

RESEARCH GROUP ON INTRODUCED SPECIES - ABSTRACTS OF PAPERS PUBLISHED IN PEER-REVIEWED JOURNALS

BIRDS:

(1) Gaston, Anthony J., Jean-Louis Martin, and Sylvain Allombert. 2005. **Oceanography affects breeding biology for the terrestrial avifauna of a temperate coastal rainforest.** *Avian Conservation and Ecology* 1: 4. [online] URL: <http://www.ace-eco.org/vol1/iss1/art4/>

We studied the timing of breeding and juvenile/adult ratios among songbirds in temperate rainforest over four years on the Haida Gwaii (Queen Charlotte Islands) archipelago, British Columbia. Timing of breeding, measured by the first capture of juveniles, or by direct observations of hatching, varied by approximately 19 d between the earliest (1998) and latest (1999) year. In 1998, the proportion of juveniles among birds trapped increased steeply as soon as young birds began to appear. In other years the rate of increase was slower. In 1999, the peak proportions of hatching year individuals among foliage gleaning insectivores (Orange-crowned and Townsend's warblers and Golden-crowned Kinglet) were lower than in other years, with almost no young Orange-crowned Warblers at all captured. May air temperatures in Haida Gwaii in 1999 were the lowest in 20 years, while those in 1998 were above average: the other two years were closer to normal, although 2001 was almost as cold as 1999. These temperatures closely followed patterns of Sea Surface Temperatures created by the 1997/98 El Niño (warm) event and the subsequent strong La Niña (cool) event. Although rainfall also differed among years, the pattern of variation in timing of breeding and in the proportion of hatching year individuals trapped, fitted the temperature data better. We conclude that SST changes off northern British Columbia, through their effects on air temperatures, had a strong effect on the breeding of forest birds, to the point of causing nearly complete reproductive failure for one species in 1999.

(2) Allombert, Sylvain, Anthony J. Gaston and Jean-Louis Martin. 2005. **A natural experiment on the impact of overabundant deer on songbird populations.** *Biological Conservation* 126 (2005) 1–13.

Declines in songbird populations have been identified both in North America and in Europe. Several explanations have been proposed but few studies have evaluated the possibility that deer overabundance might affect songbird populations, and none have identified general rules to predict such an impact. We used a group of islands in the Haida Gwaii archipelago (British Columbia, Canada), where islands without deer co-exist near islands with deer, as a natural experiment to test if

the dependence of each species on understorey vegetation was a good predictor of deer impact. Forest bird assemblages were compared on six islands that either had no deer, had deer for less than 20 years or for more than 50 years, and on an enlarged set of 31 islands for which vegetation data and an index of deer impact were available. In the six islands data-set, songbird abundance on islands browsed for more than 50 years was 55–70% lower than on deer-free islands. There was a significant decrease in alpha diversity on islands browsed by deer, but gamma diversity remained unchanged. Bird species with the highest dependence on understorey vegetation were most affected and their abundance decreased by 93%. Bird communities flipped from being 73% dependant on understorey vegetation on deer-free islands to 79% not dependant on understorey vegetation on islands with deer for more than 50 years. A canonical correspondence analysis on the 31 island data-set allowed us to further separate the interactions between bird abundance and distribution, vegetation features and deer presence. We propose that deer overabundance results in a decrease in songbird habitat quality through decreased food resources and nest site quality and may explain part of current continental-scale decreases in songbird populations.

(3) Martin, Jean-Louis and Mathieu Joron. 2003. **Nest predation in forest birds: influence of predator type and predator's habitat quality.** *Oikos* 102: 641–653.

We used the introduction of a generalist nest predator, the red squirrel *Tamiasciurus hudsonicus*, and of a large herbivore, the Sitka black-tailed deer *Odocoileus hemionus sitkensis*, to the islands of Haida Gwaii (Queen Charlotte Islands, British Columbia, Canada) to study how predator assemblage and habitat quality and structure influenced nest predation in forest birds. We compared losses of natural nests to predators on islands with and without squirrels. We selected nine islands with or without squirrel or deer and used 506 artificial nests put on the ground or in shrubs to further analyse variation of nest predation with predator assemblage and habitat quality for the predators. For both natural and artificial nests predation risk was higher in presence of squirrels. But predation risk varied within island categories. In presence of squirrels it was highest in stands with mature conifers where it fluctuated from

year to year, in response to fluctuations in squirrel abundance. Vegetation cover around the nest had little effect on nest predation by squirrels. Where squirrels were absent, nest predation concentrated near predictable food sources for corvids, the main native predators, and increased with decreasing vegetation cover, suggesting that removal of the vegetation by deer increased the risk of predation by native avian nest predators that use visual cues. Predation risk in these forests therefore varies in space and time with predator composition and with quality of the habitat from the predators' perspective. This temporal and spatial variation in predation risk should promote trade-offs in the response of birds to nest predation, rather than fine-tuned adaptations to a given predation pattern.

B: FORESTRY

(4) Martin, Jean-Louis and Christophe Baltzinger. 2002. **Interaction among deer browsing, hunting, and tree regeneration.** *Can. J. For. Res.* 32: 1254–1264. The intentional removal or addition of species or specific human impacts on ecosystems trigger changes that can help us understand species interactions. In many temperate forests, deer populations are increasing and so is the need to understand how they influence ecosystems. We took advantage of the introduction of Sitka black-tailed deer (*Odocoileus hemionus sitchensis* Merriam) to the Queen Charlotte Islands (Haida Gwaii), British Columbia, Canada, to study how hunting pressure affects the impact of deer on tree regeneration after logging. We show that although the regeneration of western redcedar (*Thuja plicata* Donn ex D. Don) is drastically reduced in presence of deer, regeneration is better and browsing stress lower, in areas where deer are more exposed to hunting. Similar effects of accessibility for hunters are observed on browsing stress of Sitka spruce (*Picea sitchensis* (Bong.) Carrière). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is not significantly affected, and its regeneration is not correlated to hunting. We suggest that the effect of hunting on tree regeneration could be explained by the incidence of hunting on deer behaviour rather than by the actual number of deer killed by hunters. These results suggest that the future occurrence of redcedar stands in second-growth forests on this archipelago may depend on the amount and distribution of deer hunting.

(5) Vila, Bruno, Thierry Keller and Frédéric Guibal. 2001. **Influence of browsing cessation on *Picea sitchensis* radial growth.** *Ann. For. Sci.* 58 (2001) 853–859.

Picea sitchensis is an ecological and economical component of North America north temperate rain forest. In Haida Gwaii which is one of the most productive forest land of British Columbia archipelago (Canada), it is an important and a valuable commercial species. The present study aims at precisising [*sic*]deer browsing consequences on growth regeneration of *Picea sitchensis*. Using ring-width series, an empirical model is built which describes browsing impact on radial growth and removal of these pressure. Taking into account deer pressure and browsing upper limit when building predictive height growth models proves valuable for comparing growth pattern of different species under browsing pressure and deducing changes in forest dynamics.

(6) Vila, Bruno, Frédéric Guibal. 2001. **Assessing browsing influence in forest understory using dendrochronology on Haida Gwaii archipelago (British Columbia, Canada).** *Dendrochronologia* 19: 139 – 151.

The impact of introduced deer (*Odocoileus hemionus sitchensis*) on understory vegetation is assessed by analyzing browsed and non browsed individuals of a shrub (*Gaultheria shallon*) and a tree species (*Picea sitchensis*). Browsing is expressed in terms of morphology change, diameter growth patterns differences and traumatic anatomical characteristics occurrence on cross-sections. At the impacted site, an upper browsing limit at a height of 1.10 m is evidenced. Abrupt growth change associated with scars are evidenced on shrubs but deer impact on shrub growth is not directly assessed because of high inter-shrub variance among ring-width series. Deer impact can be assessed taking into account particular anatomical features as pith position, pith and stem form, wedging rings and scar occurrence for which impacted and non impacted populations differ statistically. Samples from the impacted population display non circular cross-sections with altered wood areas, eccentric piths and several discontinuous or wedging rings. As regards with spruce, browsing pressure decreases apical growth and induces at severely browsed individuals a shrubby port. Narrow ring patterns are caused by browsing; these patterns are followed by a sudden growth change occurring when herbivore pressure stops. That involves

a lengthening of the recruitment period in windthrows which results in a delay of the habitat closing processes.

(7) Vourc'h, Gwenaël, Bruno Vila, Dominique Gillon, José Escarré, Frédéric Guibal, Hervé Fritz, Thomas P. Clausen and Jean-Louis Martin. 2002. **Disentangling the causes of damage variation by deer browsing on young *Thuja plicata***. *Oikos* 98: 271–283.

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 defence 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 defences were able to escape deer. This suggests that selection by deer could occur on a long-lived tree.

(8) Vila, Bruno, Gwenaël Vourc'h, Dominique Gillon, Jean-Louis Martin, Frédéric Guibal. 2002. **Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach**. *Trees* 16: 488–496

We combined chemical and dendroecological analyses to understand the mechanisms that are involved in escaping deer browse by young Sitka spruce (*Picea sitchensis*) exposed to browsing by Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Haida Gwaii (British Columbia, Canada). We compared chemical defences (terpenes), nutritive compounds (nitrogen, non-structural constituents, cellulose, and lignin), as well as age and radial growth of two young spruce categories growing side by side: (1) stunted spruces that were heavily browsed, shorter than the browse line, and (2) escaped spruces that were taller than the browse line but still browsed below the browse line. Escaped and stunted spruces did not differ in terpene concentrations, or in nutritive compound contents, suggesting that they had similar palatability. Escaped spruces were older than stunted spruces. Stunted and escaped trees had similar slow growth when young, suggesting no difference in initial browsing between the two spruce categories. For escaped spruce, there was a dramatic increase in radial growth at about 12–13 years old, suggesting that the apex of the trees had escaped deer browse. Because the two categories of spruces were equally accessible and did not differ in chemical defences or in nutritive compounds, and because escaped spruces were older than stunted trees and had a similar slow radial growth in their first 12–13 years, we conclude that morphological differences between stunted and escaped browsed trees are due to age and that it is only a matter of time before spruce escape deer on Haida Gwaii.

(9) Vila, Bruno, Franck Torre, Frédéric Guibal, Jean-Louis Martin. 2003. **Growth change of young *Picea sitchensis* in response to deer browsing**. *Forest Ecology and Management* 180: 413–424.

Taking advantage of the introduction of the black-tailed deer to the Queen Charlotte Islands (British Columbia, Canada), used dendrochronological analyses to understand the consequences of deer browsing on Sitka spruce growth. We compared shape, radial growth, height growth and age of young spruce in three sites. We identified two types of trees growing side by (1) stunted and heavily browsed spruce, smaller than the browsing limit and (2) escaped spruce that were taller than the browsing limit but still browsed in their lower

part. The compact and heavily ramified shape in stunted spruce was the result of repeated and intense browsing. In escaped spruce this was also the case below the browsing limit (1:16m_ 0:07 m), in sharp contrast with the normal shape that escaped spruce resumed above the browsing limit. We show that the release of browsing pressure, once the tree reaches the browsing limit, is characterised by an abrupt increase in radial growth. Before release, trees show growth stagnation characterized by narrow rings (0.5 mm per year) and small annual height increments (<5 cm per year). After release, trees show a growth stabilisation characterised by wider rings (3 mm per year) and larger annual height increments (20 cm per year). We use this pattern to estimate frequency and age at release and their possible variation over time. Differences between stunted and escaped spruce are highly significant and indicate that, despite of browsing, most if not all will ultimately reach the browsing limit and escape. Heavy deer pressure (30 deer per km²) delays spruce sapling recruitment about 8 years. This delay varies in relation to site quality and seems to have increased over time, suggesting an increase browsing pressure.

(10) Vila, Bruno, Franck Torre, Jean-Louis Martin Frédéric Guibal. 2003. **Response of young *Tsuga heterophylla* to deer browsing: developing tools to assess deer impact on forest dynamics.** *Trees* 17: 547–553.

We used dendroecology to describe and understand the consequences of deer browsing on regenerating western hemlock (*Tsuga heterophylla*). We compared tree shape, growth rate, height and age at four different sites in Haida Gwaii (British Columbia, Canada) that had trees representative of the range of deer impact on trees: (1) trees showing no sign of browsing, (2) escaped trees which were still browsed below the browse line and (3) stunted and heavily browsed trees. Repeated and intense browsing resulted in the small size, compact heavily ramified shape of stunted trees and in the short compact and ramified lower branches of escaped trees. These contrasted with the shape of non-browsed trees, a shape that was also found in escaped trees above the browse line. Before release, all browsed trees experienced stagnation in growth characterised by narrow rings (0.3 mm/year) and a small annual height increment (2.5 cm/year). At release, growth rate increased and stabilised: rings were wider (1.3 mm/year) and annual height increments were greater (10.5 cm/year). Nonbrowsed trees had a mean ring-width of 1.3 mm/year and an annual height increment of 22 cm/year. Delay in tree recruitment

caused by deer varied from site to site. It had been about 15 years for the escaped trees and is estimated at 30–40 years for the stunted trees. Spatial variation in deer impact may reflect spatial variation of browsing pressure resulting from local differences in the availability of preferred forage or to differences in tree chemical defences/nutritional values.

(11) Vila, Bruno, Frank Torre, Frédéric Guibal, Jean-Louis Martin. 2004. **Can we reconstruct browsing history and how far back? Lessons from *Vaccinium parvifolium* Smith in Rees.** *Forest Ecology and Management* 201: 171–185.

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

(12) Vila, Bruno, Frédéric Guibal, Franck Torre and Jean-Louis Martin. 2004. **Assessing spatial variation in browsing history by means of fraying scars.** *Journal of Biogeography* 31: 987–995.

Aim: We used fraying scars to understand spatial variation in browsing history. Information on browsing history is an essential background in studies on the long-term effect of deer browsing on the flora and fauna and of its variation in space. **Location:** We focused on two small neighbouring islands of Haida Gwaii (British Columbia, Canada), Reef Island and South-Skedans Island, colonized by introduced black-tailed deer (*Odocoileus hemionus sitkensis*). **Methods:** We searched for sites where trees with fraying scars were clustered. We studied the trees that deer selected (species, size) and the characteristics of scars (number, position, size). Using a cross-dating procedure, we dated fraying scars with dendrochronology, obtaining an accurate estimate of the year the scar was formed. **Results:** On Reef Island, *Thuja plicata* was the tree species chosen for fraying. On South-Skedans Island, where *Thuja plicata* is missing, deer chose *Salix* sp. and *Alnus rubra*. Deer chose only trees with a circumference of less than 50 cm. About two to three fraying scars were recorded per tree. All of them extended between 30–40 and 70–80 cm from the ground and were between 5 and 6 cm in width. On Reef Island, 95% of the scars were formed during the last 50 years. On South-Skedans Island, 95% were formed over the last 10 years. Age distribution of scars showed a constant increase of the number of scars over time. It indicated that deer had colonized Reef Island 53 years prior to this study but were absent or rare on South-Skedans Island until 13 years prior to this study. **Main conclusions:** These results indicate different colonization dates and thus different length of browsing histories for the islands studied and provide the historical background necessary to analyse the involvement of deer in the current differences in the flora and fauna observed between islands.

(13) Vila, Bruno, Frédéric Guibal, Franck Torre and Jean-Louis Martin. 2005. **Can we reconstruct deer browsing history and how? Lessons from *Gaultheria shallon* Pursh.** *Ann. For. Sci.* 62: 153–162.

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.

(14) Vila, Bruno, Thierry Keller and Frédéric Guibal. 2001. **Influence of browsing cessation on *Picea sitchensis* radial growth.** *Ann. For. Sci.* 58: 853–859. *Picea sitchensis* is an ecological and economical component of North America north temperate rain forest. In Haida Gwaii which is one of the most productive forest land of British Columbia archipelago (Canada), it is an important and a valuable commercial species. The present study aims at precisising deer browsing consequences on growth regeneration of *Picea sitchensis*. Using ring-width series, an empirical model is built which describes browsing impact on radial growth and removal of these pressure. Taking into account deer pressure and browsing upper limit when building predictive height growth models proves valuable for comparing growth pattern of different species under browsing pressure and deducing changes in forest dynamics.

(15) Vourc'h, Gwenaël, Jean-Louis Martin, Patrick Duncan, José Escarré, Thomas P. Clausen. 2001. **Defensive adaptations of *Thuja plicatata* to ungulate browsing: a comparative study between mainland and island populations.** *Oecologia* 126: 84–93.

Forests on the Haida Gwaii (HG) archipelago (British Columbia, Canada) evolved for about 10,000 years in the absence of large-mammal browsing. The introduction of black-tailed deer (*Odocoileus hemionus sitkensis*) from the mainland prior to 1901 provides an opportunity to evaluate changes in the adaptive defensive responses of plants to herbivory. We compared (1) food choice by deer and (2) chemical defence (terpene concentrations) between HG and mainland red cedars (*Thuja plicata*) using (1) nursery-grown seedlings never exposed to deer, (2) branches from trees that grew before the introduction of deer (“old trees”) and (3) saplings exposed to deer herbivory on the mainland and on HG. We used the first two plant categories to test the hypothesis that plants that evolve

under low herbivory levels have lower anti-herbivore defences. We used saplings to study the consequences of the dramatic increase in browsing on HG. During food experiments, deer preferred HG seedlings and old tree branches compared to those from the mainland. Total monoterpene concentrations were much higher than diterpene concentrations in all plant categories. Within plant categories, multivariate analysis showed that terpene profiles differed significantly between HG and mainland red cedars: HG seedlings and old trees had lower monoterpene levels. These results suggest that some monoterpenes may be determinants of deer food choice and that the defences of HG plants are less effective than those of mainland plants. The deer used branches from HG and mainland saplings indiscriminately. However, terpene profiles differed significantly between HG and mainland saplings, with multivariate analysis suggesting a higher defensive response in browsed HG saplings. Monoterpene profiles were different in lightly and heavily browsed saplings from HG, suggesting that under the current browsing regime, individuals with the greatest constitutive defences, or with greatest potential for induced defences, grow better and are selected on HG.

(16) Vourec'h, Gwenaël, Michel DE Garine-Wichatitsky, Alice Labbe, Dimitri Rosolowski, Jean-Louis Martin and Hervé Fritz. 2002. **Monoterpene effect on feeding choice by deer.** *Journal of Chemical Ecology*. 28, No. 12.

A previous study showed that Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) consumption was negatively correlated with monoterpene content in western redcedar (*Thuja plicata*). To test whether these monoterpenes were deterrent to Sitka black-tailed deer, we performed feeding choice experiments with four hydrocarbon (sabinene, myrcene, α -pinene, and *d* C *l*-limonene) and one oxygenated (α , β -thujone) monoterpene solution at their highest natural concentration in western redcedar foliage. To test whether deer response was species specific, we ran similar experiments on European roe deer (*Capreolus capreolus*) and rusa deer (*Cervus timorensis russa*). In all experiments, monoterpenes were repellent. Solutions with α , β -thujone, the major monoterpene in redcedar leaves, were the most repellent of the solutions tested. We then analyzed how black-tailed and roe deer responded to (1) an increase in concentration of the monoterpenes with the weakest repellent effects (hydrocarbon monoterpenes) and (2) a decrease in concentration of the monoterpene with strongest effect (α , β -thujone). Repellency tended to increase with

concentration for hydrocarbon monoterpenes, but remained strong for α , β -thujone. As wild deer regularly feed on plants containing monoterpenes, this raises the question as to how the animals deal with these molecules.

(17) Vourec'h, Gwenaël, J. Russell, and J.-L. Martin. 2002. **Linking deer browsing and Terpene production among genetic identities in *Chamaecyparis nootkatensis* and *Thuja plicata* (Cupressaceae).** *Journal of Heredity* 2002: 93(5).

To investigate whether differential herbivore browsing reflects genetic variation in plant defense expression, variation in needle terpenes and damage caused by black-tailed deer (*Odocoileus hemionus*) was analyzed on yellow-cedar (*Chamaecyparis nootkatensis*) and western redcedar (*Thuja plicata*). In a 100-genet yellowcedar population, three genets that were heavily browsed and had extremely low levels of monoterpenes (0–0.36% dry matter), sesquiterpenes, and diterpenes were compared to unbrowsed genets (0.85–3.83% monoterpenes in dry matter). These differences were maintained in individuals protected from browsing, suggesting genetically based variation in constitutive terpene production. In western redcedar, heavily browsed trees had significantly lower total monoterpene concentrations (1.69% dry matter) than lightly browsed trees (3.32% dry matter). One heavily browsed tree expressed no monoterpenes. No differences were found for diterpenes. In both species, the genotypes with extremely low monoterpene concentrations came from the same openpollinated families.

(18) Vourec'h, Gwenaël, Bruno Vila, Dominique Gillon, José Escarré, Frédéric Guibal, Hervé Fritz, Thomas P. Clausen and Jean-Louis Martin. 2002. **Disentangling the causes of damage variation by deer browsing on young *Thuja plicata*.** *Oikos* 98: 271–283.

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 defences were able to escape deer. This suggests that selection by deer could occur on a long-lived tree.

(19) Vourc'h, Gwenaël, John Russell, Dominique Gillon and Jean-Louis Martin. 2004. **Short-term effect of defoliation on terpene content in *Thuja plicata***. *Ecoscience* 10: 161-167.

Insect herbivory or mechanical wounding in conifers can induce monoterpene biosynthesis. Low risk of herbivory coupled with low availability of resources, are hypothesized to favour induced responses and to decrease constitutive defences. We studied the response to defoliation in western redcedars (*Thuja plicata*) from two regions: the Haida Gwaii archipelago, where mammalian herbivores were lacking until black-tailed deer were introduced at the end of the 19th century and previous work indicated that trees were less well defended, and the north coast mainland (British Columbia, Canada). We predicted that higher induced defences in the island population would compensate for reduced constitutive defences. We used one- and two-year-old nursery grown seedlings to test (1) if defoliation would cause a short-term chemical response in island western redcedar and (2) if mainland western redcedars that have always been exposed to large mammalian herbivores respond differently. The

concentration in monoterpene and diterpenes did not vary significantly in response to defoliation over the 5 day period analyzed regardless of the defoliation intensity or the plant's origin.

C: VEGETATION

(20) Stockton, Stephen A., Sylvain Allombert, Anthony J. Gaston, Jean-Louis Martin. 2005. **A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests**. *Biological Conservation* 126 : 118–128.

The introduction of Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) to Haida Gwaii (Queen Charlotte Islands, BC, Canada) in the late 19th century, provided an opportunity to understand the long-term effects of deer populations on the vegetation of temperate rain forests in the absence of their natural predators wolves (*Canis lupus* L.), and cougars (*Puma concolor* L.). Using seven small islands with different browsing histories (no deer, deer for <20 years, deer for >50 years), we tested the long-term forest edge habitats. Overall vegetation cover exceeded 80% in the lower vegetation layers on islands without deer and was less than 10% on the islands with deer for more than 50 years. Although overall plant species richness was similar on islands with or without deer, plant species richness at the plot scale (314m²) was reduced by 20–50% on islands with deer for >50 years. The differences were most pronounced for the species rich edge communities and among herb and shrub species. These results suggest that in the absence of predators, deer have the potential to greatly simplify the forest ecosystem.

(21) Gaston, Anthony J., Stephen A. Stockton and Joanna L. Smith. *In press*. **Species-area relationships and the impact of deer-browse in the complex phytogeography of the Haida Gwaii archipelago (Queen Charlotte Islands), British Columbia**. *Ecoscience*. We studied the biogeography of vascular plants on ten islands in Laskeek Bay, Haida Gwaii (Queen Charlotte Islands), British Columbia. The islands varied in size from 4.5-395 ha, and experienced a range of different browse pressures from introduced black-tailed deer (*Odocoileus hemionus*). We examined how island size interacted with browse pressure in determining the total species counts for individual islands. Numbers of plant species recorded increased with island area. The regression exponent for the log-log plot of species number on island area was 0.18: at the lower end of the range for such

exponents. Many species absent from islands <25 ha in area were characteristic of forest interiors and consequently, part of the increase in richness on larger islands probably was the result of increased forest interior area. Among the islands <25 ha in area, the normal species-area and species-isolation relationships were reversed, with smaller, more isolated, islands supporting more plant species than larger islands and, for a given area, more isolated islands supporting more species, than less isolated ones. This reversal of the normal trend appears to be the result of deer browsing. Small, isolated islands were the only islands without deer and were richer, especially in wildflowers, than the larger, less isolated islands. On large islands, total species complement remains as predicted by area because the effect of deer was mitigated by the presence of deer-free refugia on cliffs and in isolated gullies. We concluded that deer were a major factor structuring the island plant communities and continued protection of island habitats from introduced deer is essential to maintain the native flora of Haida Gwaii.