

Disentangling the causes of damage variation by deer browsing on young *Thuja plicata*

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Long-lived trees experience different levels of damage due to mammalian herbivores. To untangle the mechanisms that underlie this variation, we combined chemical with dendrochronological analyses to study variation in browsing on Western redcedars (*Thuja plicata*) on Haida Gwaii (British Columbia, Canada). Since the last glaciation, Haida Gwaii forests had lacked large herbivore browser until Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) were introduced at the beginning of the 20th century. Dendrochronology yielded information on radial growth and plant annual responses to environmental stresses including herbivory. Secondary metabolite content and plant nutritional quality provided insights into proximate causes of food choices made by herbivores. We sampled lightly- and heavily-browsed young trees at four sites: three clear-cut sites with high browsing pressure and one old-growth forest site where browsing pressure had, until recently, been lower. Heavily-browsed young trees had lower concentrations of secondary metabolites and were of lower nutritive value than lightly-browsed trees at all sites. Under high browsing pressure, tree growth patterns suggested that all young trees were initially severely browsed until some trees, currently scored as lightly-browsed, started to escape deer. At the old-growth site, both lightly- and heavily-browsed trees tended to have lower overall average secondary metabolite concentrations than those of all other sites, a trend possibly related to greater canopy closure. Lightly-browsed trees were older than heavily-browsed ones which resulted, during the period of lower browsing pressure, in higher growth rate and a same pattern of change in growth from one year to the next year. This suggests that, under low browsing pressure, selection of young trees related to chemical defense was weak and that growth differences due to other factors than browsing could be expressed. Under strong browsing pressure, however, all young trees had equally low growth rates until trees with better genetic potential to produce effective defenses were able to escape deer. This suggests that selection by deer could occur on a long-lived tree.

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By feeding on vegetative and reproductive plant parts, herbivores affect plant population dynamics by limiting plant growth, reproductive success, competitive ability

and ultimately survival (Harper 1977, Crawley 1983, Tilghman 1989, McInnes et al. 1992, Stromayer and Warren 1997, Kielland and Bryant 1998). Plant

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palatability to herbivores depends on the interplay between plant nutritional quality and physical and chemical characteristics which determine overall nutritional and toxic value (Provenza et al. 1992, McArthur et al. 1993, Hanley 1997, Berteaux et al. 1998). Several studies have demonstrated a correlation between intraspecific variation in herbivory damage and plant defense traits (Bryant and Kuropat 1980, Cooper and Owen-Smith 1985, Duncan et al. 1994, Suomela et al. 1997, Lawler et al. 1998, Pass et al. 1998). However, correlation between two factors does not prove causality.

Variation of plant defense within a plant population could result from four interrelated factors. First, environmental variation in resource availability could influence plant palatability through effects on defense chemical expression (Coley et al. 1985, Boira and Blanquer 1998, Loreau and de Mazancourt 1999). Second, variation could result from genetic differences. Several studies have shown that defense against browsing has a strong additive genetic variance (Dimock II et al. 1976, Silen et al. 1986), and that genetic variation exists in plant resistance to browsing (Danell et al. 1990, Roche and Fritz 1997, Rousi et al. 1997). Third, plant defense may vary with ontogeny due to developmental constraints or stronger selection for defense against herbivores and pathogens at the juvenile rather than the adult stage (Watkinson 1986, Kearsley and Whitham 1989, Bryant and Julkunen-Tiitto 1995, Karban and Thaler 1999, Fritz et al. 2001, Swihart and Bryant 2001). Finally, defense levels can be influenced by an individual plant's history of herbivory. After browsing, plant nutritional quality may increase through changes in carbon-nitrogen ratio (Chapin III et al. 1985) or decrease as a result of chemical defense induction (Tallamy and Raupp 1991, Karban and Baldwin 1997, Agrawal and Karban 1999).

Thus, it is difficult to pinpoint the exact source when variation in herbivore damage is observed in a plant population. One approach to solving this problem is to conduct a common garden experiment where herbivory and developmental factors are controlled. For long-lived species, however, time constraints restrict use of this technique. Genotype-by-environment interactions also are useful for determining plant resistance to herbivores under field conditions (Maddox and Cappucino 1986). In this paper, we propose an alternate approach to working with long-lived species, one that combines chemical analysis with dendrochronological measurements of wild populations. The analysis of plant chemicals that are relevant to the herbivore's food choice provides a link between plant damage and plant traits. Dendrochronological analyses yield data on tree age and growth rate that can be used to assess the longer-term impacts of environmental stresses on radial tree

growth (Schweingruber 1988). With proper sampling, differences in growth patterns of trees growing at the same sites can be attributed to biotic factors, such as herbivory, as opposed to abiotic factors such as climatic variation. Payette (1987), for instance, successfully used the record of animal disturbance found in tree ring series to determine the spatial and temporal variations of several animal species. Integrating dendrochronological analyses with chemical data provides a powerful tool for examining both the short- and long-term causes and consequences of differential plant damage.

The study was conducted on Haida Gwaii (The Queen Charlotte Islands), an archipelago off the coast of British Columbia, Canada, where Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) were introduced at the beginning of the 20th century (Carl and Guiguet 1972). We looked at the impact of the introduced deer on one of the dominant long-lived conifers of the forest, Western redcedar (*Thuja plicata* Donn ex D. Don). Currently, Western redcedar recruitment is greatly reduced by deer browsing in old-growth forests (Martin and Daufresne 1999). However young trees can be found in clear-cuts where abundant light and vegetation facilitate recruitment (Martin and Baltzinger 2002) as well as in a few old-growth forest stands on small isolated islands where deer pressure is or has recently been low. At all these sites, there is variation in the current amount of browsing observed on young Western redcedars.

Our goals were (1) to determine whether defensive secondary compounds accounted for the differences in browsing by Sitka black tailed-deer on young Western redcedars while controlling for nutritional compounds; (2) to determine the effect of plant age and past herbivory history on the observed variation using dendrochronology; (3) to integrate these data sets to determine to what extent plant chemical phenotype influences overall browsing and growth patterns in Western redcedar; and (4) to compare sites with histories of high and low browsing pressure to analyze how site-specific browsing intensity affects population-level attributes such as chemical defense levels, growth rate and form, and survivorship.

Materials and methods

Study area

Haida Gwaii (Fig. 1) is an oceanic archipelago ca. 300 km long and ca. 80 km from mainland Canada. There are two major islands (Graham and Moresby), and over a hundred smaller islands. This work took place on the eastern side of the archipelago, an area which belongs to the Coastal Western Hemlock zone in the wet hypermaritime sub-zone and receives 1100 to 1300 mm precipitation (Banner et al. 1989). At

these low elevations, forests consist of a mixture of Western hemlock (*Tsuga heterophylla*, Raf. Sarg.), the dominant species, Western redcedar, which is often co-dominant but sometimes dominant, and Sitka spruce (*Picea sitchensis*, Bong. Carriere).

Before deer were introduced, there were no large forest browsers over most of the archipelago. The only large terrestrial herbivore native to the archipelago, the now extinct Dawson caribou (*Rangifer tarandus dawsonii* Setton), was restricted to lowland boggy areas of the northern island (Cowan 1989). The only deer predators are human hunters and black bear (*Ursus americanus* Pallas). Deer are now abundant. The only accurate density estimates available at present on the archipelago are for old growth forests and suggest density of about 33 deer per km² (Daufresne and Martin 1997).

Plant material and sampling

Western redcedar

Western redcedar is a preferred food source of Sitka black-tailed deer (Pojar et al. 1980, Coates et al. 1985). Deer severely reduce Western redcedar regeneration on Haida Gwaii by browsing seedlings and saplings (Martin and Daufresne 1999). Young trees are virtually missing from the understory of old-growth forests, although, after clear-cutting some regeneration does occur (Martin and Baltzinger 2002).

Sites

In May 1999, we sampled twenty lightly- and twenty heavily-browsed young trees at each of three sites that were logged 20–30 years ago (Fig. 1): North Graham, South Graham and North Moresby. The trees sampled within each site were at least 2 m apart to avoid intraspecific competition influence. Slashes were typically burned after logging and no subsequent treatment was carried out after burning. All the sites were sampled within a week with one site per day. Regeneration was exclusively natural and all the trees were accessible to deer. All the sites were on flat ground covered with typical second growth regeneration (Sitka spruce and Western hemlock) and shrubs (*Gaultheria shallon* Pursh, *Vaccinium* spp, *Rubus* spp). All young trees had been exposed to deer for their entire lifetimes, while their ancestors grew in an environment with reduced browsing (Vourc'h et al. 2001).

We also sampled fifteen lightly- and fifteen heavily-browsed young trees in the old-growth forest on Skedans Island, a small isolated island that has been colonized by deer. Vegetation structure indicated that recruitment had occurred under moderate browsing pressure at least during the late 1980s after which the browsing pressure increased (Rodway et al. 1988, J.-L. Martin and B. Vila, pers. obs.). This site was located ca 20–100 m away from the shore on a flat area. The soil was covered by moss or dead leaves. Shrubs were mostly *Gaultheria shallon*, and trees mostly young and mature Sitka spruce and Western hemlock. Because

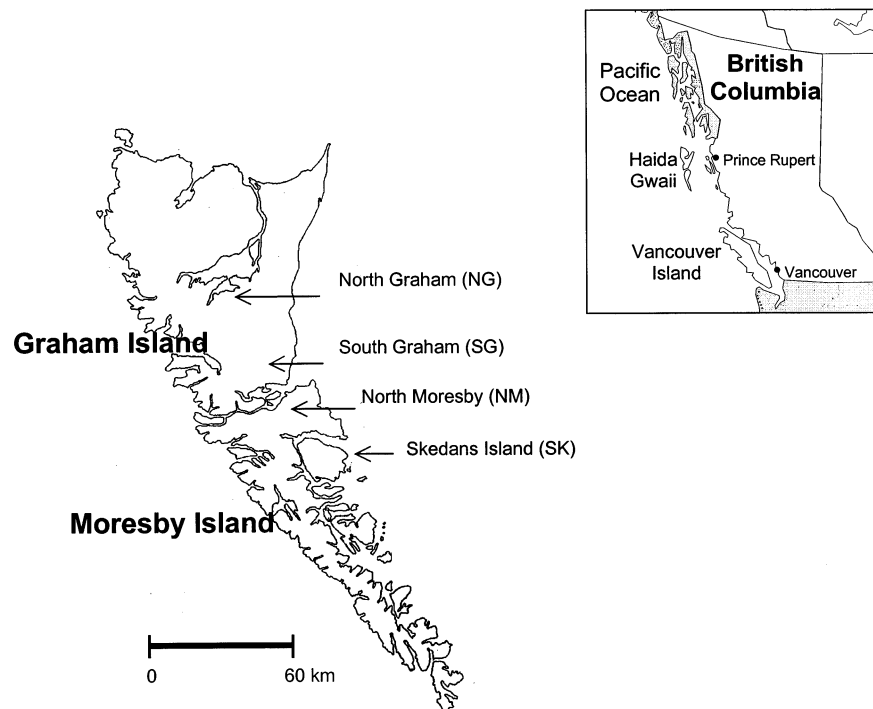


Fig. 1. British Columbia (Canada) and Haida Gwaii with the three clear-cut sites with high deer impact (NG, SG, MN) and the one site in old-growth forest with low deer impact until recently (SK) where young Western redcedars were sampled.

Western redcedar is often rare on the small isolated islands (Martin et al. 1995), it was not possible to find replicate islands with low browsing and sufficient Western redcedar for additional sampling.

Tree sampling criteria

Young trees were defined as non-mature Western redcedars, with a woody stem between 0.5 and 5 cm of diameter, accessible to deer. Estimates of the browsing intensity an individual tree had experienced were based on two criteria: the frequency of browsing scars and growth morphology. The former was calculated as a percentage by taking the ratio of the number of leaves with scars over the total number of leaves. The measurements were done over the entire trees with the exception of a few very heavily and homogeneously browsed individuals for which the ratio was determined on one quarter of the tree volume and multiplied by four to get the whole tree ratio. This volume was sampled by dividing the tree volume in four on its length according to cardinal direction and randomly choosing one quarter. Lightly-browsed young trees were defined as trees with less than 35% of leaves with browsing scars, straight stems and long branches of small diameter. Heavily-browsed young trees were defined as trees with more than 65% of leaves with browsing scars and with short, large diameter branches and numerous small leaves growing from the trunk. Tree heights also were measured.

Plant damage and chemical composition

To correlate the variation in damage with a set of plant traits, we collected leaves that were accessible to deer, and green. In the leaves, we analyzed terpenes (mono- and diterpenes) and nutritive compounds (nitrogen, cell solubles, hemicellulose, cellulose, lignin, ash). Terpenes are abundant in conifers (Banthorpe and Charlwood 1980) including Western redcedar (Rudloff and Lapp 1979, Vourc'h et al. 2001) and are known to be correlated with decrease foliage consumption by cervids (Personius et al. 1987, Duncan et al. 1994, Vourc'h et al. 2001).

Chemical analyses

Terpenes: Three grams of fresh leaf material from each plant sample were extracted with 30 ml methanol for 48 h. After filtration the extracts were stored at -20°C until analyzed for terpene content by gas chromatography (GC). Extracts were analyzed on a Hewlett Packard 6890 GC equipped with a flame ionization detector, and monoterpene peaks identified using the same method described in Vourc'h et al. (2001). Leaf material from the same samples were dried at 55°C for 24 h to get the dry matter content to calculate terpene percentage in dry matter.

Nutritive compounds: All samples were dried at 55°C for 24 h, ground in a cyclone mill (Cyclotec Sample Mill, Tecator) and then scanned with a near-infrared reflectance spectrophotometer (NIRSystems 6500). Wet chemical analyses were performed on selected samples representative of the whole range of spectral variation found in the populations. Samples were extracted with methanol to remove phenolics after extraction with dichloro-methane to remove the lipid fraction (Waterman and Mole 1994). On the extractive-free samples, nitrogen analysis was performed on a LECO (FP-428) instrument. Fibres were measured using Van Soest procedures (Van Soest 1963). Ash was measured after combustion of oven-dried samples at 550°C (Allen 1989). Calibration equations were monitored according to the methods described by Shenk and Westerhaus (1991b), Joffre et al. (1992) and Gillon et al. (1999). Data analysis was conducted using the ISI software system (Shenk and Westerhaus 1991a). Using these calibration equations, contents in nitrogen, hemicellulose, cellulose, lignin, and ash were measured on all samples. The measured values were obtained with standard errors of calibration of 0.02% for nitrogen, 1.82% for hemicellulose, 0.59% for cellulose, 0.95% for lignin, and 0.12% for ash. Cell solubles were calculated for all samples by subtracting fibre (hemicellulose + cellulose + lignin) from organic matter (organic matter = $100 - \text{ash}$).

Statistical analyses

Because differences in profiles of individual secondary compounds or combinations of compounds of the same group can be important (Connolly et al. 1980), we first looked at the correlation of the concentration of mono- and diterpene molecules within their compound group. All monoterpenes were significantly and positively correlated ($r > 0.65$, $P < 0.001$), as well as all the diterpenes except two minor peaks (mean $< 0.015\%$ in dry matter). Therefore, after checking that the results were consistent, we chose to run the analysis on the total concentration of mono- and diterpene rather than considering every peak as a response variable. Total mono- and diterpene concentration met the normality criteria so that no transformation was needed. We ran a MANOVA (SAS 1999) to test the difference between lightly- and heavily-browsed trees using the total concentrations of mono- and diterpenes as quantitative response variables. We considered "browse" (lightly- versus heavily-browsed) and "site" (North Graham, South Graham, North Moresby, and Skedans Island) as the qualitative predictor variables. We identified the significant response variables using ANOVA (SAS 1999). We corrected the level of significance, α , by the improved Bonferroni procedure for multiple tests proposed by Simes (1986). The method orders the p-values $P_{(1)}, \dots, P_{(n)}$ in increasing order for testing hypotheses $H_0 = \{H_{(1)}, \dots, H_{(n)}\}$. H_0 is rejected if $P_{(j)} \leq j\alpha/n$ for any

$j = 1, \dots, n$, so that corrected $P_{c(j)} = P_{(j)}/n$ can be compared to α . Tests of significance for differences in means were made by LSMEANS test of GLM procedure (SAS 1999) and were corrected the same way. We used the same procedure with nitrogen, cell solubles, hemicellulose, cellulose, lignin, and ash concentrations as quantitative response variables to test the difference in nutritive value.

Plant damage, age and growth pattern

Tree ring analysis

At each site, a sub-sample of 12 to 14 lightly- and heavily-browsed trees was randomly collected for dendrochronological analyses among trees sampled for chemical analyses. Cross-sections of these individuals were sampled at the bottom of their stem just above the collar to obtain the longest ring series. To analyze ring series, tissue structure was made visible by polishing a transverse section of the sample with sandpaper of different grades. The number of rings was counted to obtain tree age. Because changes in environmental conditions can affect ring width and other anatomical characteristics, the occurrence and duration of these changes can often be identified and dated (Schweingruber 1988, 1996). The identification of ring sequences with similar patterns in different samples was used in the cross-dating method to accurately date each ring (Fritts 1976). Once the rings had been dated, we measured ring widths with a precision of 1/100 mm, with an Eklund measuring device, along two suitable radii that avoided irregularities (Fritts 1976, Schweingruber 1988, 1996, Cook and Kairiukstis 1990). The average value of each ring width was calculated to obtain an individual chronology for each tree. Individual chronologies were visually cross-dated and a mean chronology for each population was constructed (Fritts 1976, Cook and Kairiukstis 1990). All individuals for which cross dating failed were discarded. We graphed the mean chronology for each lightly or heavily-browsed population per site including only data points with at least 3 individuals.

Statistical analyses

Age differences were assessed by ANOVA (SAS 1999) with "browse" and "site" as the qualitative predictor variables. Means were compared by the LSMEANS procedure (SAS 1999). Because of unbalanced sample sizes, type III sums of squares were used.

To test the effect of browsing on tree growth pattern, ring-width series within each site were analyzed by multivariate repeated-measure analyses. We used multivariate (MANOVA) as opposed to univariate (ANOVA) analyses to avoid data circularity problems and because some of the sample sizes were unbalanced (Ende 1993). Data were log transformed to normalize

the distributions. Because young trees were not necessarily of the same age, we started the analyses at the date where data were available for at least all trees but one. We tested the effects of time and time \times browse interaction. The former tests whether there was a significant ring width variation when averaged over both browse levels. The latter interaction tested whether the shape of the response was different. When this interaction was not significant, we tested ring width mean difference by LSMEANS (SAS 1999) for each date within each site in the period analyzed in the MANOVA. Because of unbalanced sample sizes, we used type III sums of squares. We corrected the level of significance, by the improved Bonferroni procedure (Simes 1986).

Results

Amount of plant damage

On the clear-cut sites, heavily-browsed trees had a mean height of 71 cm (standard error (SE) = 5 cm), and 88% (SE = 3%) of leaves had browsing scars. Trees were stunted with short, large diameter branches and many small leaves growing from the trunk. In contrast, lightly-browsed trees had a mean height of 116 cm (SE = 5 cm), and 22% (SE = 2%) of leaves had browsing scars. They had straight stems with long branches of small diameter and leafless trunks.

On Skedans Island, none of the heavily-browsed trees had the characteristic stunted shape of heavily-browsed trees at the other sites. Here, heavily-browsed trees measured 120 cm (SE = 18 cm), and 96% (SE = 3%) of leaves had browsing scars and their top leaves browsed. Their growth form was straight but they were branched at their base. Lightly-browsed trees were 250 cm (SE = 16 cm). They showed signs of browsing up to the height that can be reached by deer with browsing scars averaging 39% (SE = 4%) of the tree, a percentage value slightly greater than the 35% threshold that we chose a priori to define low levels of browsing.

Plant damage and chemical composition

Secondary metabolites

We focused on the 19 major terpene peaks (9 monoterpenes and 10 diterpenes) present in most of the samples. Five of the nine monoterpenes were identified and were the same as those found by Vourc'h et al. (2001): α -pinene, sabinene, β -myrcene, limonene and α,β -thujone.

The MANOVA on the total mono- and diterpene concentrations showed significant browse and site effects (browse effect: Roy's Greatest Root (RGR) = 0.40, $F_{2,141} = 28.45$, $P < 0.001$; site effect: RGR = 1.17,

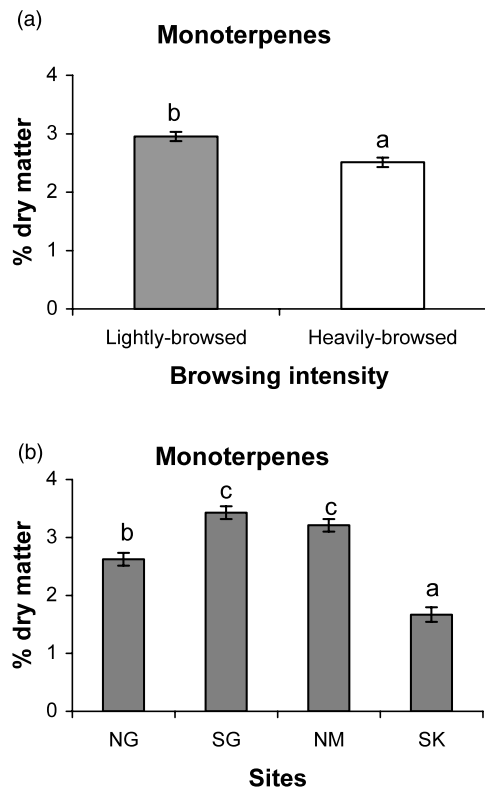


Fig. 2. Means with standard error bars of monoterpene concentrations in (a) heavily- and lightly-browsed young Western redcedars, (b) across the 4 sites on Haida Gwaii (see Fig. 1). Difference letters mean that means are different ($P_c < 0.05$).

$F_{3,142} = 55.24$, $P < 0.001$) but no browse \times site interaction ($RGR = 0.03$, $F_{3,142} = 1.37$, $P = 0.253$). Lightly-browsed trees had more monoterpenes ($F_{1,142} = 15.38$, $P < 0.001$) and diterpenes ($F_{1,142} = 55.99$, $P < 0.001$) than heavily-browsed trees (Fig. 2 and 3). In addition, mono- and diterpene concentrations were lower at the old-growth site than for young trees in clear-cut sites (site effect monoterpene: $F_{3,142} = 43.53$, $P < 0.001$; diterpenes: $F_{3,142} = 34.33$, $P < 0.001$) (Fig. 2 and 3). The same patterns were observed for all individual monoterpene peaks and all diterpene except two small peaks.

Nutritive compounds

The MANOVA for nutritive foliage compound content showed a significant browse \times site interaction ($RGR = 0.23$, $F_{5,140} = 6.50$, $P < 0.001$). MANOVA performed within each site showed a significant browse effect at every site (North Graham: $RGR = 0.82$, $F_{5,34} = 5.58$, $P < 0.001$; South Graham: $RGR = 1.83$, $F_{5,34} = 12.46$, $P < 0.001$; North Moresby: $RGR = 1.17$, $F_{5,34} = 7.99$, $P < 0.001$; Skedans: $RGR = 1.67$, $F_{5,24} = 8.04$, $P < 0.001$). For each nutritive compound, the difference between lightly- and heavily-browsed trees was consistent across sites. Lightly-browsed trees tend to have

more nitrogen, cell solubles, and hemicellulose, and less cellulose, lignin, and ash than heavily-browsed trees (Fig. 4). The MANOVA within each browse category shows a significant site effect (Lightly-browsed: $RGR = 1.30$, $F_{5,69} = 18.00$, $P < 0.001$; heavily-browsed: $RGR = 1.84$, $F_{5,69} = 25.36$, $P < 0.001$), and the site effect was significant for each compound within browse category (for every compound, $P_c < 0.024$) except for hemicellulose in lightly-browsed trees.

Plant damage and plant age and growth

Five lightly-browsed trees (one at North Graham, three at South Graham and one at North Moresby) were discarded because of failure in cross-dating.

Age

As the browse \times site interaction term was statistically significant ($F_{3,79} = 3.58$, $P = 0.017$), we compared the age of lightly and heavily-browsed trees within each site. Lightly-browsed trees from South Graham and Skedans were older than heavily-browsed trees (Fig. 5). At the two other sites, there was no significant difference in tree age between browsing categories.

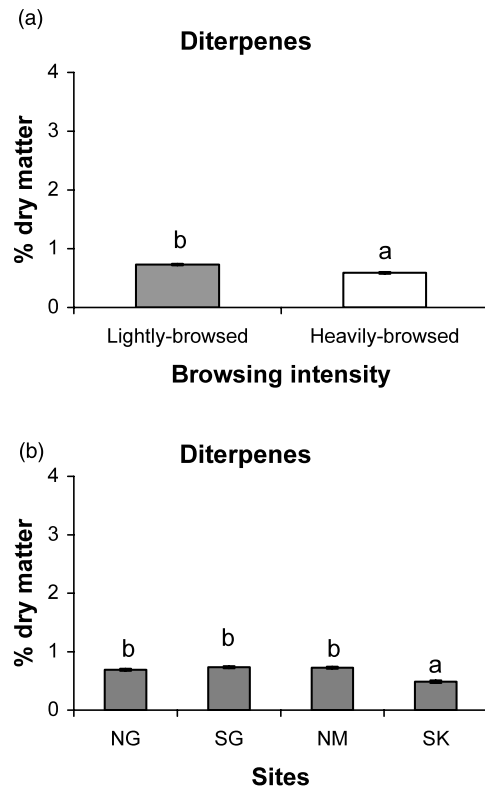
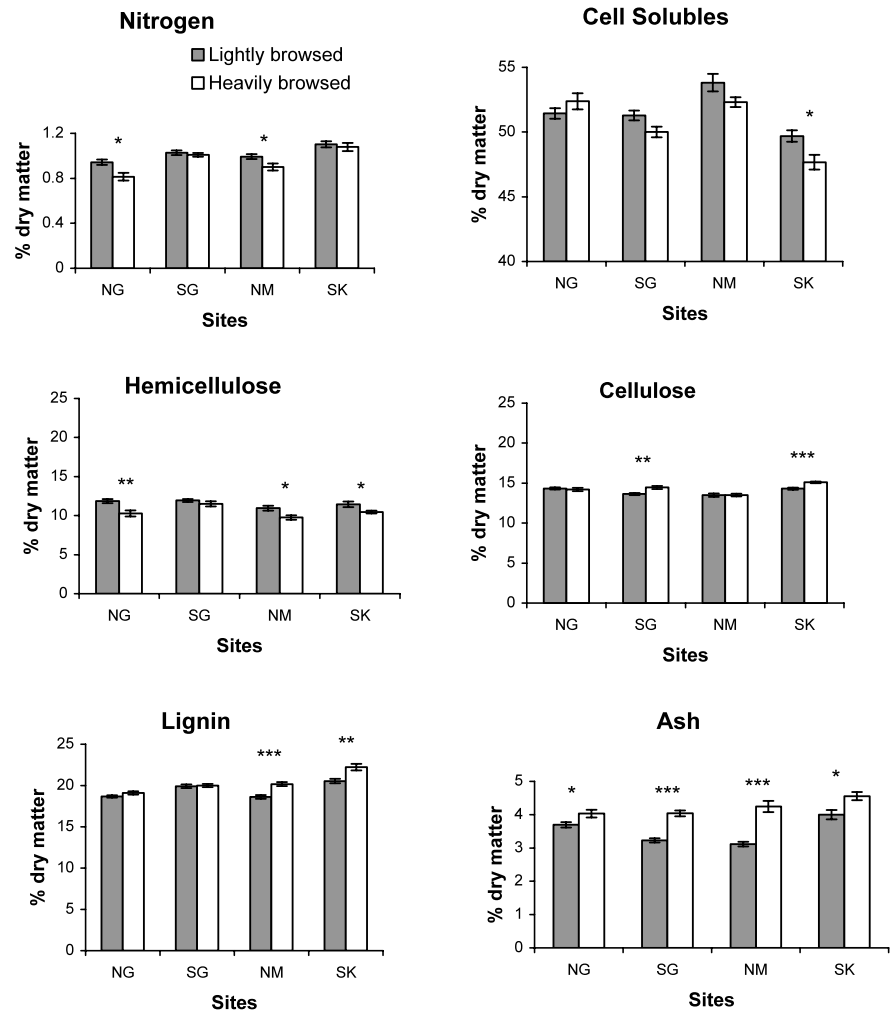


Fig. 3. Means with standard error bars of diterpene concentrations in (a) heavily- and lightly-browsed young Western redcedars, (b) across the 4 sites on Haida Gwaii (see Fig. 1). Difference letters mean that means are different ($P_c < 0.05$).

Fig. 4. Means with standard error bars of nutritive compound concentrations in heavily- and lightly-browsed young Western redcedars sampled in 4 sites on Haida Gwaii (see Fig. 1). Stars (*) indicate the P-values (corrected with the improved Bonferroni method, see text) for the comparison between lightly- and heavily-browsed young Western redcedars within a site. *: $P_c < 0.05$, **: $P_c < 0.01$, ***: $P_c < 0.001$. Note that the y-axis for cell solubles starts at 40% dry matter.



Growth rate and pattern

Visual inspection of the four chronology graphs (Fig. 6) shows that browsing categories have generally overlapping growth patterns during a given period until the growth rate of lightly-browsed trees diverged and increased. This pattern was most obvious for the two clear-cut sites (North Graham and North Moresby) where both browsing categories had identical age ranges, and for Skedans Island during the period of 1990–1998. A similar effect was evident at the South Graham site, but the growth rate of heavily-browsed plants was more variable and lightly-browsed trees appeared to grow very slowly in 1987. During the time of low browsing pressure on Skedans Island (before 1990), lightly-browsed trees, which were older than heavily-browsed trees, had a higher growth rate, but a parallel growth curve.

For the multivariate repeated-measure analyses within each site, we used the largest complete data sets available. These included the years 1993–98 (North Graham and South Graham), 1992–98 (North Moresby) and 1987–98 (Skedans). We found that the time \times browse interactions were significant for North Graham and North Moresby sites and that the time effect was significant at all sites (Table 1). Since the time \times browse interaction was not significant at South Graham and Skedans, we tested the mean difference in ring width for each date of the multivariate analyses (LSMEANS, SAS 1999). After correction by the improved Bonferroni procedure (Simes 1986), we found no significant differences at South Graham. At Skedans, however, lightly-browsed trees had significantly higher growth in 1987, 1988, marginally higher in 1997, and higher again in 1998 (Table 2).

Discussion

Variation in damage is correlated with defenses

On Haida Gwaii, young Western redcedars subject to high rates of browsing had fewer monoterpenes and diterpenes than did lightly-browsed trees. This result is consistent with Vourc'h et al. (2001) finding that, in cafeteria experiments, Sitka black-tailed deer preferentially feed on branches from Western redcedar collected on Haida Gwaii rather than on branches collected on the mainland redcedar, even though Haida Gwaii branches had only slightly lower monoterpene concentration (ca. 0.15%). Monoterpenes deter feeding by cervids (Welch et al. 1981, Elliott and Loudon 1987, Duncan et al. 1994). Furthermore, Vourc'h et al. (in press) demonstrated that the five monoterpenes identified in Western redcedar in this paper were repellent to wild Sitka black-tailed deer when offered in feeding choice experiment at the concentration of lightly-browsed young Western redcedar. Monoterpenes, being volatile, could act as olfactory deterrent signals and/or have toxic effects on ruminal microbial fermentation or nervous system (Nagy et al. 1964, Oh et al. 1967, Millet et al. 1981, Provenza et al. 1992, Villalba and Provenza 2000). Diterpenes occurred in much lower concentrations than monoterpenes. The number of diterpenes isolated was greater than that found in Vourc'h et al. (2001) due to the use of an improved gas-chromatography column in the present study. Diterpene effects on cervids have not been studied as thoroughly as those of monoterpenes, but Danell et al. (1990) showed that diterpene concentrations were negatively correlated with browsing on Scots pine (*Pinus sylvestris*) by moose (*Alces alces*).

Heavily-browsed trees also differed from lightly-browsed trees in their nutritional value. They tended to be poorer in nitrogen, hemicellulose, and cell solubles and richer in cellulose, lignin, and ash. This pattern could be a consequence of long-term browsing stress and of the resulting smaller leaf size ensuing in increased structural (cellulose, lignin, and ash) and decreased parenchyma (nitrogen and cell solubles) tissues (Raffa et al. 1998). Cell solubles correspond to the cell cytoplasm, that is intracellular glucides and proteins that are readily digestible. On the other hand, lignin is a digestion-reducing fiber (Hanley 1992) and ash is the remnant of foliar combustion that consists mainly of minerals that are present in structural tissues or chelators of organic molecules (Allen 1989). Nitrogen decrease in heavily-browsed trees differs from Löyttyniemi (1985) and Edenius (1993) findings showing an increase in nitrogen content of Scots pine leaves after browsing or clipping, and suggests that intense browsing stress induced root mortality.

In summary, heavily-browsed young Western redcedars had less secondary compounds but were also of poorer nutritive value. This is consistent with the findings that food choice by mammal herbivores, especially in ecosystem dominated by woody vegetation, is primarily determined by secondary metabolite content of plant tissues rather than by nutrient content alone (Bryant and Kuropat 1980, Bryant et al. 1983, McArthur et al. 1993, Hanley 1997). Similarly, other studies have shown that within the same population, target trees have the lowest levels of secondary compounds (for moose, *Alces alces*, Danell et al. 1990; for Abert's squirrels, *Sciurus aberti*, Snyder 1993).

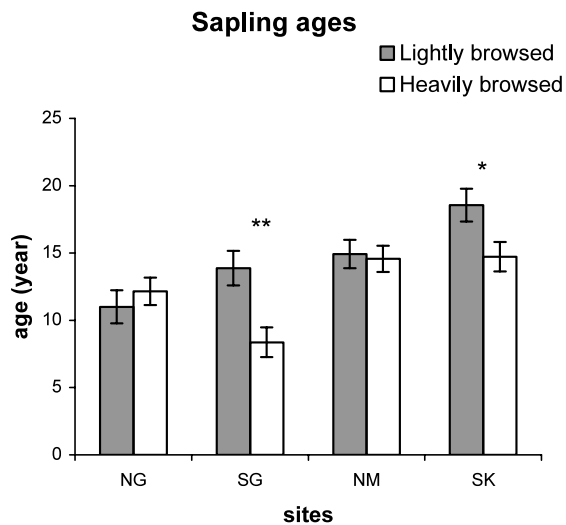


Fig. 5. Mean age of lightly- and heavily-browsed young Western redcedars at the 4 sites (see Fig. 1). Vertical bars are standard errors (*: statistically different means $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

Browsing history suggests variation in defense

One of our goals was to use browsing history, as inferred through dendrochronological measurements, to inform our understanding of the current differences in overall plant damage and defense levels. Because heavily- and lightly-browsed trees occurred on the same sites, often side by side, and thus were similarly accessible to deer, the differences in defense levels within sites cannot be explained by variation in environmental factors that would influence the production of chemical defense nor by differences in deer browsing due to differences in accessibility.

Therefore we were left with three mechanisms to explain our results. First, young redcedars may differ genetically in their potential to express chemical defenses under browsing pressure. Second, higher level of defense in juvenility lightly-browsed plants may be a result of their greater age. Indeed, Vourc'h et al. (2001) found that monoterpene concentrations were low in one-year-old seedlings and reached a peak at the sapling stage. Under this hypothesis, escaping deer

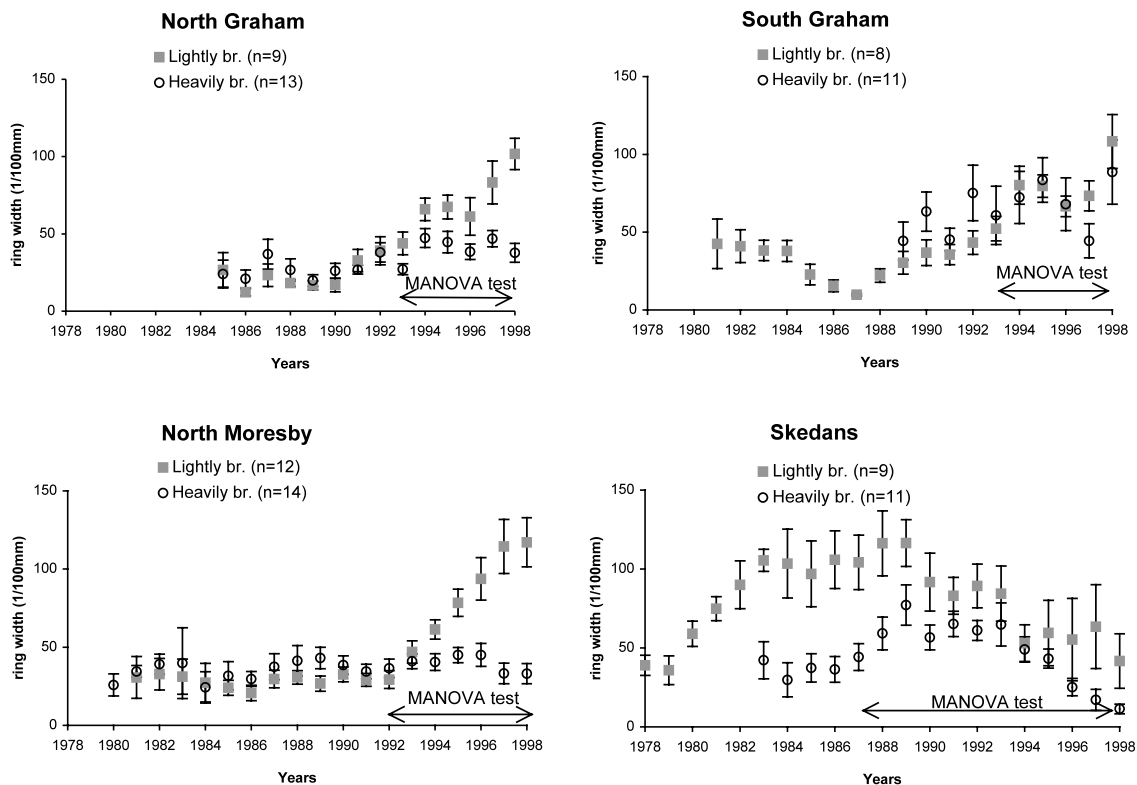


Fig. 6. Mean ring widths of lightly- and heavily-browsed young Western redcedars at the 4 sites (see Fig. 1) by year. Vertical bars are standard errors. Means are shown when at least 3 trees per category per site are present for a given year. The numbers (n =) in brackets are the total number of trees. Arrows indicate the period where all trees or all trees but one are present and where the multivariate repeated-measure tests have been done.

browsing will simply be a matter of time as observed for Sitka spruce (Vila and Guibal 2001). Finally, trees may differ chemically due to browsing history. Under this hypothesis, all young trees have the same initial defense potential but random browsing creates subsequent variation in palatability among them. First, evergreen species usually store more of their carbon and nutrient reserves in leaves than do deciduous trees (Chapin III 1980). Severe and repetitive defoliation of evergreens by mammals could reduce the carbon available for producing defense chemicals and increase the suitability of evergreens to herbivores, ultimately leading browsed trees into a vicious circle (Bryant et al. 1983, Tuomi et al. 1991, Raffa and Smalley 1995). Second, insect herbivory or mechanical wounding can to the contrary induce an increase monoterpene biosynthesis in several conifers (induced defenses, Marpeau et al. 1989, Lewinsohn et al. 1991, Lerdau et al. 1994, Litvak and Monson 1998). However, we failed to observe any induced defense to artificial defoliation in one- and two-year-old nursery-grown redcedars (Vourc'h, unpubl.).

The historical approach provided by dendrochronological analysis enables us to further evaluate the merits of the remaining hypotheses. Ring-width series provide

data for analyzing tree response to environmental stress (Cook and Kairiukstis 1990). By decreasing the annual growth of branches, and consequently leaf formation and photosynthetic rate, deer browsing has a strong effect on overall growth. When young trees are below the upper browsing limit, their radial growth is hampered. Thus, a low growth rate can be interpreted as a direct consequence of browsing (Vila et al. 2001).

When browsing pressure was high, as at clear-cut sites and on Skedans between 1990 and 1998, both tree categories showed the same growth pattern until the growth rate of lightly-browsed trees diverged and increased. This suggests that all trees experienced similar browsing pressure until lightly-browsed trees started to escape deer. This conclusion is strongly supported for North Graham and North Moresby, where lightly and heavily-browsed trees were the same age. Therefore neither growth divergence nor differences in defense level can be explained by age. The fact that (i) all trees were accessible to deer, (ii) herbivore defense (Berenbaum and Zangerl 1992) and monoterpene production are principally under genetic control (Hanover 1966, Merk et al. 1988, Bohlmann et al. 1998), (iii) Vourc'h et al. (submitted) found evidence for significant additive genetic variation for monoterpene production and

Table 1. MANOVA repeated-measures analyses of young Western redcedar ring width for the 4 sites. The years in brackets are the years included in the analyses. Years were chosen when data was available for all trees or all trees but one. P = p-value.

| Sites | Effect | Roy's greatest root | F value | Num DF ^a | Den DF ^b | P |
|------------------------------|---------------|---------------------|-----------|---------------------|---------------------|---------|
| North Graham (1993–1998) | Time | 1.76 | 5.28 | 5 | 15 | 0.005** |
| | Time × Browse | 1.30 | 3.91 | 5 | 15 | 0.018* |
| South Graham (1993–1998) | Time | 1.61 | 4.19 | 5 | 13 | 0.017* |
| | Time × Browse | 0.25 | 0.65 | 5 | 13 | 0.668 |
| North Moresby (1992–1998) | Time | 1.16 | 3.69 | 6 | 19 | 0.013* |
| | Time × Browse | 1.54 | 4.89 | 6 | 19 | 0.003** |
| Skedans (1987–1998) | Time | 11.41 | 7.26 | 11 | 7 | 0.007** |
| | Time × Browse | 2.34 | 1.49 | 11 | 7 | 0.306 |

^a Nm DF = Numerator Degree of Freedom.

^b Den DF = Denominator Degree of Freedom.

Table 2. P-values of LSMEANS tests between ring width of lightly- and heavily-browsed young Western redcedars at Skedans during the 1987–1998 period. Corrected p-values (P_c) are corrected for multiple tests with the procedure proposed by Simes (1986). We did $n = 12$ tests. Corrected p-values: $P_{c(j)} = P_{(j)}/j$.

| Years | Uncorrected p-values $P_{(j)}$ | Order of the p-values (j) | Corrected p-values $P_{c(j)}$ |
|-----------|--------------------------------|---------------------------|-------------------------------|
| 1987 | 0.003 | 2 | 0.018* |
| 1988 | 0.008 | 3 | 0.032* |
| 1989 | 0.039 | 5 | 0.094 |
| 1990–1996 | ≥ 0.129 | ≥ 6 | ≥ 0.256 |
| 1997 | 0.019 | 4 | 0.057 |
| 1998 | < 0.0001 | 1 | < 0.001 *** |

browsing intensity in common garden experiments on young Western redcedars, all suggest that ultimately only trees with greater chemical defense potential will escape deer. Once young trees start to escape deer by producing sufficiently concentrated defenses, they can produce more foliage, and allocate more resources to growth and defense. Young trees that do not have sufficient genetic potential to deter deer become caught in a circle of heavily browsing leading to lower defense as well as (Machida 1979, Bryant et al. 1983, Tuomi et al. 1991, Raffa and Smalley 1995).

At South Graham, lightly-browsed trees followed roughly the same pattern as at the other two clear-cut sites, but heavily-browsed trees were younger and had a higher and more variable growth rate. The main difference was that the divergence was not significant and growth seemed to decrease severely in 1987. We can only propose a speculative interpretation at this stage. An unknown local event around 1987, such as flooding, might have seriously hampered growth and killed the weakest trees, those that were the most heavily-browsed. This would explain the low growth rate in 1987 and why there were no heavily-browsed trees older than 10 years. The growth rate fluctuations suggest that browsing pressure has not been constant. Because the site was close to the main forest logging road and to the main town (Queen Charlotte City), hunting pressure and disturbance due to logging activities could lead to more variable browsing pressure. This interpretation would be consistent with the findings of Martin and Baltzinger (2002) on the relation between hunting pres-

sure, browse stress and amount of Western redcedar regeneration.

Low browsing pressure allows variation in growth and lower defenses

At Skedans, the absence of stunted, heavily-browsed trees that were typical of all other sites suggested that trunks and branches were formed during a period of low to moderate browsing pressure. This was consistent with earlier observations of low browsing pressure during the late 1980's (Rodway et al. 1988, J.-L. Martin, pers. obs.). As indicated by their growth curves (Fig. 6), lightly-browsed trees showed greater growth rates than did heavily-browsed ones during this period of low browsing pressure. The curves were parallel and lightly-browsed trees were older, suggesting that the difference in growth rate was more likely due to age than to better growth potential. This suggests that, under low browsing pressure, growth differences due to age, genetic or environmental factors are more apparent than they are under high browsing pressure.

Although we lack information on chemical composition of young trees on Skedans when browsing pressure was low, the comparison with the other sites gives us some information about the selective pressure caused by browsing. Young trees on Skedans had lower mono- and diterpene contents than trees from the other sites. This suggests that under low browsing pressure, selection against trees with low terpene concentration was

weaker, so trees with very low defense were still part of the pool. This would be consistent with the results of Vourc'h et al. (2001) showing that seedlings and mature Western redcedars from Haida Gwaii, which were never exposed to deer, tended to be less well defended than their mainland counterparts. However, in the absence of replicate sites, we cannot rule out the effect of environment to explain the lower defenses observed in redcedars on Skedans. There, young trees grow under the canopy where shading and relatively better soils can limit carbohydrate production for secondary metabolites (Gleizes et al. 1980, Mihaliak and Lincoln 1985, Muzika et al. 1989, Bryant et al. 1991, Wainhouse et al. 1998).

Conclusion

Intraspecific variation in damage by deer to young Western redcedars was correlated with variation in secondary metabolite content. Furthermore, young trees were not all equally susceptible to browsing: those with superior potential for deploying chemical defenses escaped deer on Haida Gwaii; those without the ability to express sufficient concentrations of deterrent compounds become mired in an endless cycle of browsing and slow growth. Through an integration of chemical and dendrochronological analyses, we have shown that short-term variations in chemical defense have readily observable long-term effects on plant growth and likely on plant fitness.

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References

Agrawal, A. A. and Karban, R. 1999. Why induced defenses may be favored over constitutive strategies in plants. – In:

- Tollrian, R. and Harvell, C. D. (eds), *The ecology and evolution of inducible defenses*. Princeton Univ. Press, pp. 45–61.
- Allen, S. E. 1989. Analysis of vegetation and other organic materials. – In: Allen, S. E. (ed.), *Chemical analysis of ecological materials*, 2nd ed. Blackwell Scientific Publications, pp. 46–61.
- Banner, A., Pojar, J., Schwab, J. W. and Trowbridge, R. 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. – In: Scudder, G. G. E. and Gessler, N. (eds), *The outer shores*. Queen Charlotte Islands Museum Press, Skidegate, Haida Gwaii, BC, Canada, pp. 261–279.
- Banthorpe, D. and Charlwood, V. 1980. The terpenoids. – In: Bell, E. and Charlwood, V. (eds), *Encyclopedia of plant physiology*, Berlin. Vol. 12B., pp. 185–220.
- Berenbaum, M. R. and Zangerl, A. R. 1992. Genetics of secondary metabolism and herbivore resistance in plants. – In: Rosenthal, G. A. and Berenbaum, M. R. (eds), *Herbivores: their interactions with secondary plants metabolites*. In: *Evolutionary and ecological processes*. Vol. II, 2nd. Academic Press, pp. 415–438.
- Berteaux, D., Crête, M., Huot, J. et al. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. – *Oecologia* 115: 84–92.
- Bohlmann, J., Meyer-Gauen, G. and Croteau, R. 1998. Plant terpenoid synthases: molecular biology and phylogenetic analysis. – *Proc. Natl. Acad. Sci. USA* 95: 4126–4133.
- Boira, H. and Blanquer, A. 1998. Environmental factors affecting chemical variability of essential oils in *Thymus piperella* L. – *Biochem. Syst. Ecol.* 26: 811–822.
- Bryant, J. P. and Julkunen-Tiitto, R. 1995. Ontogenetic development of chemical defense by seedling resin birch: energy cost of defense production. – *J. Chem. Ecol.* 21: 883–896.
- Bryant, J. P. and Kuropat, P. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. – *Annu. Rev. Ecol. System.* 11: 261–285.
- Bryant, J. P., Chapin, F. S. and Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. – *Oikos* 40: 357–368.
- Bryant, J. P., Kuropat, P. J., Reichardt, P. B. and Clausen, T. P. 1991. Controls over the allocation of resources by woody plants to chemical antiherbivore defense. – In: Palo, R. T. and Robbins, C. T. (eds), *Plant defenses against mammalian herbivory*. CRC Press Inc., pp. 83–102.
- Carl, G. C. and Guiguet, C. J. 1972. Alien animals in British Columbia. – B.C. Provincial Museum Handbook No. 14, Victoria B.C.
- Chapin III, F. S. 1980. The mineral nutrition of wild plants. – *Annu. Rev. Ecol. System.* 11: 233.
- Chapin III, F. S., Bryant, J. P. and Fox, J. F. 1985. Lack of induced chemical defense in juvenile Alaska woody plants in response to simulated browsing. – *Oecologia* 67: 457–459.
- Coates, K. D., Pollack, J. C. and Barker, J. E. 1985. The effect of deer browsing on the early growth of three conifer species in the Queen Charlotte Islands. – In: *Research Report No. RR85002-PR*. BC Ministry of Forest, Canada.
- Coley, P. D., Bryant, J. P. and Chapin III, F. S. 1985. Resource availability and plant antiherbivore defense. – *Science* 230: 895–899.
- Connolly, G. E., Ellison, B. O., Fleming, J. W. et al. 1980. Deer browsing of Douglas-fir trees in relation to volatile terpene composition and in vitro fermentability. – *Forest Sci.* 26: 179–193.
- Cook, E. R. and Kairiukstis, L. A. 1990. *Methods of dendrochronology. Applications in the environmental sciences*. – Kluwer Academic Press.
- Cooper, S. M. and Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. – *Oecologia* 67: 142–143.

- Cowan, I. M. 1989. Birds and mammals on the Queen Charlotte Islands. – In: Scudder, G. G. E. and Gessler, N. (eds), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, Haida Gwaii, BC, Canada, pp. 175–187.
- Crawley, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. Studies in ecology Volume 10. – Blackwell Scientific Publications.
- Danell, K., Gref, R. and Yazdani, R. 1990. Effects on mono- and diterpenes in Scots Pine needles on moose browsing. – *Scand. J. For. Res.* 5: 535–539.
- Dauffresne, T. and Martin, J.-L. 1997. Changes in vegetation structure and diversity in relation to the presence of a large herbivore: the impact of introduced black-tailed deer on old-growth forests in Haida Gwaii (Queen Charlotte Islands). – In: Annual scientific Report 7. Laskeek Bay Conservation Society, Queen Charlotte City, BC, Canada.
- Dimock II, E. J., Silen, R. R. and Allen, V. E. 1976. Genetic resistance in Douglas-fir to damage by Snowshoe Hare and Black-tailed Deer. – *Forest Sci.* 22: 106–121.
- Duncan, A. J., Hartley, S. E. and Iason, G. R. 1994. The effect of monoterpene concentrations in Sitka spruce (*Picea sitchensis*) on the browsing behaviour of red deer (*Cervus elaphus*). – *Can. J. Zool.* 72: 1715–1720.
- Edenius, L. 1993. Browsing by moose on scots pine in relation to plant resource availability. – *Ecology* 74: 2261–2269.
- Elliott, S. and Loudon, A. 1987. Effects of monoterpene odors on food selection by Red deer calves (*Cervus elaphus*). – *J. Chem. Ecol.* 13: 1343–1349.
- Ende, C. N. von 1993. Repeated-measures analysis: growth and other time-dependant measures. – In: Scheiner, S. M. and Gurevitch, J. G. (eds), Design and analysis of ecological experiments. Chapman & Hall, pp. 113–137.
- Fritts, H. C. 1976. Tree-rings and climate. – Academic Press.
- Fritz, R. S., Hochwender, C. G., Lewkiewicz, D. A. et al. 2001. Seedling herbivory by slugs in a willow hybrid system: developmental changes in damage, chemical defense, and plant performance. – *Oecologia* 129: 87–97.
- Gillon, D., Houssard, C. and Joffre, R. 1999. Using near-infrared reflectance spectroscopy to predict carbon, nitrogen and phosphorus content in heterogeneous plant material. – *Oecologia* 118: 173–182.
- Gleizes, M., Pauly, G., Bernard-Dagan, C. and Jacques, R. 1980. Effects of light on terpene hydrocarbon synthesis in *Pinus pinaster*. – *Physiol. Plant.* 50: 16–20.
- Hanley, T. A. 1992. Predictiong digestibility protein and digestible dry matter in tannin-containing forages consumed by ruminants. – *Ecology* 73: 537–541.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). – *Oikos* 79: 209–218.
- Hanover 1966. Genetics of terpenes. I. Gene control of monoterpene levels in *Pinus monticola* Dougl. – *Heredity* 21: 73–84.
- Harper, J. L. 1977. Population biology of plants. – Academic Press.
- Joffre, R., Gillon, D., Dardenne, P. et al. 1992. The use of near-infrared reflectance spectroscopy in litter decomposition studies. – *Ann. Sci. For.* 49: 481–488.
- Karban, R. and Baldwin, I. T. 1997. Induced responses to herbivory. – The Univ. of Chicago Press.
- Karban, R. and Thaler, J. S. 1999. Plant phase change and resistance to herbivory. – *Ecology* 80: 510–517.
- Kearsley, M. J. C. and Whitham, T. G. 1989. Developmental changes in resistance to herbivory: implications for individuals and populations. – *Ecology* 70: 442–444.
- Kielland, K. and Bryant, J. P. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. – *Oikos* 82: 377–383.
- Lawler, I. R., Foley, W. J., Pass, D. M. and Handasyle, K. 1998. Intraspecific variation in *Eucalyptus* secondary metabolites determines food intake by folivorous marsupials. – *Oecologia* 116: 160–169.
- Lerdau, M., Litvak, M. and Moson, R. 1994. Plant chemical defense: monoterpenes and the growth-differentiation balance hypothesis. – *Trends Ecol. Evol.* 9: 58–61.
- Lewinsohn, E., Gijzen, M. and Croteau, R. 1991. Defense mechanisms of conifers. Differences in constitutive and wound-induced monoterpene biosynthesis among species. – *Plant Physiol.* 96: 44–49.
- Litvak, M. E. and Monson, R. K. 1998. Patterns of induced and constitutive monoterpene production in conifer needles in relation to insect herbivory. – *Oecologia* 114: 531–540.
- Loreau, M. and de Mazancourt, C. 1999. Should plants in resource-poor environments invest more in antiherbivore defence? – *Oikos* 87: 195–200.
- Löyttyniemi, K. 1985. On repeated browsing of Scots pine saplings by mosse (*Alces alces*). – *Silva Fenn.* 19: 387–391.
- Machida, S. 1979. Differential use of willow species by moose in Alaska. – Univ. of Alaska Fairbanks, Alaska, USA.
- Maddox, G. D. and Cappucino, N. 1986. Genetic determination of plant susceptibility to a herbivorous insect depends on environmental context. – *Evolution* 40: 863–866.
- Marpeau, A., Walter, J., Launey, J. et al. 1989. Effects of wounds on the terpene content of twigs of maritime pine (*Pinus pinaster* Ait.): 2. Changes in the volatile terpene hydrocarbon composition. – *Trees* 3: 220–226.
- Martin, J.-L. and Baltzinger, C. 2002. Interaction between deer browse, deer predation risk, and tree regeneration. – *Can. J. Forest Res.* 32: 000–000.
- Martin, J.-L. and Dauffresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. – In: Wiggins, G. (ed.), Proc. Cedar Symp., Victoria, BC, Canada, South Moresby Forest Replacement Account., pp. 69–89.
- Martin, J.-L., Gaston, A. J. and Hitier, S. 1995. The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). – *Oikos* 72: 115–131.
- McArthur, C., Robbins, C. T., Hagerman, A. E. and Hanley, T. A. 1993. Diet selection by ruminant generalist browser in relation to plant chemistry. – *Can. J. Zool.* 71: 2236–2243.
- McInnes, P., Naimen, R. J., Pastor, J. and Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royal, Michigan, USA. – *Ecology* 73: 2059–2075.
- Merk, L., Kloos, M., Schönwitz, R. and Ziegler, H. 1988. Influence of various factors on quantitative composition of leaf monoterpenes of *Picea abies* (L.) Karst. – *Trees* 2: 45–51.
- Mihaliak, C. A. and Lincoln, D. E. 1985. Growth pattern and carbon allocation to volatile leaf terpenes under nitrogen-limiting conditions in *Heterothea subaxillaris* (Asteraceae). – *Oecologia* 66: 423–426.
- Millet, Y., Jouglard, J., Steinmetz, M. D. et al. 1981. Toxicity of some essential plant oils. Clinical and experimental study. – *Clin. Toxicol.* 18: 1485–1498.
- Muzika, R. M., Pregitzer, K. S. and Hanover, J. W. 1989. Changes in terpene production following nitrogen fertilization of grand fir (*Abies grandis* (Dougl.) Lindl.) seedlings. – *Oecologia* 80: 485–489.
- Nagy, J. G., Steinhoff, H. W. and Ward, G. M. 1964. Effects of essential oils of Sagebrush on deer rumen microbial function. – *J. Wildl. Manage.* 28: 785–790.
- Oh, H. K., Sakai, T., Jones, M. B. and Longhurst, W. M. 1967. Effect of various essential oils isolated from Douglas fir needles upon sheep and deer rumen microbial activity. – *Appl. Microbiol.* 15: 777–784.
- Pass, D. M., Foley, W. J. and Bowden, B. 1998. Vetebrate herbivory on *Eucalyptus*-Identification of specific feeding deterrents for common ringtail possums (*Pseudocheirus peregrinus*) by bioassay-guided fractionation of *Eucalyptus ovata* foliage. – *J. Chem. Ecol.* 24: 1513–1527.
- Payette, S. 1987. Recent porcupine expansion at tree line: a dendroecological analysis. – *Can. J. Zool.* 65: 551–557.

- Personius, T. L., Wambolt, C. L., Stephens, J. R. and Kelsey, R. G. 1987. Crude terpenoid influence on Mule deer preference for Sagebrush. – *J. Range Manag.* 40: 84–88.
- Pojar, J., Lewis, T., Roemer, H. and Wilford, D. J. 1980. Relationships between introduced Black-tailed deer and the plant life in the Queen Charlotte Islands, British Columbia. – In: Unpublished Report BC Ministry of Forest, Smithers, BC, Canada.
- Provenza, F. D., Pfister, J. A. and Cheney, C. D. 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. – *J. Range Manag.* 45: 36–45.
- Raffa, K. F. and Smalley, E. B. 1995. Interactions of pre-attack and induced monoterpene concentration in host conifer defense against bark beetle-fungal complexes. – *Oecologia* 102: 285–295.
- Raffa, K. F., Krause, S. C. and Reich, P. B. 1998. Long-term effects of defoliation on red pine suitability to insects feeding on diverse plant tissues. – *Ecology* 79: 2352–2364.
- Roche, B. M. and Fritz, R. S. 1997. Genetics of resistance of *Salix sericea* to a diverse community of herbivores. – *Evolution* 51: 1490–1498.
- Rodway, M. S., Lemon, M. J. F. and Kaiser, G. W. 1988. British Columbia seabird colony inventory: report # 1-East coast Moresby Island. – In: Technical report series No. 50 Canadian wildlife Service, Pacific and Yukon Region, BC, Canada.
- Rousi, M., Tahvanainen, J., Henttonen, H. et al. 1997. Clonal variation in susceptibility of white birches (*Betula* spp.) to mammalian and insect herbivores. – *Forest Sci.* 43: 396–402.
- Rudloff, E. von and Lapp, M. S. 1979. Populational variation in the leaf oil terpene composition of western red cedar, *Thuja plicata*. – *Can. J. Bot.* 57: 476–479.
- SAS 1999. Release 8.00. – SAS Institute Inc., NC, USA.
- Schweingruber, F. H. 1988. Tree-rings, Basics and applications of dendrochronology. – D. Reidel Publ. Company, Dordrecht.
- Schweingruber, F. H. 1996. Tree-rings and environment. Dendroecology. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research. – Paul Haupt, Berne, Stuttgart.
- Shenk, J. S. and Westerhaus, M. O. 1991a. ISI NIRS-2 software for near-infrared instruments. – Infrasoftware International, Silverspring.
- Shenk, J. S. and Westerhaus, M. O. 1991b. Population definition, sample selection, and calibration procedures for near-infrared reflectance spectroscopy. – *Crop Sci.* 31: 469–474.
- Silen, R. R., Randall, W. L. and Mandel, N. L. 1986. Estimates of genetic parameters for deer browsing of Douglas-fir. – *Forest Sci.* 32: 178–184.
- Simes, R. J. 1986. An improved Bonferroni procedure for multiple tests of significance. – *Biometrika* 73: 751–754.
- Snyder, M. A. 1993. Interactions between Abert's squirrel and Ponderosa pine: the relationship between selective herbivory and host plant fitness. – *Am. Nat.* 141: 866–879.
- Stromayer, K. A. and Warren, R. J. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? – *Wildl. Soc. Bull.* 25: 227–234.
- Suomela, J., Suominen, O. and Törvi, M. 1997. Variation in quality of mountain birch and tea-leaved willow for mammal and insect herbivores: differences among trees, among sites and between tree species. – *Ecography* 20: 224–232.
- Swihart, R. K. and Bryant, J. P. 2001. Importance of biogeography and ontogeny of woody plants in winter herbivory by mammals. – *J. Mamm.* 82: 1–21.
- Tallamy, D. W. and Raupp, M. J. 1991. Phytochemical induction by herbivores. – J. Wiley & Sons, Inc, New York.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. – *J. Wildl. Manage.* 29: 486–489.
- Tuomi, J., Fagerström, T. and Niemelä, D. W. 1991. Carbon allocation, phenotypic plasticity, and induced defenses. – In: Tallamy, D. W. and Raupp, M. J. (eds), Phytochemical induction by herbivores. J. Wiley & Sons, Inc, New York, pp. 85–104.
- Van Soest, P. J. 1963. Use of detergent in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. – *J. Assoc. Off. Anal. Chem.* 46: 829–835.
- Vila, B. and Guibal, F. 2001. Browsing influence in the understory of Haida Gwaii (British Columbia) forests using dendrochronology. – *Dendrochronologia* in press.
- Vila, B., Keller, T. and Guibal, F. 2001. Influence of browsing cessation on *Picea sitchensis* radial growth. – *Ann. For. Sci.* 58: 853–859.
- Villalba, J. J. and Provenza, F. D. 2000. Roles of flavor and reward intensities in acquisition and generalization of food preferences: do strong plant signals always deter herbivory? – *J. Chem. Ecol.* 26: 1911–1922.
- Vourc'h, G., de Garine-Wichatitsky, M., Labbé, A. et al. in press. Monoterpene effect on feeding choice by deer. – *J. Chem. Ecol.*
- Vourc'h, G., Martin, J.-L., Duncan, P. et al. 2001. Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. – *Oecologia* 126: 84–93.
- Vourc'h, G., Russell, J. and Martin, J.-L. submitted. Linking deer browsing, monoterpene production, and genetic variation: case study in *Chamaecyparis nootkatensis* and *Thuja plicata* (Cupressaceae).
- Wainhouse, D., Ashburner, R., Ward, E. and Rose, J. 1998. The effect of variation in light and nitrogen on growth and defence in young Sitka spruce. – *Funct. Ecol.* 12: 561–572.
- Waterman, P. G. and Mole, S. 1994. Methods in ecology. Analysis of phenolic plant metabolites. – Blackwell Scientific Publications.
- Watkinson, A. R. 1986. Plant population dynamics. – In: Crawley, M. J. (ed.), Plant ecology. Blackwell Scientific Publications, pp. 137–184.
- Welch, B. L., MacArthur, E. D. and Davis, J. N. 1981. Differential preference for wintering mule deer for accessions of big sagebrush and for black sagebrush. – *J. Range Manag.* 34 (5): 409–411.