

Interaction among deer browsing, hunting, and tree regeneration

Jean-Louis Martin and Christophe Baltzinger

Abstract: 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.

Résumé : L'éradication ou l'addition d'espèces, ainsi que l'impact de certaines activités humaines sur les écosystèmes, peuvent déclencher des modifications dans les communautés permettant de mieux comprendre les mécanismes qui gouvernent les interactions entre espèces. Dans une grande partie des forêts tempérées nous assistons à un accroissement important des populations de cervidés; d'où la nécessité de mieux comprendre comment la présence du cerf influence les écosystèmes. Nous avons tiré profit de l'introduction du cerf à queue noire de Sitka (*Odocoileus hemionus sitchensis* Merriam) sur les îles de la Reine-Charlotte (Haida Gwaii) en Colombie-Britannique (Canada) pour étudier comment la pression de chasse exercée sur le cerf affecte la régénération naturelle des conifères après une coupe à blanc. En présence du cerf, la régénération du thuya géant (*Thuja plicata* Donn ex D. Don) est très fortement réduite, mais elle est meilleure dans les zones facilement accessibles aux chasseurs, zones où le taux d'abrutissement est par ailleurs plus faible. Nous avons observé la même chose avec l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière). La pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) n'est pas significativement affectée et la chasse n'a pas d'impact sur la régénération de cette essence. L'impact de la chasse sur la régénération des arbres est davantage dû à l'effet de la chasse sur le comportement du cerf qu'au nombre de cerfs tués par les chasseurs. L'avenir du thuya géant dans les forêts de seconde venue de cet archipel est donc fonction de l'intensité et de la distribution de la chasse.

Introduction

Interactions between species are an essential part of ecosystem functioning (Miller and Travis 1996; Bonsall and Hassel 1997). The removal or addition of species can give rise to complex chain reactions affecting other components of the ecosystem (Lindström et al. 1994; Abrams 1996; Simberloff and Stiling 1996; Hobbs and Mooney 1998). This effect is likely to be greater on islands where species have often evolved within a relaxed competitive context (Elton

1958; Vourc'h et al. 2001). The local overabundance of a native species that results from changes in land-use practices can also cause changes in the distribution and abundance of other species at different trophic levels and modify community structure (Waller and Alverson 1997). Such changes, when they can be documented, allow us to better understand ecosystem functions. Conversely, identifying how human-induced factors affect species distribution or abundance, may suggest means for mitigating undesired effects and help define management options.

Deer can significantly affect the absolute and relative abundance of woody species (Hough 1965; Ross et al. 1970; Anderson and Katz 1993; see review of Waller and Alverson 1997), and in extreme situations, the consequences of deer browsing will override the effect of climate or of other environmental variables (Boerner and Brinkman 1996).

Brown et al. (1999) have argued, on the basis of theoretical and empirical evidence, that deer abundance and deer habitat use are significantly affected when the animals face a risk from a predator. Their point was that the expected reduction in effects of the herbivore on the vegetation resulted more from behavioural changes in the animals facing such a risk (Swenson 1982; Kufeld et al. 1988; Nicholson et al.

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J.-L. Martin¹ and C. Baltzinger² Centre d'Écologie Fonctionnelle et Évolutive – Centre National de la Recherche Scientifique, 1919 route de Mende, 34293 Montpellier CEDEX 5, France.

¹Corresponding author
(e-mail: martin@cefe.cnrs-mop.fr).

²Present address: *Cemagref*, Institut de Recherche pour l'Ingénierie de l'Agriculture et de l'Environnement, Domaine des Barres, 45290 Nogent-sur-Vernisson, France.

1997; Kilgo et al. 1998) than from the actual number of animals killed. In a situation where hunters are the dominant predator, this suggests a negative correlation between browsing intensity or hunting pressure irrespective of the number of animals shot.

Pojar et al. (1980), Pojar and Banner (1984), Baltzinger and Martin (1998), and Martin and Daufresne (1999) have shown that the introduction of Sitka black-tailed deer (*Odocoileus hemionus sitchensis* Merriam) to the Queen Charlotte Islands (Haida Gwaii, British Columbia, Canada) has significantly affected the recruitment and coexistence of plant species in the forests of this archipelago. They demonstrated an absence of regeneration for one of the dominant tree species, western redcedar (*Thuja plicata* Donn ex D. Don), in primary forests where deer had become established (Martin et al. 1994; Martin and Daufresne 1999; see also Cornett et al. 2000 for *Thuja occidentalis* L. under high white-tailed deer (*Odocoileus virginianus* Zimmerman) browsing pressure). It has also been suggested (e.g., Pojar et al. 1980; Coates et al. 1985) that redcedar regeneration was similarly reduced by deer in secondary forests created by the cutting of primary forest. However, this has been the subject of debate (Wiggins 1999), as the assessment of the consequences of deer browsing for tree regeneration in clearcuts in the Queen Charlotte Islands was mainly based on technical studies done at a restricted geographic scale and for planted trees (see Bennett 1996).

Other than hunters, major predators that could regulate deer populations are absent from the Queen Charlotte Islands. Although fawns are preyed on by black bear (*Ursus americanus*), the bulk of adult deer predation results from human hunting. However, hunting is unevenly distributed in space and is concentrated in places readily accessible from the local communities (Pojar et al. 1980). Therefore, these islands provide a rather unique and simplified situation in which to investigate how hunting rate affects the impact of deer on natural tree regeneration after clear-cutting and to explore the predictions of Brown et al. (1999) on the consequences of fear on such an impact.

Materials and methods

The islands, their trees, and the deer

The Queen Charlotte Islands is an archipelago 80 km from the mainland of British Columbia, extending 300 km, north to south. There are two main islands (Graham to the north and Moresby to the south) and about 200 smaller islands of various sizes. The present physiography has been divided into three natural units: the Queen Charlotte Ranges in the west-southwest; the Skidegate Plateau, which runs northwest to southeast across the central part of the archipelago; and the Queen Charlotte Lowlands in the northwest (Sutherland Brown and Yorath 1989). The natural biotas have been divided into three major biogeoclimatic zones (Banner et al. 1989): the Coastal Western Hemlock zone, the Mountain Hemlock zone, and the Alpine Tundra zone. Part of the archipelago was free of ice throughout the last ice age providing refugia for certain organisms (Heusser 1989), including some endemic taxa (Foster 1989). The climate is humid and temperate. Precipitation is highest along the west coast (to 5000 mm) and lowest in the lowlands on the east

(to 1100 mm). Three species of tall conifers (typically >40 m height and >0.7 m diameter at breast height (DBH)) dominate the mature forests: western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar, and Sitka spruce (*Picea sitchensis* (Bong.) Carrière). The first two are partially replaced at higher altitudes by mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) and yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) (Hopkinson 1931; Fowells 1965; Banner et al. 1989). Western redcedar often occurs in single-species clumps as a consequence of self-fertilization and short-distance seed dispersal (El-Kassaby et al. 1994). It forms extensive pure stands in areas of poor drainage. Although frequently dominant in wood volume, redcedar is usually less abundant in terms of stem density (data from Weyerhaeuser Canada).

Since colonization by Europeans in the last century, the lowland rainforests have been subject to two major human-induced changes: extensive commercial felling of primary forest and the introduction of exotic species, of which 11 are mammals (compared with only 8 indigenous species of terrestrial mammals, one now extinct; Cowan 1989). Among these, the Sitka black-tailed deer, introduced in the early part of the 20th century, is a forest-dwelling ungulate that has colonized the entire archipelago. Its willingness to swim has allowed it to reach all but the most remote offshore islets.

Commercial forestry is concentrated mainly on the large islands including Graham, Moresby, and Louise (Fig. 1). Areas with commercial timber exploitation can be divided into those easily accessible to hunters from the major communities (Masset, Port Clements, Queen Charlotte City, and Sandspit) by a network of logging roads and those only accessible by sea or air and, so, sparsely hunted. Consequently, hunting mainly takes place on the parts of central Graham Island and of northeastern Moresby Island accessible from the population centres. From interviews with hunters, we confirmed that hunting pressure diminishes with increasing isolation and that deer seemed more abundant (or less shy) in areas less accessible to hunting. Until recently the only deer abundance estimate available for the archipelago was based on deer abundance in similar habitats on the mainland. It suggested that there were between 50 000 and 65 000 animals on the archipelago (S. Sharpe, Head, Skeena Regional Wildlife, Smithers, B.C., personal communication). Between 1996 and 2000, deer censuses and deer cull programs on three medium-sized islands (Daufresne and Martin 1997; S. Sharpe, unpublished data) yielded density estimates that were all around 30 deer/km². Finally, pellet group counts from transects in old-growth forest patches on Graham Island and northeastern Moresby Island (Engelstoft 2001) yielded estimates of about 13 deer/km². If we extrapolate these figures to the roughly 8500 km² of habitat available to deer on the archipelago we obtain a much higher estimate of the total deer population: between 113 000 and 250 000 deer. The local summary statistics data base indicates that in 1998, 672 deer (of which 565 were bucks) were killed by licensed hunters on the northern island, and 311 (of which 252 bucks) in the central section of the archipelago (southern island). These figures have regularly decreased since 1980 when 1525 deer were killed in the north and 704 in the central section. This decrease was paralleled by a regular decrease in the number of licensed hunters that declined from

1377 in 1980 to 521 in 1998. An additional but unrecorded number of deer were killed by the Haida hunters. The Haida represent about 50% of the local population. The total number of deer killed per year by all hunters, could be about 2000 deer/year (about 1300 on the northern island and 600 on the southern island).

Study protocol and data analysis

We chose two study areas, one in the northern part of the archipelago, on Graham Island and one in the central part on Moresby and Louise Islands. Both areas are situated on the eastern slope of the archipelago, within the same physiographic unit, the Skidegate Plateau, and both belong to the Coastal Western Hemlock biogeoclimatic zone. We treated these two areas as replicates. At each area we selected two sites: one that was readily accessible to hunters (Mainline on Graham Island, and Alliford Bay on Moresby Island) and one that was difficult to access (Ian Lake on Graham Island, and Louise Island near Moresby Island; Fig. 1).

To study the natural regeneration of redcedar after logging at each site we selected naturally regenerating blocks clear-cut 10–15 years ago, rather than plantations. This age range was chosen so that (i) natural regeneration had time to take place and (ii) terminal shoots of the oldest redcedar could have escaped deer browsing.

A first selection of all the blocks of suitable age in the study sites was carried out from a 1 : 50 000 scale map derived from Landsat 5 Thematic Mapper data. This map identified blocks that were clear-cut on the archipelago by 10-year intervals (Gowgaia Institute, September 1997). We then recorded the pre-felling information (stem density and volume by species per DBH class and per hectare before cutting) and the year when cutting actually occurred for each of these forest blocks using the archives kept by the forest company Weyerhaeuser Canada. This pre-felling information was based on (i) British Columbia Ministry of Forests inventories based on photo-interpretation originally done in 1967 and regularly updated by surveys and (ii) operational cruise information. For second growth that was less than 30 years old, inventories were based on stocking survey information. On the basis of the records of silvicultural operations we rejected blocks for which herbicides or fertilizer had been applied or planting or spacing carried out. Thus, the blocks that were ultimately retained as suitable had regenerating forests that resulted exclusively from natural regeneration.

Because our emphasis was on western redcedar and because western redcedar regeneration can be expected to be higher for blocks that had a higher proportion of redcedar before cutting (Ferguson et al. 1986; in Graham et al. 1988; but see Schmidt 1955), we controlled for the effect of redcedar abundance before cutting on redcedar regeneration by assigning all the blocks selected so far to four classes of relative abundance of redcedar before cutting (nil; low, <10%; medium, 30–40%; high, >60%). As the composition of the original, ≥ 250 -year-old, forest was established in the absence of deer, we decided to use it as an estimator of redcedar regeneration potential (Ferguson et al. 1986; in Graham et al. 1988) in the absence of browsing by mammals. There was no direct information available on advance regeneration left after harvest in these cut blocks. However,

the current lack of redcedar advance regeneration in the mature forests of the archipelago (see Introduction), and the fact that 100% of the small redcedar trees ($N = 35$) sampled by B. Vila (personal communication) in 20-year-old cut blocks on Graham Island were issued from post-logging germination (as opposed to 50% of small Sitka spruce trees issued from advance regeneration) suggest an absence, or an extreme rarity, of western redcedar advance regeneration in these forests.

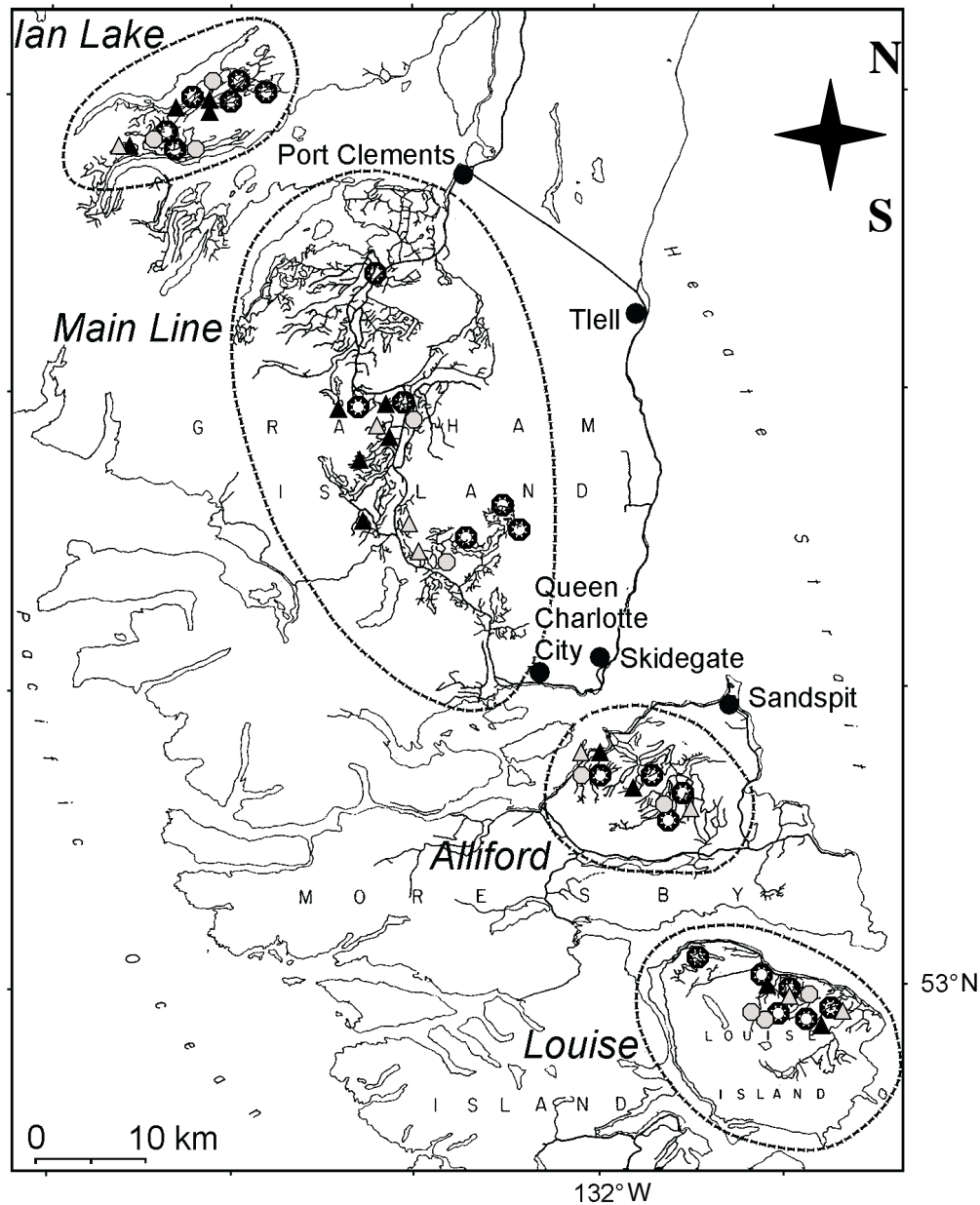
The final selection of blocks to be actually sampled under the a priori stratification by hunting pressure and redcedar relative abundance before cutting was achieved as follows: in each study site we selected at least two blocks for each class of pre-cutting redcedar abundance (Table 1). For the class with highest proportion of redcedar before cutting the minimum number of blocks available per site was always larger than four. We selected blocks that covered about 10 ha whenever possible and blocks that maximized, within a study site, the distance between blocks of the same class of redcedar abundance before cutting. In each of the selected blocks we placed standard circular plots (50 m² in area, 3.99 m radius) at a density of one per hectare to sample the vegetation. As a result the mean number of plots per block varied from 7.8 (low pre-cutting cedar abundance class) to 9.8 (high pre-cutting cedar abundance class). In each plot, we counted the number of individuals for each tree species within four size classes: germinants (height <10 cm, stem not woody), seedlings (height 10–50 cm, woody stem), saplings (height >50 cm and diameter <2.5 cm), and small trees (DBH >2.5 cm). The latter class (small trees) was further subdivided into 5-cm DBH classes (2.5 < DBH < 7.5 cm, and so on). In the case of redcedar, because of the lack of advance regeneration, most if not all the small trees probably grew after the original forest was cut.

We recorded the mean height (h) and estimated the percent cover of the shrub species (horizontal projection of the volume of vegetation in the plot) using a chart with rectangles representing black and white patterns in which the proportion of black varied from 1, 5, 10, 20, 30, ..., up to 90% of the area of the rectangles. In each plot we estimated browsing stress for each tree species (per size class) and each shrub species by estimating the percentage of branch and twig tips that was browsed. This measure combined all browsing that affected an individual during its growth (Martin and Daufresne 1999). We distinguished four browsing scores: (1) nil; (2) low, <20%; (3) medium, 20–60%; (4) high, >60%.

To estimate overall impact of deer on redcedar regeneration we compared the density of redcedar in the seedling, sapling, and small tree classes from our >60% pre-cutting redcedar class to the density of redcedar from a small 625-m² enclosure studied by Bennett (1996) on Moresby Island (Queen Charlotte Islands). This reference sample was part of a 10-year-old cut block with more than 60% of redcedar before cutting and with natural redcedar regeneration.

We tested the effect of accessibility to hunters (that is, of the risk to deer to be killed) on (i) tree density per size class, (ii) shrub cover and height, and (iii) percent browsing of trees and shrubs by using general linear models (GLIM,

Fig. 1. Sampling localities: shaded triangles, cut blocks with no western redcedar prior to logging; solid triangles, cut blocks with less than 10% redcedar before logging; shaded polygons, cut blocks with 30–40% redcedar prior to cutting; solid polygons, cut blocks with more than 60% of redcedar before cutting.



Payne 1986; Aitkin et al. 1989). We controlled for the effect of study area and of the proportion of redcedar before cutting.

We treated each circular plot as a single observation in relation to the independent variables (study area, access, and proportion of redcedar before cutting). We tested the significance of the effects of each independent variable and of their interaction on the different vegetation variables by the method of backward stepwise elimination, starting with the complete model and progressively eliminating effects defined as insignificant (rejection level at $P < 0.05$) (Aitkin et al. 1989). In the case of data with Poisson distributions, the difference of deviance (estimated by GLIM) generated by the elimination of one main factor or interaction follows a

chi-square distribution with degrees of freedom equal to the difference between the degrees of freedom of that main factor or interaction. The stem density of a given tree species within each size class was normalized by log transformation (Crawley 1993).

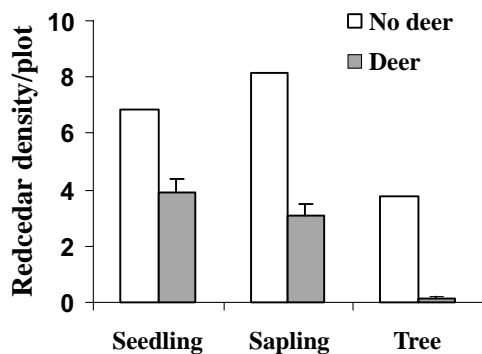
We selected the sapling stage as the most appropriate to compare browsing on redcedar to that on the other two main canopy trees. Sapling stage was old enough to give deer the time to have an impact but small enough to still be easily accessible to the deer.

We treated browsing stress and shrub cover as continuous variables, because they formed a continuous gradient. Both browsing score and shrub cover were tested for normal distribution. When necessary the data were corrected for over-

Table 1. Number of sampling blocks and number of standard circular plots (in parentheses; each plot 50 m² in area, 3.99 m in radius) per study site in relation to redcedar proportion before cutting, and accessibility to hunters.

Redcedar abundance before cutting	Northern area		Central area	
	Easy access (Mainline)	Difficult access (Ian Lake)	Easy access (Alliford)	Difficult access (Louise Island)
Nil	3 (29)	2 (19)	2 (16)	2 (12)
Low (<10%)	5 (47)	4 (22)	2 (13)	4 (35)
Medium (30–40%)	2 (17)	3 (25)	2 (20)	2 (20)
High (>60%)	6 (52)	5 (43)	4 (36)	5 (45)
Total	16 (145)	14 (109)	10 (85)	13 (112)

Fig. 2. Western redcedar seedling, sapling, and small tree densities in 10- to 15-year-old regeneration after logging in one site without deer (open bars; after Bennett 1996) and in a sample of blocks from sites with deer (shaded bars, this study).



dispersion following recommendations in Crawley (1993), and the significance of the effect of the independent variable on browsing score or on shrub cover was estimated by a *F* test (Crawley 1993), after we removed from the analysis the plots in which the species under consideration was not observed.

Results

Impact of deer on redcedar regeneration

The abundance of naturally regenerating redcedar in our samples from sites with more than 60% of redcedar before cutting, was lower in presence of deer than in the enclosure sampled by Bennett (1996) (Fig. 2). Seedling density was 1.7 times lower on the sites with deer than inside the enclosure; sapling density was 2.6 times lower; and tree density was 187.5 times lower. In the small tree class the highest stem density on sites with deer was about 80 stems/ha (2.5 < DBH < 7.5 cm). Before harvesting, the mean density of trees with 17.5 cm DBH or more was 105 trees/ha.

Relation between regeneration and proportion of redcedar before cutting

Germination stage

The density of germinants varied among the four study sites and among classes of redcedar abundance before cutting (Fig. 3). There was a significant interaction between study area and redcedar abundance before cutting ($\chi^2 = 10.4$, *df* = 3, *P* < 0.05). In the northern sites (Mainline and Ian Lake), germination of redcedar was highest in blocks that had a high redcedar abundance before cutting. At the south-

ern sites (Alliford and Louise), density of germination was low at Alliford and high at Louise. At Louise, the density of germinants was highest in the blocks that had no or little redcedar before cutting. The other variables had no effect on the amount of germination at a given site.

Post-germination stage

At all post-germination stages, redcedar density was highest for blocks that had the highest proportion of redcedar before cutting (Fig. 4; $\chi^2 = 55.9$, *df* = 3, *P* < 0.001 for seedling density; $\chi^2 = 53.1$, *df* = 3, *P* < 0.001 for sapling density; $\chi^2 = 30.4$, *df* = 3, *P* < 0.001 for small tree density).

Effect of access to hunters on redcedar regeneration

There was no significant effect of accessibility to hunters on redcedar seedling abundance. Overall, seedling abundance was significantly higher in the northern pair of sites (Mainline and Ian Lake; Fig. 5) than in the southern sites (Alliford and Louise) ($\chi^2 = 7.32$, *df* = 1, *P* < 0.01). Saplings were, on average, three times more abundant in areas more accessible to hunters (920 vs. 330 saplings/ha; $\chi^2 = 11.74$, *df* = 1, *P* < 0.001). The northern pair of sites had, as for seedlings, a significantly higher overall abundance of redcedar saplings per plot than the southern ones ($\chi^2 = 8.07$, *df* = 1, *P* < 0.01). There was a mean of 56 small redcedar trees/ha in accessible sites, compared with at most 16/ha in isolated sites ($\chi^2 = 10.86$, *df* = 1, *P* < 0.001). Mean abundance of small trees was also significantly higher in the northern sites than in the southern ones ($\chi^2 = 5.67$, *df* = 1, *P* < 0.05).

The amount of browsing on seedlings and saplings was significantly lower in areas easily accessible to hunters (Fig. 6) (seedlings: $F_{[3,118]} = 7.58$, *P* < 0.001, saplings: $F_{[3,91]} = 11.14$, *P* < 0.001). Browsing scores were low for the 28 redcedar stems that reached the small tree stage among these plots, because these individuals were tall enough such that most of their foliage was beyond the reach of deer. The small sample size for the small tree class precluded comparing browsing stress among sites, so we plotted the same overall mean value for trees at all sites (Fig. 6).

Comparing redcedar saplings with saplings of other canopy trees and with dominant shrub species

At all sites, redcedar was one of the least abundant species of sapling size despite the fact that these sites had >60% of redcedar before cutting (Fig. 7). The abundance of Sitka spruce saplings was of the same order of magnitude than the abundance of redcedar saplings. There was no significant effect of accessibility on the abundance of Sitka spruce sap-

Fig. 3. Mean number of germinants of western redcedar per plot in the four study sites in relation to the proportion of western redcedar before cutting.

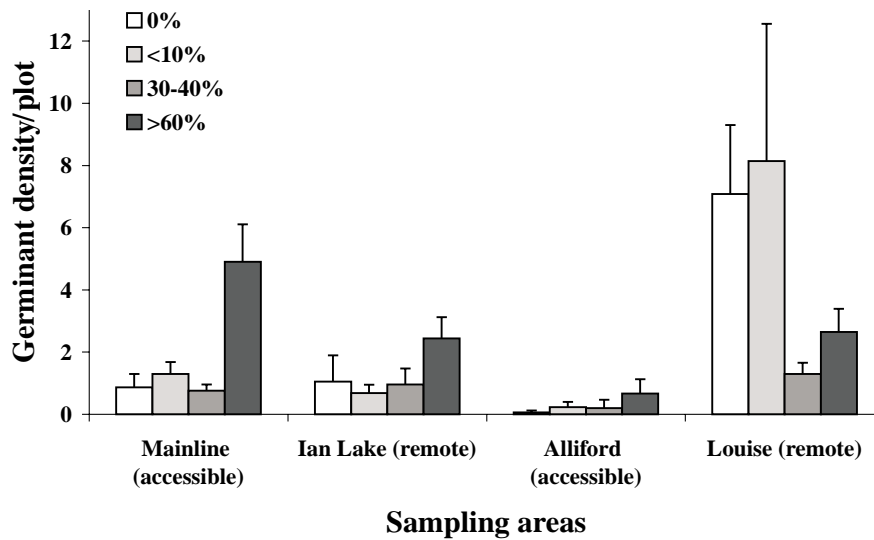


Fig. 4. Density of western redcedar seedlings, saplings, and small trees in relation to the proportion of western redcedar before cutting, all samples pooled.



lings. Western hemlock saplings were 5–10 times more abundant as redcedar or Sitka spruce saplings on all sites. The abundance of hemlock saplings did not differ significantly between accessible and remote sites. At all sites, browsing stress on saplings was highest for redcedar and least for hemlock (almost no signs of browsing; Fig. 8). Browsing scores of redcedar and Sitka spruce were higher in remote areas than in areas easily accessible to hunters ($F_{[3,91]} = 11.14, P < 0.001$ for redcedar; $F_{[3,123]} = 8.46, P < 0.001$ for Sitka spruce). Browsing scores of saplings varied from 1.52 to 3.84 (i.e., approximately 12–74%) for redcedar, from 1 to 1.98 (i.e., 0–22%) for Sitka spruce and were almost nil (<1%) in western hemlock (Fig. 8).

Red huckleberry (*Vaccinium parvifolium* Andrews) was the only shrub species present on our plots to yield a suffi-

cient sample size for analysis. Its cover was significantly higher ($F_{[3,121]} = 19.38, P < 0.001$), and individuals were taller ($F_{[3,121]} = 8.95, P < 0.001$) and less browsed ($F_{[3,121]} = 13.34, P < 0.001$) in areas easily accessible to hunters than in areas inaccessible to hunters (Fig. 9). Browsing scores of huckleberry ranged from 2.6 to 3.2 (i.e., 30–70%) and were comparable with the damage observed on western redcedar.

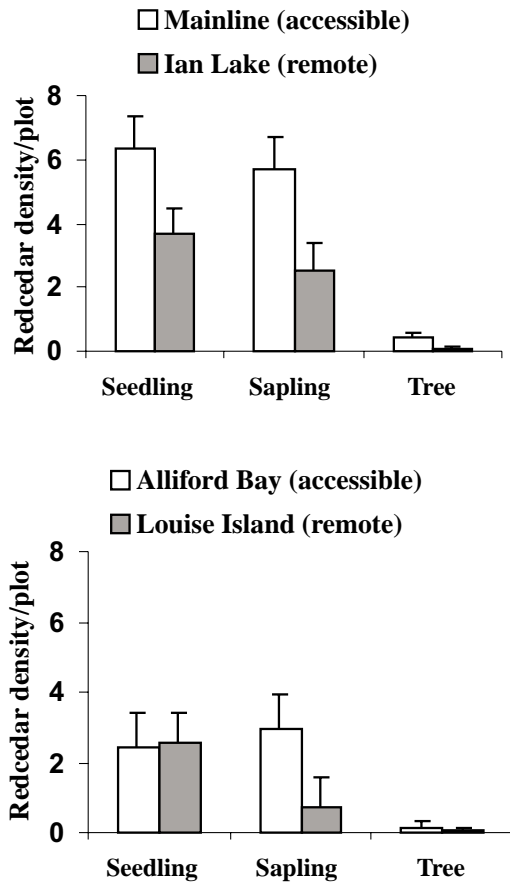
Discussion

The effect of redcedar abundance before cutting on redcedar regeneration

Germination stage

The density of germinants was highest in sites with highest proportion of redcedar in the original old-growth forest

Fig. 5. Density of western redcedar seedlings, saplings, and small trees in plots sampled in sites that had >60% of redcedar before cutting: open bars, localities easily accessible to hunters; shaded bars, localities difficult to access.

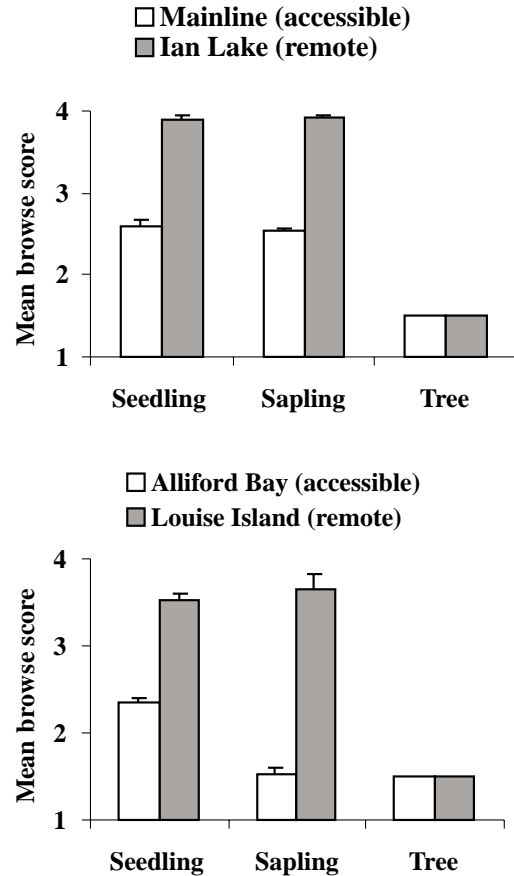


for three of four sampling sites, but the pattern was the reverse at the fourth one. Germination abundance is variable because of strong variation among years (Klinka and Feller 1993; Daniels 1994) and of high seedling mortality (Schmidt 1955; Curran and Dunsworth 1988). Other factors that may influence germination following disturbances are the size of opening of the canopy, which permits better seed dispersal, or the exposure of mineral soils (Graham et al. 1988; Edwards and Leaden 1988). J.-L. Martin and C. Baltzinger (unpublished data) found that germination in closed forests was patchy and relatively uncommon, even where redcedar was the dominant species, but germinants in these small patches were usually abundant.

Post-germination stages

Unlike for germinants, the pattern of size-class distribution for post-germination stages resembled the relative distribution in the pre-existing forests; that is, redcedar seedlings, saplings, and small trees were all more abundant where redcedar had been predominant in the primary forest, confirming earlier results by Ferguson et al. (1986). However, the low relative frequency of redcedar in the regeneration cohort of all tree species in the blocks with >60% of redcedar before cutting, suggests that recruitment was low relative to the abundance of redcedar in the original forest (0.5–17% for the sapling and small tree stages in our sam-

Fig. 6. Browse scores of seedlings, saplings, and small trees in plots from sites that had >60% of redcedar before cutting: open bars, localities easily accessible to hunters; shaded bars, localities difficult to access. Note that, for small trees, there were too few samples to average out between sites; the score given is the overall mean for all 28 trees recorded in the four sites. Scores are as follows: (1) nil, (2) <20%, (3) 20–60%, (4) >60%.

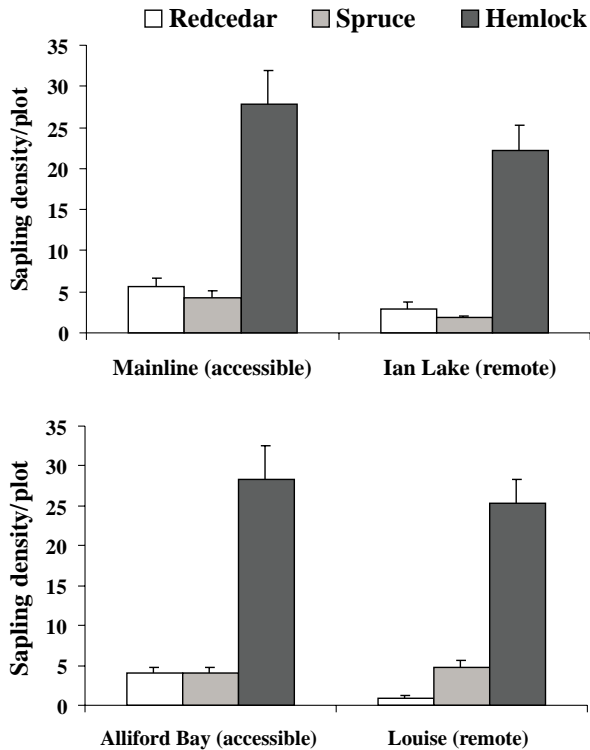


ples). Such a low proportion of redcedar when deer were present was also found by Bennett (1996) and in the inventories carried out by MacMillan-Bloedel 5 years after logging. However, it is difficult to project the composition of the mature forest (>100 years) based on composition at 10–15 years after cutting. On one hand, these young stands will suffer further mortality, but on the other hand, redcedar is a long-lived, pest-resistant tree (Fowells 1965), which can see its proportion in a stand increase over time relative to shorter lived trees even with its lower, slower, and irregular recruitment (Daniels et al. 1995).

The effect of accessibility to hunters on redcedar regeneration

Comparison of our data with the results from Bennett (1996), although the latter were collected on a single site, confirmed earlier observations (Pojar et al. 1980; Coates et al. 1985) that redcedar regeneration on the Queen Charlotte Islands, 10–15 years after logging, has been significantly reduced by deer browsing. Our comparison of sites easily accessible to hunters with those more difficult to reach showed that impact by deer was significantly lower on sites with

Fig. 7. Mean density per plot of the three main tree species (sapling stage) in the four sampling sites in relation to access to hunters.

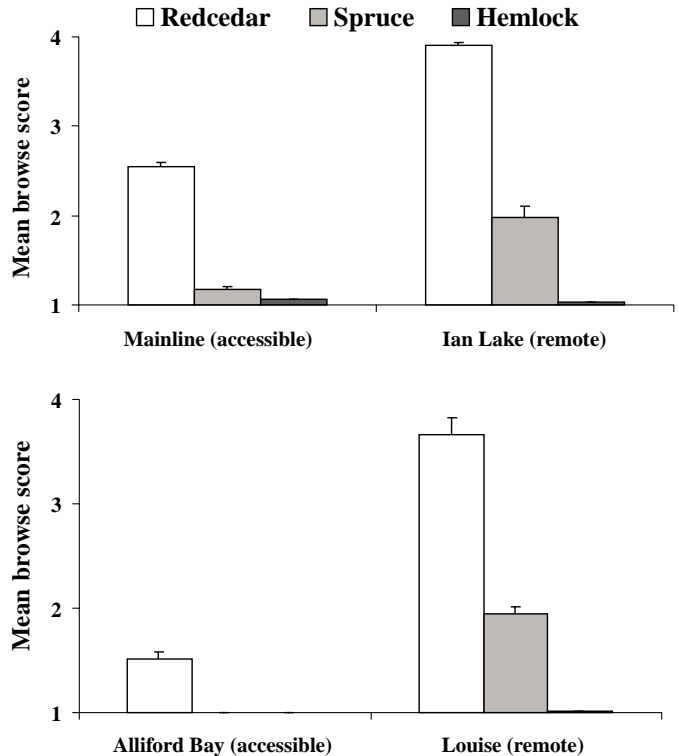


better access, where the risk of being shot is presumably higher.

If we assume, on the basis of the few deer density estimates available for the archipelago, a mean deer density of about 20 deer/km², then the deer population exposed to hunting in the 625 km² accessible to hunting from the population centres on Graham Island is about 12 500 animals. A similar estimation would yield a figure of about 10 000 animals for the approximately 500 km² area accessible from population centres on northeastern Moresby Island. On the basis of our kill estimates, the number of deer killed per year would amount to about 10% of the deer living in the areas exposed to hunting. This low level of harvest suggests that the differences in deer impact on the vegetation that we observe between sites in relation to hunting rate are more likely to reflect changes in the way deer use their home range when they risk being killed than a significant reduction in deer density. These changes in habitat use could include increased amount of time spent in areas with dense cover, such as remnant patches of old-growth forest; increased avoidance of areas near human activity, or increased proportion of nocturnal activity (e.g., Kufeld et al. 1988; Nicholson et al. 1997; Kilgo et al. 1998). This interpretation emphasizes the need to better understand the ecology of fear (Brown et al. 1999), if we want to better understand trophic interactions.

There is no indication from the pre-cutting records that there was any systematic difference in the occurrence of redcedar between accessible and isolated sites in the original forest. Lowest densities of redcedar were observed in the ac-

Fig. 8. Mean browsing scores per plot for the three main tree species (sapling stage) in the four sampling localities at the sapling stage in relation to access to hunters.

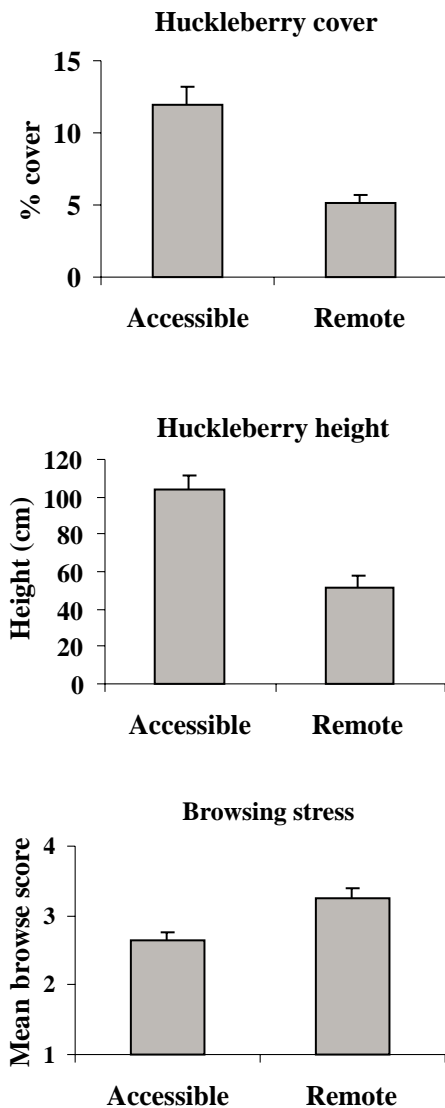


cessible site in the north and in the remote site in the south (with 94 and 82 stems/ha, respectively) and highest values in the remote site in the north and accessible site in the south (123 and 119 stems/ha, respectively). This seems to eliminate the possibility of differences between site categories prior to deer introduction.

Our observation that browsing on seedlings and saplings was significantly greater in isolated sites than in accessible sites is consistent with our assumption that accessibility influences impact by deer. Thus, those sites with the lowest densities of redcedar were also those with the heaviest browsing pressure.

In summary, our results suggest that current regeneration of secondary forests on the Queen Charlotte Islands will result in a species composition that is deficient in redcedar, compared with the pre-existing forest that had developed in the absence of deer. However, they also reveal a pattern for redcedar to be better represented in second growth on Graham Island than on Moresby Island, for both accessible and isolated areas. There is no evidence for such a pattern in the pre-cutting data, and we cannot provide an explanation. Finally, the relative palatability of tree species to deer suggested by the browsing scores that we observed is in agreement with the results of Pojar et al. (1980), Pojar and Banner (1984), Martin et al. (1994), and Martin and Daufresne (1999). Redcedar is most preferred, then Sitka spruce, and finally western hemlock. Thus, Sitka spruce can become an alternative source of food, where redcedar is missing or reduced. However, the amount of Sitka spruce regeneration does not vary with accessibility to hunters, a result that confirms the findings of Vila et al. (2002) showing

Fig. 9. Mean cover, height, and browsing stress for red huckleberry in relation to access to hunters.



that even under heavy browsing pressure young Sitka spruce will ultimately manage to escape deer browsing and recruit into the overstory. Deer, by reducing shrub cover, also reduce the competition for resources between trees and shrubs (Fraser et al. 1995; Chang et al. 1996) favouring, therefore, the development of the trees least affected by browsing.

Management implications

In view of the current absence of redcedar regeneration in primary forest (Martin and Daufresne 1999), we speculate that the long-term prospect for the persistence of redcedar in the forests of the Queen Charlotte Islands, assuming the persistence of the black-tailed deer, will depend on the amount and distribution of deer hunting. Despite the modest number of deer actually killed, we observed a significant correlation between higher hunting rate and better tree regeneration. McIntosh et al. (1995) have shown that hunting, if intensive enough, can also be an efficient way to actually reduce deer abundance in an area, even in a context where immigration

from adjacent areas with lower hunting rate can take place. The evidence available suggest that there is a threshold density below which damage to the vegetation is negligible (Gill 1992). This threshold will depend on the habitat and plant targeted.

Our study has shown that even a relatively modest hunting pressure can improve cedar regeneration in young forests. In old-growth forests, evidence obtained from experimental culls on isolated islands of the Queen Charlotte Islands (A.J. Gaston, T. Golumbia, J.L. Martin, and S. Sharpe, unpublished data) indicate that redcedar regeneration can take place when deer density is reduced to about 4 deer/km². In the situation of the Queen Charlotte Islands, three trends are critical to consider in the evaluation of the potential of hunting as a tool to control deer impact on the vegetation: (i) the regular decrease in the number of hunters over the past 20 years; (ii) the low proportion of does killed, which represents at most 1% of each local population, leaving the effective deer population size practically unaffected by hunting; and (iii) the reduction in access to some areas through road deactivation. Dealing with the problems caused by the overabundance of white-tailed deer in the eastern United States, Brown et al. (2000) recommended that deer population management should combine hunting regimes that (i) promote recreational hunting with great per-hunter harvests of antlerless deer and (ii) site-specific hunts and programs in areas where access to hunters is limited. A policy of increased hunting rate in landscapes composed by a mosaic of old-growth forest patches, recent clearcuts, and patches of regenerating forests should also include the monitoring of the consequences of high hunting rate on the whole pattern of habitat use by deer and especially on the possible increase of deer impact in the remaining patches of mature forest (e.g., Nicholson et al. 1997).

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