in shrubs such as salal and red huckleberry (*Vaccinium parvifolium* Smith in Rees) [3]. Today deer are abundant over most of the area and current density estimates range from 13 to 30 deer per km² [15, 28, 29]. In most places the understory has been reduced to a few old isolated and senescent shrubs as a result of heavy deer browsing [38, 39] (pers. obs.). According to Reimoser et al. (1999) [41] the absence of ground vegetation, the existence of a browse line and of palatable species confined to sites inaccessible to deer observed in these places, all indicate a very heavy browsing pressure.

2.1.2. Salal

Salal is an erect, evergreen and loosely branched shrub with an extensive root system allowing effective vegetative spread [13, 17, 19]. It is a dominant understory species in lowland coniferous coastal forests and it is very abundant in open shoreline habitats because light increases its vigor and growth. It is recognized to be a valuable wildlife food in British Columbia. Salal supplies about 10% of the total diet of black-tailed deer and it is of special importance in winter [18]. Birds commonly eat salal berries, which can represent 45% of the diet of juveniles in August [18]. In short, salal plays an essential role in vegetation succession, habitat structure, soil protection and ecology of several native animal species [17, 40].

On the few deer-free islands, 40% of the shrub cover consists of salal [28], often in the form of continuous almost impenetrable thickets. The cover of vegetation on these 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 [49, 50]. On the deer-affected islands adjacent to the deer-free islands, vegetation cover averages 26.2%, 10.7% and 20.3% in these three vegetation layers. Salal occurs only as isolated individuals (cover less than 1%) that are taller than the browse line situated between 1.1 and 1.5 m high [28, 49, 50]. These individuals are remnants of once impenetrable thickets [38, 39]. On the islands with deer situated at the very south of the archipelago, shrub remnants are abundant and salal thickets more widespread (pers. obs.).

2.2. Sampling and sample preparation

The work took place on 4 deer-free islands (Low Island, South-Low Island, Lost Island and Tar Island) and 4 deer-affected islands (Reef Island, Ramsay Island, Burnaby Island and the south of Moresby Island) (Fig. 1). On each island we selected sites that had sufficient representation (> 200 m²) of salal, growing under an open canopy, and situated near the forest edge along the coastline. Because salal has an extensive root system that allows vegetative spread [18], we sampled individual salal stems that were at least 2 m away from any other stem sampled [19]. On deer-free islands, all characterized by a small area (< 10 ha), we sampled stems every 2 meters along transects that were parallel to the coastline and which run across most of the area favourable to salal on these islands. On deer-affected islands, we sampled salal stems in plots situated 10 to 30 m away from remnant salal thickets. Areas sampled, exposure, slope, soil depth and the number of individuals collected are reported in Table I.

2.2.1. Radial growth

Because cambial activity starts at the tip of the stem, easily identifiable growth rings are restricted to the upper part of a stem, whereas very narrow rings characterise the lower part of a stem. This causes

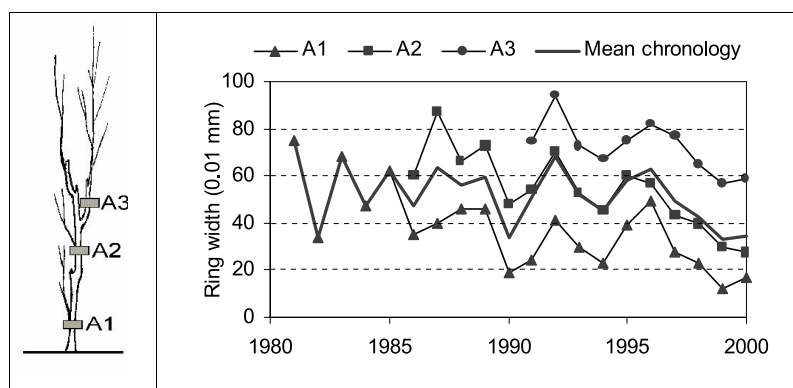


Figure 2. Example of a stem sectioned at different intervals from the base to the top. A1 to A3: ring-width chronologies from each section and mean individual chronology built by averaging all chronologies from the same stem.

Table I. Characteristics of the sites sampled. RW § MC = Ring-Width and Morphological Characters and AS § HS = Age Structure and Height Structure.

Analyses	Island / Site number	Deer	Area (m) sampled	Slope (°)	Aspect (°)	Soil depth (cm)	Number of individual
RW § MC	South-Low (1)	absent	5 × 15	0	–	20	8
RW § MC	Low (2)	absent	5 × 20	15	40	15	10
RW § MC	Reef (3)	present	30 × 10	10	180	30–45	5
RW § MC	Reef (4)	present	30 × 20	14	160	35	10
AS § HS	Lost (5)	absent	5 × 20	3	280	60	25
AS § HS	Lost (6)	absent	5 × 20	3–18	300–340	50–75	26
AS § HS	Low (7)	absent	10 × 40	18	40	15–20	50
AS § HS	Tar (8)	absent	5 × 10	8	290	30	25
AS § HS	Reef (9)	present	20 × 40	0–12	180	30–40	30
AS § HS	Reef (10)	present	20 × 150	19	130	25	17
AS § HS	Ramsay (11)	present	20 × 60	9	160	35	39
AS § HS	Burnaby (12)	present	10 × 60	10	170	40	15
AS § HS	South-Moresby (13)	present	10 × 60	14	275	75	51
AS § HS	South Moresby (14)	present	10 × 60	13–15	110	45	43

difficulties in cross-dating ring-width chronologies. To properly investigate the dynamics of shrub growth, we used the method proposed by Kolishchuk (1990) [23], sectioning each stem at different intervals from the top to the base. When choosing the distance between sections, it was essential to provide sufficient overlap between ring-width series of neighbouring sections and to cover the zone of the normal annual increment formation (Fig. 2). This method has also the advantage to allow identifying missing rings linked to particular conditions prevailing in shrub growth [23]. We therefore collected, for each stem, 5 cm sections at each inter-node. Adjacent sections were, on average, separated by about 20 cm. When stems were branched, sections were collected for all axes. We numbered each section according to its position on the stem with codes identifying sections from different branches of the same stem. Because this method is time consuming, we had to restrict sampling to a limited number of shrubs (5 to 10) collected on two of the four deer-free islands, Low and South-Low islands, and on one of the deer-affected island, Reef Island.

2.2.2. Stem age and height

We studied stem age structure and stem height in samples from three of the four deer-free islands (Lost, Low and Tar Islands) and from all four of the deer-affected islands (Reef Island, Ramsay Island, Burnaby Island and south of Moresby Island). The latter were roughly distributed along a north-south gradient parallel to the route of deer colonization. These sites were separated from each other by about 20–25 km. Reef Island was closest to the point of deer introduction whereas Moresby Island was the most distant from the point of deer introduction. For each salal stem taller than 20 cm and with a diameter >0.5 cm, we measured total height and the height of the first leaves (at 5 cm accuracy). Basal cross-sections were collected and labeled.

2.2.3. Sample preparation

The sections were meticulously sanded using successively finer grits of sand paper (80 – 180 – 320 – 400), a procedure described by

Stokes and Smiley (1968) [48]. After removing the sanding marks left by the preceding grit, each section was polished to further improve the legibility. Section preparation was examined through a microscope ($\times 40$) and preparation done once again in case of reading difficulty.

2.3. Analyses

2.3.1. Radial growth and morphological characters

2.3.1.1. Ring chronologies

The dating of ring series is based on the identification of rings with characteristic features, generally rings that are unusually narrow. Years characterized by such isolated narrow rings are termed pointer years [21]. They are used by dendrochronologists for (1) directly cross-dating wood samples by comparing, under the microscope, ring patterns of successive sections [37] or (2) to produce skeleton plots describing ring sequences which are compared to synchronise ring series [45]. To achieve cross-dating, ring width curves are also compared under a light table using either raw data or standardized series. Standardization allows emphasizing narrow rings and allows removing non inter-annual variations [37]. In the present study standardisation is achieved by replacing x_t by $(x_{t+1} - x_t) / (x_{t+1} + x_t)$. We used these methods (1) to cross-date all sections within a stem and (2) to cross-date the stems.

For each section, ring-widths were measured with a precision of 0.01 mm along a radial line of cells using an Eklund measuring device from the bark to the centre and from upper sections to lower sections. Two radii (separated at least by 90°) were measured on each section to calculate a mean value for each ring. For each stem we obtained: (1) partial chronologies which length depended on the position of the section on the stem, the closer to the apex, the shorter the partial chronology; (2) a basal chronology corresponding to the longest ring width series obtained from the basal section.

2.3.1.2. Stem and population mean chronologies

Once sections from a stem were cross-dated, all section chronologies from that stem were averaged to build the mean chronology for that stem. Finally individual stem chronologies were compared by the same cross-dating method in order to build a mean population chronology for plants from deer-free islands and plants from deer-affected islands. Visual agreement between individual stem chronologies was backed up by correlation coefficient calculated on standardized series and validated by a Student *t*-test.

2.3.1.3. Morphological characters and signatures

Browsers can consume various parts of woody plants such as leaves, twigs, bark or wood. By doing so, they induce cambium destruction and expose wood to pathogens. This can, in turn, induce the alteration of morphological characteristics of the stem. These alterations can be classified into direct damage (section and pith deformation, lobes, pith position) and indirect damage (decaying wood).

On each of the sections collected we analysed morphological characteristics. We recorded (1) the shape of the stem section: circular or deformed, (2) the presence of lobes (if cambium is removed locally along the stem future rings will only develop where the cambium is intact, forming a lobe), (3) the presence of decaying wood which corresponds to decomposition by fungi and other micro-organisms that may induce changes in wood texture and colour, (4) pith form (circular or deformed), (5) pith position (centred or not), (6) wedging rings (*sensu stricto*; rings that are wedging out due to localised failure of cambial activity) [21]. It also allows quantifying character occurrences by the % of sections of a stem in which the character is present. This

quantity is then used to compare average character frequencies/stem between deer-free and deer-affected islands using Student *t*-test in situations with equal variances or with Welch's approximate *t*-test when variances were unequal [47]. Finally, we estimated the sensitivity of each morphological character to deer browsing by comparing *t*-value between deer-affected and deer-free islands. The same approach can be used to estimate within island type variation in the occurrence of these characteristics.

2.3.2. Age structure and stem height

2.3.2.1. Age determination

We selected the area of the cross-section that was most legible. We pointed rings for each cross-section and counted them along two radii from the pith to the bark of each cross-section in order to be sure we missed no ring. Following Bunnell (1990) [6], who failed to find missing or double rings, we considered ring count as the best estimate of age.

2.3.2.2. Analyses

We log₁₀ transformed age data to stabilize the variance [47]. In order to document the height up to which deer damage this species, we compared mean heights of first leaves between deer-free and deer-affected sites with a *t*-test. We also plotted the distribution of the height of the first leaves. We compared mean age and mean stem height with a nested analysis of variance correcting the degree of freedom by Satterthwaite's correction for unequal sample size [47]. In addition to comparing stem age between deer-affected and deer-free categories, we also compared stem age between northern (Reef Island), intermediate (Ramsay and Burnaby Islands) and southern (southern Moresby Island) deer-affected islands using the "least significant difference" (l.s.d.) post-hoc test. We compared total stem height between deer-affected and deer-free categories, between islands within each of these two categories and between sites within each island. We used categories, islands and sites as factors, the category being the factor the higher in the hierarchy and the site being the lower. We considered categories and islands as fixed factors and sites as a random factor. Intervals with 95% of confidence were obtained at each level of hierarchy.

We plotted age structures (percentage per 10-year classes) and used a chi-squared test of independence with Bonferroni correction for multiple comparisons [47] to test the similitude or the difference of age structures between sites within islands, islands within a geographical area and between geographical areas. We used age structures to assess a date at which the understory modification by deer browsing had become prominent on the islands with deer that we studied.

3. RESULTS

3.1. Ring-width chronologies and morphological characters

3.1.1. Ring-width chronologies

3.1.1.1. Cross dating on deer-free islands

On deer-free islands, sections within each stem were easy to cross-date with the help of pointer years on skeleton plots. These results were confirmed by comparing the curves representative of ring series. Mean chronologies were built for each stem collected on deer-free islands. The agreement between

Table II. Comparison of the occurrence of morphological characteristics of salal stems within (1) deer-free island (comparison between sites 1 and 2, $df = 16$), deer-affected island (comparison between sites 3 and 4, $df = 13$) and between deer-free and deer-affected islands ($df = 31$). $t = t$ -values and the $P = P$ -values.

Category		Free				Affected				Free		Affected	
Site number		1	2	t	P	3	4	t	P	1 + 2	3 + 4	t	P
Pith position	centred	48.9	51.7	0.60	0.28	85.7	72.3	0.18	0.43	75.7	50.8	2.68	0.01
	not centred	51.1	48.3			14.3	27.8			24.4	49.2		
Pith form	circular	79.9	85.9	0.75	0.23	43.3	71.5	2.56	0.05	83.2	64.9	2.83	0.01
	not circular	20.1	14.1			56.7	28.5			16.8	35.1		
Section form	circular	85.3	82.7	0.22	0.41	29.5	36.8	0.51	0.31	83.8	34.3	5.77	0.001
	not circular	14.8	17.3			70.5	63.3			16.2	65.7		
Decaying wood	presence	9.7	5.0	0.73	0.24	38.6	25.1	1.67	0.06	7.1	29.6	4.42	0.001
	absence	90.3	95.0			61.4	74.9			92.9	70.4		
Lobes	presence	7.8	12.1	0.68	0.25	60.9	42.0	1.62	0.07	10.2	48.3	5.79	0.001
	absence	92.2	87.9			39.1	58.0			89.8	51.7		
Wedging rings	presence	1.6	3.8	0.85	0.20	8.5	7.9	0.13	0.45	2.8	8.1	2.17	0.04
	absence	98.5	96.2			91.5	92.1			97.2	91.9		

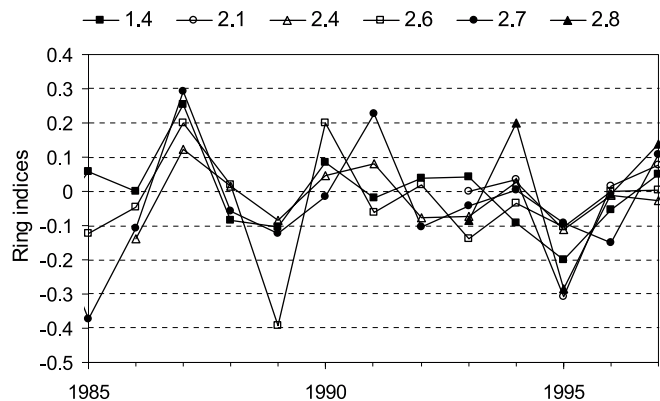


Figure 3. Good agreement obtained with the method of plotted curves (standardized ring series) between mean chronologies of salal individuals 1.4, 2.1, 2.4, 2.6, 2.7 and 2.8 (inter-stem cross-dating) on deer-free islands (samples 1 and 2).

different stem chronologies was poor (inter-stem cross-dating): only 6 out of the 18 stems cross-dated ($P < 0.001$) (Fig. 3). The skeleton plot confirmed that it was impossible to build a mean chronology for the samples from deer-free islands.

3.1.1.2. Cross-dating on a deer-affected island

On the deer-affected island, most sections within each stem could not be cross-dated whatever the method used. This prevented building individual mean stem chronologies, except for 2 stems for which a negative abrupt growth change was observed in all sections (Fig. 4). This change coincided with scars identifiable by visual examination. Before a scar, ring width varied from year to year. The ring on which the scar occurred was characterised by an abrupt negative growth change. Then, from year ($t + 1$) onwards ring were very narrow with little variation.

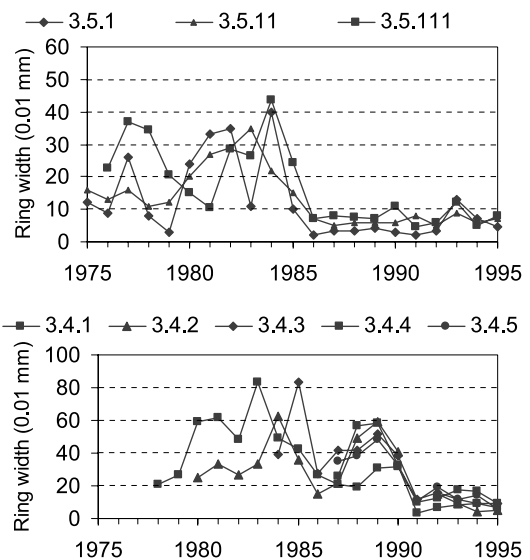


Figure 4. Good agreement showing negative abrupt growth changes of all sections within a stem collected from the base to the top on the two browsed individual (salal 3 and 4) collected on the deer-affected island. The section 3.5.1 is the basal section of the individual 5 of the sample 3, the section 3.5.111 is the apical section. The section 3.4.1 is the basal section of the individual 4 of the sample 3, the section 3.4.5 is the apical section.

3.1.2. Morphological characteristics

A total of 325 sections were analysed. There was no significant variation between samples within the same category (deer-free or deer-affected islands) except for the form of the pith (Tab. II). This character differed significantly ($P < 0.05$) between different samples from the deer-affected island. Although all morphological characters were observed on both

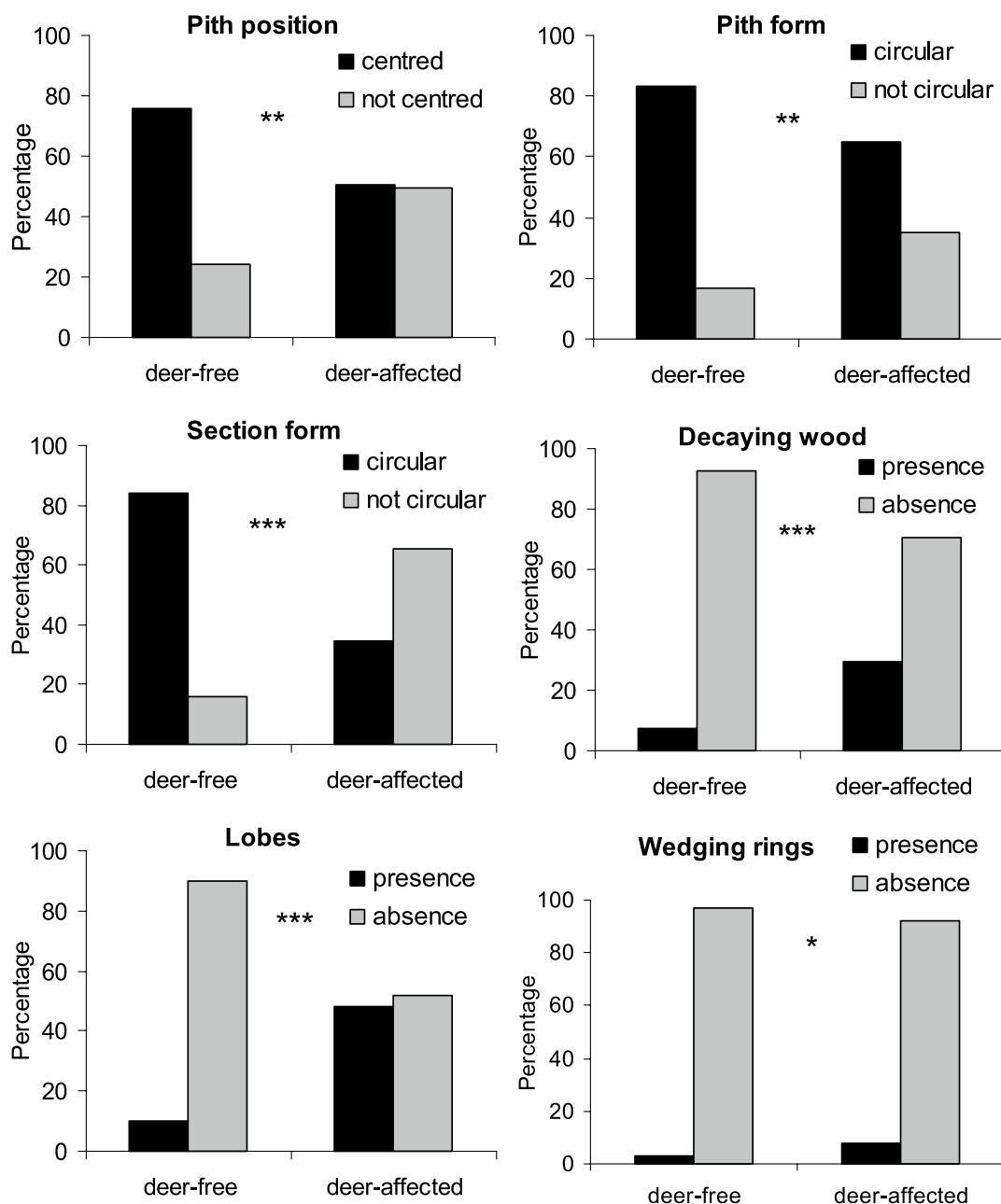


Figure 5. Percentage of each morphological character observed between individuals of deer-free and deer-affected islands. Stars indicate significance related to P -values. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

deer-free and deer-affected islands, their frequency varied significantly between the two island categories ($P < 0.01$) except for wedging rings (Fig. 5 and Tab. II). The major contrast between deer-free and deer-affected islands was observed for the frequency of lobes and of non circular sections and, to a lesser extent for decaying wood, pith position and pith form (Tab. II). On deer-free islands, salal stems were (1) circular, (2) their pith was centred, not deformed, (3) rings were concentric and (4) bark was continuous around the circumference. Com-

pared to deer-free islands salal stems from deer-affected islands were characterised by (1) altered stem geometry near a scar, (2) distorted pith towards the scar, with sometimes pith laid against the bark and not centred, (3) the presence of callous tissue enclosing the wounded tissue, a process which is slow and not always effective, (4) the presence of a brown and white coloration with changes in wood texture and compartmentalisation through structural and chemical boundaries in order to resist the diffusion of pathogens.

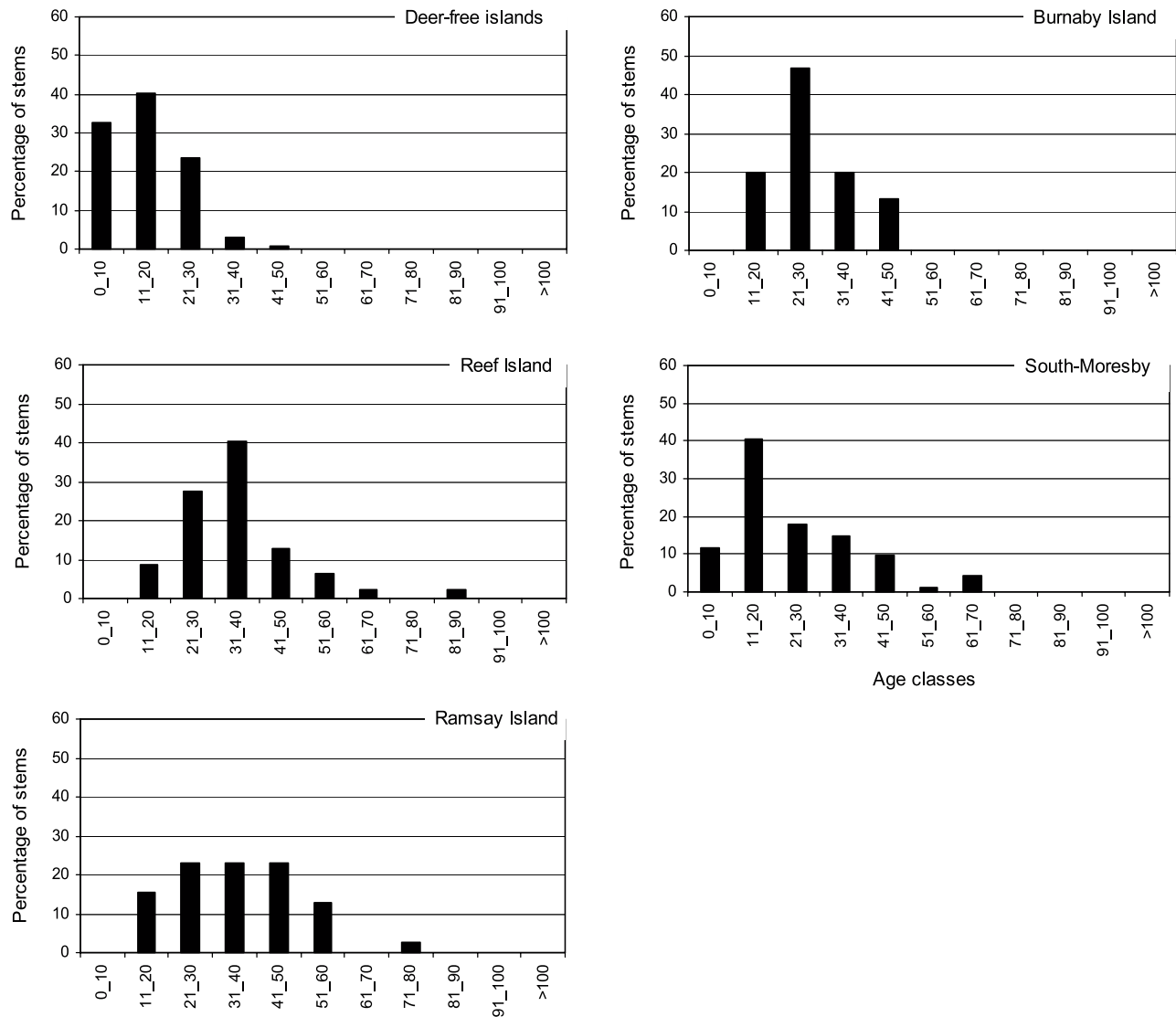


Figure 6. Age structures (% of stems per 10-year-classes) on the different islands. Deer-affected islands are ordered from north to south.

3.2. Stem age structure

3.2.1. Variation in stem age, height and foliage distribution

Stems were significantly older on the deer-affected islands (mean \pm S.E. = 29.89 ± 2.10) than on the deer-free islands (16.02 ± 1.38 ; nested ANOVA, $P < 0.05$). Within the deer-affected islands, post-hoc tests show (1) that there were no significant differences in mean age of salal stems between Reef, Ramsay and Burnaby Islands ($P > 0.05$) all with deer and (2) that mean age at the south of Moresby Island (with deer) did not differ significantly from mean age observed on Burnaby Island ($P > 0.05$) but was significantly lower than mean age observed on Reef and Ramsay Islands ($P < 0.001$) (also with deer). The post-hoc tests reveal also that mean stem age was

significantly different between the sites from south of Moresby Island and the sites from the deer-free islands ($P < 0.001$).

Stem height varied significantly from site to site ($P < 0.001$) but the variation was not correlated to the presence or absence of deer ($P = 0.25$) or to islands ($P = 0.76$).

Mean height of the first salal leaves along a stem was higher ($P < 0.001$) and less variable on the deer-affected islands (mean \pm SE = 1.26 ± 0.05 m) than on the deer-free islands (0.90 ± 0.09 m). In presence of deer, there were no stems with leaves under the browse line.

3.2.2. Age structures

There was no variation in age structure between sites within a given island ($P > 0.05$). We therefore grouped sites from a given island to compare age structures between islands (Fig. 6).

Stem age structures on deer-free islands differed significantly from the age structure on deer-affected islands ($P < 0.001$ for comparison with pooled data for Reef, Ramsay and Burnaby and $P < 0.001$ for comparison with south-Moresby).

On deer-free islands, 96% of the stems were less than 30 years old and 100% were less than 40 years old. Each of the first 3 age classes contained at least 20% of the stems. Age structure was similar on all deer free islands ($P < 0.05$).

On deer-affected islands, age structure varied with locality. The percentage of stems older than 30 years decreased from north to south. On Reef Island over 63% of the stems were older than 30 years, on Ramsay Island over 61%. On Burnaby Island this percentage dropped to 33.3% and on the south of Moresby Island to 29.8%. Reef and Ramsay Islands are also characterized by a deficit of stems in the age-class 11–20. There were no stems younger than 10 years on Reef, Ramsay as well as Burnaby Islands. On the southern tip of Moresby, a deficit of stems was only observed in the age-class 1–10. Although the age structure on Burnaby was statistically similar to the age structure on Reef and Ramsay ($P > 0.05$), only the age structures observed on Reef and on Ramsay did differ statistically from the age structure observed on the southern tip of Moresby ($P < 0.01$).

4. DISCUSSION

4.1. Understanding salal growth pattern and deer signatures on salal

On deer-free islands, the overall absence of correlation between stem mean chronologies suggests that individual factors exert a stronger influence upon salal diameter growth than do factors affecting the whole stand. According to Schweingruber (1988) [45], many living angiosperms seem to follow endogenous growth rhythms independent from variation induced by climate. However the poor agreement between stem chronologies in salal may also reflect inter-individual competition.

4.1.1. Deer effect on growth rate

On deer-affected islands, we analyse the abrupt negative growth change associated with browsing scars as the consequence of severe leaf and shoot removal by deer. Such reduction in growth of defoliated plant parts has been observed by Honkanen and Haukioja (1994) [20] and Krause and Raffa (1996) [24]. This pattern can also be seen as a mirror image of the pattern we observed in young trees when they escape deer browsing [51, 53]. We suggest that the repetitive, irregular and partial defoliation by deer also explains the asynchronism observed in stem sections from deer-affected islands, in contrasts to the synchronism observed for sections collected on deer-free islands. Thus identifying, counting and dating abrupt growth changes in salal populations should allow to reconstruct the local history of deer browsing in a way similar to what has been done using adult tree rings [26] to reconstruct the history of insect outbreaks [31, 32, 42] or scars to reconstruct past caribou activity [33], porcupine expansion [36], beaver occupation [4] or changes in deer population [34, 35].

4.1.2. Deer impact on ring shape, section form, pith and wood decay

On deer-affected island, the steep increase of the frequency of morphological characters in salal stems has to be attributed to deer browsing. Partial removal of cambium by deer also results in incomplete rings that produce lobes when they superpose, deforming the stem section. Pith position and pith form also are altered but less so than section form. Pith formation is actually over when browsing occurs whereas section form is produced by the cambium that is susceptible to be removed or partially destroyed by deer. As a result section form is one of the best characters to diagnose deer impact. Wood decay can be attributed to deer browsing and the pathways they create for pathogens. In the patches of decaying wood, for example, bleaching and weight reduction are caused by fungi [44]. On deer-affected island the occurrence of such patches of decaying wood, contrasts with deer-free islands and reflects the specificity of deer caused injuries. Wedging rings to the contrary are least characteristic. They occur between sequences of normal rings and result from failures in cambial activity unrelated to the presence of deer. The distribution of these morphological features in situations of known deer densities could actually produce valuable calibrations to indirectly assess deer densities where direct estimates are not available.

4.2. Reconstructing deer colonization history using stem age structure

In dense salal stands, such as those on deer-free islands, we observed a balanced stem age structure that resulted from the constant production of new sprouts [17, 19] which progressively replaced older stems that die off. On islands with deer, deer prevent such a replacement [39] and only stems that had foliage above the browse line when deer browsing started were able to remain alive, this until they eventually die from old age. The lack of stem recruitment from rhizomes on deer-affected islands had already been diagnosed by Pojar et al. [39]. On heavily browsed sites, this process can lead to the total elimination of the shrubby understory [10, 49, 50].

The variation we observed in stem age structures suggests deer impact has been prevalent for at least 20 years before this study in the sites sampled on Reef, Ramsay and Burnaby islands, suggesting comparable histories of deer impact across most of the southern half of the archipelago. On the southern tip of Moresby Island prevalent deer impact seems to have taken place only for the 10 years before this study. These north south differences could be interpreted as a result of distance to the point of introduction. However, we know that deer were present in the south of the archipelago already in 1946 [14]. This increased time lag between initial colonization and heavy impact in the south of the archipelago could result from differences in habitat and climate. The south of Moresby Island is situated in the very wet hypermaritime sub-zone, with higher precipitation and differences in vegetation composition [3], factors known to influence deer population dynamic [16, 22].

The overall pattern is remarkably consistent with the pattern observed for the other dominant long lived shrub, the red huckleberry, on the same islands [54]. However the time span of prevalent deer impact suggested on Reef, Ramsay and Burnaby

islands by red huckleberry stem age structure is about 20 years longer than the one suggested by the results from salal. In addition the study of fraying scars on some of these islands provided dates of deer presence that were about a decade earlier than those obtained from red huckleberry [54]. These different estimates on the duration of deer presence illustrate the importance to understand the processes that are behind the different types of signatures and their complementary nature. Red huckleberry shrubs, for instance, tend to occur in relatively open understories with moderate impediment to deer movement, whereas salal often comes in dense thickets that make up physical barriers to deer movement. In addition, huckleberry stems can survive the lack of replacement by new stems for about 100–120 years against 50–60 years for salal stems. Finally, most surviving salal shrubs occur near remnant thickets, their age structure will reflect more the history of deer impact on these particular thickets than the time since deer have become abundant on an island. While stem age structures provide indications about when deer impact on the understory became prevalent, fraying scars can provide date estimates for the actual date of colonisation of an island.

Investigations on plant-herbivore interactions can be considerably enhanced by the historical context provided by the study of ligneous species, especially when this information cannot be obtained from other repositories. The signatures deer have left in the wood are probably the most widespread and reliable source of information but we need to develop the tools to read them. Such tools should allow developing a better knowledge of browsing history from the regional scale to the scale of local plant populations and individual plants within these populations. Browsing signatures could also be used to monitor the changes occurring in ecosystems in which browsing pressure has been reduced and, more generally, yield essential insights on how forest ecosystems work.

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