Assessing browsing influence in forest understory using dendrochronology on Haida Gwaii archipelago (British Columbia, Canada)

Bruno Vila, Frédéric Guibal

Institut Méditerranéen d'Ecologie et de Paléoécologie, UMR 6116 CNRS, Boite 451, Faculté des Sciences et Techniques de Saint-Jérôme, 13397 Marseille cedex 20 - France

Abstract

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

Keywords: disturbance, browsing, deer, abrupt growth change, traumatic characteristics

Introduction

The impact of herbivory on plant communities has been well established (Huntly 1991; Crawley 1997) and it is recognised that ungulate herbivores may have a profound effect on forest structure (Anderson, Loucks 1979; Veblen et al. 1989). Influence of herbivory is deduced by analysing species composition and comparing structure and biomass (Hernandez, Silva-Pando 1996). When studies focus on a single species, experimental approach may be carried out and changes may be evidenced in plant morphology, in plant growth and in plant chemistry (Mopper et al. 1991; Duncan et al. 1998). Besides that, disturbance on forest ecosystem dynamics caused by herbivory can be analysed by *a posteriori* approaches based on woody plant morphology and on ring-width series analysis (Schweingruber 1996).

Dendroecology represents a valuable way to assess past and present disturbances in so far as using rings series it is possible to have an annual approach of external factors influence. That is possible because the disturbance induces diameter growth rate changes and modifies age structure. Changes peculiar to disturbances usually generate a signature of it. Identifying of the signature and taking into account its variations throughout time make it possible to reconstruct disturbance variations (Schweingruber et al. 1990; Schweingruber 1996). Dendrochronologists have been using disturbances recorded in tree ring series to precise spatial and temporal variations of several animal species (Payette 1987; Bordage, Filion 1988). Among them, Motta (1995, 1996, 1997) studied age and scars distributions (fraying scar and bark-stripping) due to

ungulates in several alpine forest species in order to assess a temporal approach of ungulates population dynamics.

Introduced in the early 20th century in many parts of the world for hunting (de Vos et al. 1956; Petrides 1975), ungulates reached densities likely to have significant impact on vegetation and animal communities in many areas due to the absence of predator and the abundance of favourable habitats (Veblen et al. 1989; Mark et al. 1991). On the Haida Gwaii archipelago (British Columbia, Canada), the 20 black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) released in the north of Graham Island in the early 20th soon colonised most of the archipelago and disturbed the ecosystem (Pojar, Banner 1984; Pojar et al., 1980). Only herbivore after endemic caribou (*Rangifer tarandus dawsoni* Seton) disappeared in the 1920s (Carl, Guiguet 1972), deer affected forest ecology hindering forest regeneration and impoverishing primary and secondary forest ecosystem (Pojar et al. 1980; Pojar, Banner 1984; Foster 1989; Martin et al. 1993). Martin and Daufresne (1999) studying understory evidenced how salal (*Gaultheria shallon* Pursh) cover is reduced from 43% in deer-free islands to less than 1% in deer-infested islands due to overbrowsing and to the fact that young stems are pruned by deer. They also evidenced how deer suppressed red cedar (*Thuja plicata* D. Don. Ex Lamb.) recruitment whereas Pojar and Banner (1984) underlined the increasing pressure on regenerating spruce (*Picea sitchensis (*Bong.) Carrière).

This disturbance is a main concern to forest industry as it causes wood depreciation, high seedling mortality, delay in recruitment and a possible tree composition change (Pojar et al. 1980; Pojar, Banner 1984; Martin, Daufresne 1999). It is also a concern to conservation agencies (Ogilvie 1989; Taylor 1989). The richness displayed by insular ecosystems such as those of Haida Gwaii being huge in terms of flora endemism, birds communities and timber quality produced, understory browsing by deer induces far-reaching effects on biodiversity, landscape and economy.

We chose to focus our study on salal and regenerating spruce, two major components of North Western America temperate rain forest. Salal pro-

vides many habitats which have supplied herbivores with important source of food (Haeussler et al. 1990) and it participates to nutrients cycle by reducing soil erosion. Spruce forms pure canopy stands along the outer-coast on sites affected by ocean spray and in advanced stages of primary succession on floodplains (Peterson et al. 1997); its role is capital for maintaining forest ecosystem. It is an outstanding timber species in coastal British Columbia especially in Haida Gwaii archipelago where it covers 21% of the timber harvesting landbase (British Columbia Ministry of Forests 1994). Spruce is the second preferred conifer by deer after red cedar on Haida Gwaii (Pojar et al. 1980; Martin, Daufresne 1999) and it may become an alternative food source, once red cedar regeneration has been severely reduced by deer browsing. We therefore selected salal and regenerating spruce as potential indicator understory species to assess black-tailed deer browsing pressure.

The present study is a first attempt in assessing black-tailed deer browsing pressure influence on forest understory by means of tree-ring analysis. That necessitates browsing consequences on plants and browsing signatures recorded in growth patterns are well understood. For this purpose, we took advantage of the occurrence of close islands with and without introduced deer to study age determination and ring-width analysis, identifying characteristic ring patterns according to their size or anatomical features.

In order to assess how browsing pressure is expressed, our objectives are for salal:

(i) to compare age on controlled and impacted individuals and precise the height of the browsing limit,

(ii) to examine radial growth patterns on controlled and impacted individuals,

(iii) to analyse anatomical characters and their occurrence on cross-sections from controlled and impacted individuals.

Whereas for regenerating spruce, our objectives are:

(iv) to examine and to assess how browsing pressure is expressed on radial growth patterns,

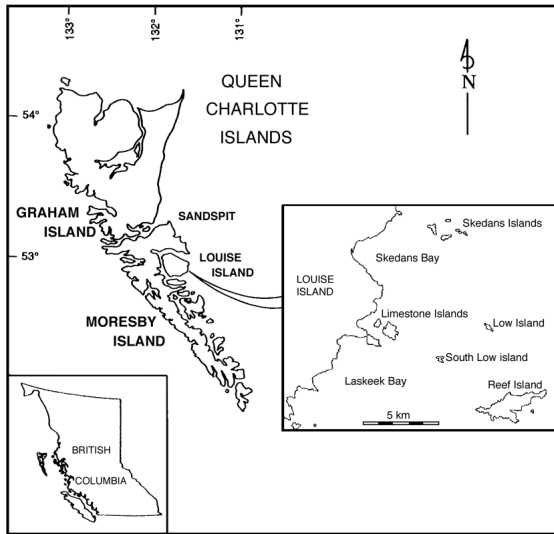(v) to study the tree age in order to precise delay in recruitment.

Fig. 1 - Haida Gwaii archipelago and Laskeek Bay islands.

Materials and methods

Study area, vegetation and deer

The Haida Gwaii archipelago (53 N, 132 W), situated off the western Canadian coast (British Columbia), includes more than 150 islands. Sampling focused on four islands of Laskeek Bay located in the eastern side of the archipelago which belongs to the Coastal Western Hemlock Zone, wet Hyper-maritime sub-zone (Fig. 1). Old-growth forests consist of a mixture of hemlock (*Tsuga heterophylla* (Raf.) Sarg.) which is the dominant species, red cedar often codominant and spruce of which regeneration depends on windthrows. The understory is composed of shrubs such as salal and red huckleberry (*Vaccinium parvifolium* Smith in Rees), of grasses, mosses and lichens (Banner et al. 1989).

Two islands are free from deer: Low and South-Low (less than 10 ha). Two other islands are settled by deer: Reef (249 ha) and Limestone (49 ha). The two deer impacted islands are characterised by a density of 0.30 deer/ha. At small islands where the study is carried out and which are totally recovered by primary forest, deer foraging is low and essentially represented by salal, red huckleberry along the shoreline, spruce recruiting and grasses in windthrows. On these islands, the absence of grasses and seedlings, the presence of an evident browsing height limit and the fact that palatable species are confined to inaccessible areas, all indicate a heavy browsing pressure (Reimoser et al. 1999).

Sampling and study site for shrub

Site selection addresses small plots in which individuals are directly affected by disturbance and control plots. Individuals are randomly sampled over an ecologically homogeneous area in order to assess the magnitude of the disturbance effects. Impacted and non impacted populations were sampled in plots situated in open canopy and shoreline habitat where conditions for salal growth are optimal. On deer free islands, non browsed individuals which form impenetrable thickets were collected randomly along a 40 m transect in order to obtain representative sample of non impacted populations. On deer impacted island, browsed individuals are isolated and result from salal thickets which were formed before deer introduction. They are very few and all individuals located in a 25 x 25 m plot were sampled.

Salals were sampled by collecting cross-sections: 17 browsed individuals were collected at Reef Island; 12 non browsed individuals were collected at each non impacted island (South-Low, Low). Given all samples were collected among stems which were distant from each other, we consider that each stem represents one individual. Ecological characteristics

Island	Slope	Exposition	Soil	Substrate depth
Reef	10°	S/SE	organic	30 cm
Low	15°	E	organic	20 cm
South-Low	absence of slope		organic	20 cm

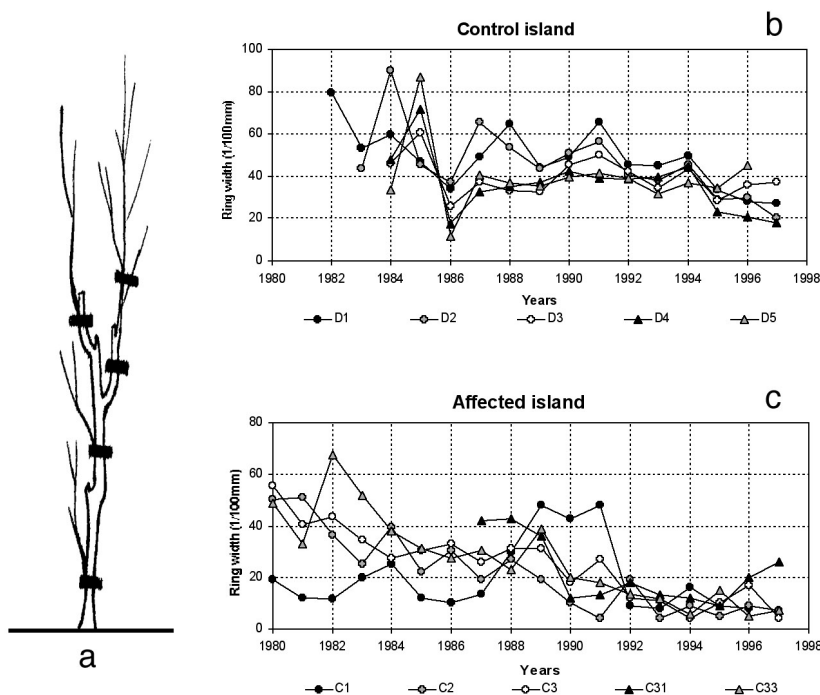Tab. 1 - Ecological characteristics of salal plots.

Fig. 2 - a. Collected stem cross-sections at different intervals. b. Good cross-dating of cross-sections from a control individual. c. Wrong cross-dating of cross-sections from an affected individual.

of the plots are reported in Tab. 1.

In order to precise growth dynamics, we applied Kolishchuk's method (1990) on shrubs which consists in cutting the trunk at different intervals from top to basis (Fig. 2a). Collected at every internode, sections provided overlaps between ring-width series from immediately neighbouring sections. Characterised by a diffuse-porous wood on which ring boundaries are difficult to be detected, salal cross-sections required a meticulous sanding in order to evidence ring limits. For each cross-section, ring-widths were measured with a precision of 1/100 mm along a radial file of cells using Eklund measuring device from the bark to the centre and from upper sections to lower sections. Two radii were measured on each cross-section, a mean value was calculated for each ring and a curve was plotted for each mean series. Then curves were compared over a light-table in order to crossdate them within a same shrub.

For each shrub, two sorts of chronologies are obtained: (i) partial chronologies which depend on the height of the cross-section along the stem (the closer the apex, the shorter the partial chronology) and (ii) a mean individual chronology (Fig. 2) built up from all partial chronologies from a same stem (Kolishchuk 1990). Then individual chronologies are compared over a light-table and correlation coefficients are calculated.

In order to assess how browsing pressure is expressed, a qualitative analysis of sections by identifying of anatomical features was carried out. Browsers can consume various parts of woody plants i. e. leaves, twigs, bark, wood. Due to cambium destruction and wood exposure to pathogens, browsing induces changes in wood anatomical features. Such features were examined on cross-sections. For that purpose, we compared cross-sections from deer free islands and deer impacted island as regards :
- presence/absence of lobes. Due to cambium removal on one side, rings are only elaborated on the other side. Rings superposition on this side forms a lobe;
- presence/absence of decaying wood following fungi or other micro-organisms attacks resulting in

texture and colour changes;
- pith form. Normally circular, pith may be distorted;
- pith position which is normally centred and may be brought of centre;
- section form which refers to stem cross-sections. Normally circular, the cross-section may be distorted;
- wedging rings are rings which ensue from cambial activity failing.

Analysis consisted in counting and comparing occurrence of these anatomical features by means of χ^2 test.

Sampling and methods for regenerating spruce

For regenerating spruce, sampling consisted in collecting cores or cross-sections as low as possible in order to precise tree age and sapling growth pattern. As many cores as possible were collected in order to get the pith. Because some browsed trees remain within the browsing limit while others are able to growth above the browsing limit, two sorts of browsed spruces were collected in two windthrows located at Reef and Limestone islands: 66 small browsed spruces (35 at Limestone and 31 at Reef island) and 68 taller free spruces which had been previously heavily browsed (34 at Limestone and 34 at Reef island). Clustered together inside windthrows, small browsed spruces and taller free spruces (escaped) where collected randomly along transects in order to obtain a representative sample of each category of affected trees.

Canopy surrounding Reef island windthrow is mainly spruces with few hemlocks. The site characterised by a slope ca. 8%, is well drained and organic soil is 50 cm thick. At Limestone Island the windthrow corresponds to the death of an old tall spruce. The site is badly drained. Soil organic is 60 cm thick. Surrounding trees are spruce and red cedar. In both sites, regeneration only concerns spruce. Plots are situated in open canopy with good light condition.

Stem cross-sections and cores were measured (1/100 mm) along two radii and the average value for each ring was calculated according to classical dendrochronology methods (Fritts 1976;

Schweingruber 1988; Cook, Kairiukstis 1990). Age is precised counting rings on cross-sections or cores with pith. Age at which taller trees escaped to deer is deduced from growth pattern analysis.

Results

Salal browsing limit and age

The height of the leader is random on deer free islands (H = 0.89 m; σ = 0.35) while it is rather constant on deer impacted island (H = 1.11 m; σ = 0.13) indicating a browsing height limit. Difference between islands is significant ($P < 0.01$). Without deer, salal are leaved from the bottom to the top whereas when deer is present, leaves appear above a level which is the browsing limit.

Ring counts on the longest ring series on basal cross-sections reveal that salal stems from deer impacted island are twice older than stems from deer free islands (control islands = 15.6 years, σ = 7.16; Reef = 35.2 years, σ = 12.57). Difference is statistically significant ($P < 0.01$).

Salal chronologies

On deer free islands, cross-sections from a same salal crossdated (Fig. 2b) and a mean chronology could be calculated for each individual. It was not possible to build up a mean chronology for the population due to low correlation between shrubs.

On deer impacted island, many difficulties were encountered in attempting to crossdate cross-sections from a same salal (Fig. 2c). Abrupt growth changes were evidenced for individuals for which it was possible to cross-date cross-sections (Fig. 3). These abrupt changes coincide with scars which were noticed during cross-dating. Before these changes occur, ring width varies much from one year to another. The ring on which the scar occurs is characterized by an abrupt growth decrease. On the following year (t+1), width still decreases to reach its minimal value. On years t+2 and t+3 width stays low and variations are small.

Salal anatomical features

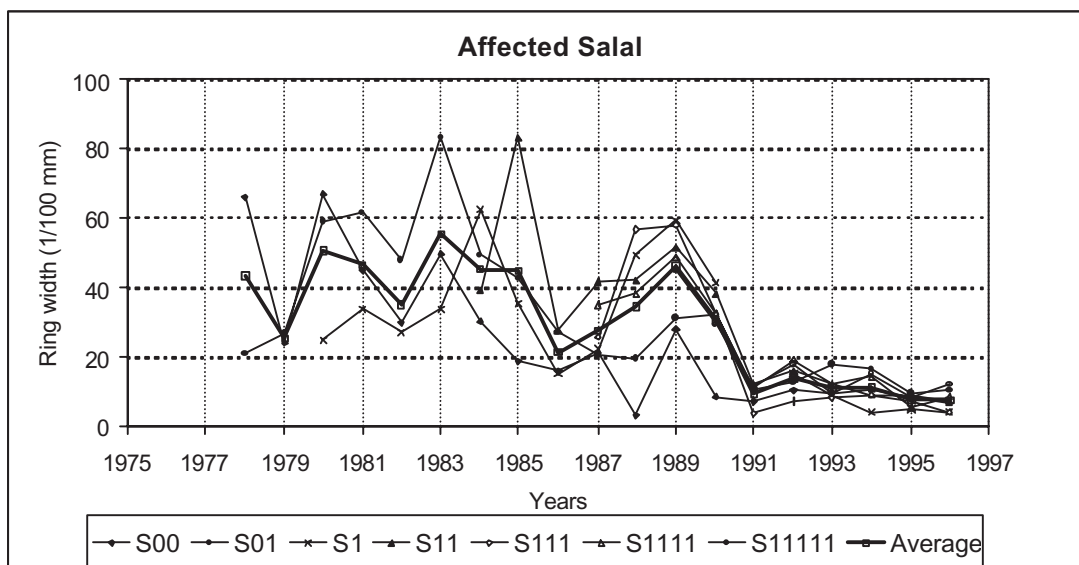On deer free islands, cross-sections are circular,

Fig. 3 - Abrupt growth changes on a browsed salal.

their pith is central and rings are concentric; bark is continuous around all the circumference. On deer impacted island, sections are not circular showing altered wood characterized by different colorations, excentred pith, lobes and wedging rings (Fig. 4).

As far as browsed salal stems are concerned, several remarks can be underlined:
- stem geometry is altered near a scar;
- at injured level callous tissue encloses the wounded tissue but this process is long and not always effective;

- most of the time, a brown coloration appears before a white coloration associated to a loss of weight. This brown coloration matching with the wood alteration is linked to deer presence; compartmentalization (Shigo 1984) is noticeable;
- pith is often distorted at the scar level and at immediate upper sections: it is distorted towards the scar. Sometimes it is laid against the bark indicating that attack was performed on bud or on a young twig and that cambium was damaged. At the upper sections,

| Observed characters		Control islands	Affected island	χ^2
Pith position	centred	122	86	19.51
	not centred	40	80	
Pith form	circular	133	100	19.03
	altered	29	66	
Section form	circular	147	48	130.0
	altered	15	118	
Alteration	absence	76	59	13.80
	presence	3	19	
Lobes	absence	77	44	37.44
	presence	2	34	
Wedging ring	absence	931	1775	4.56
	presence	4	23	

Tab. 2 - Anatomical features and χ^2 associated.
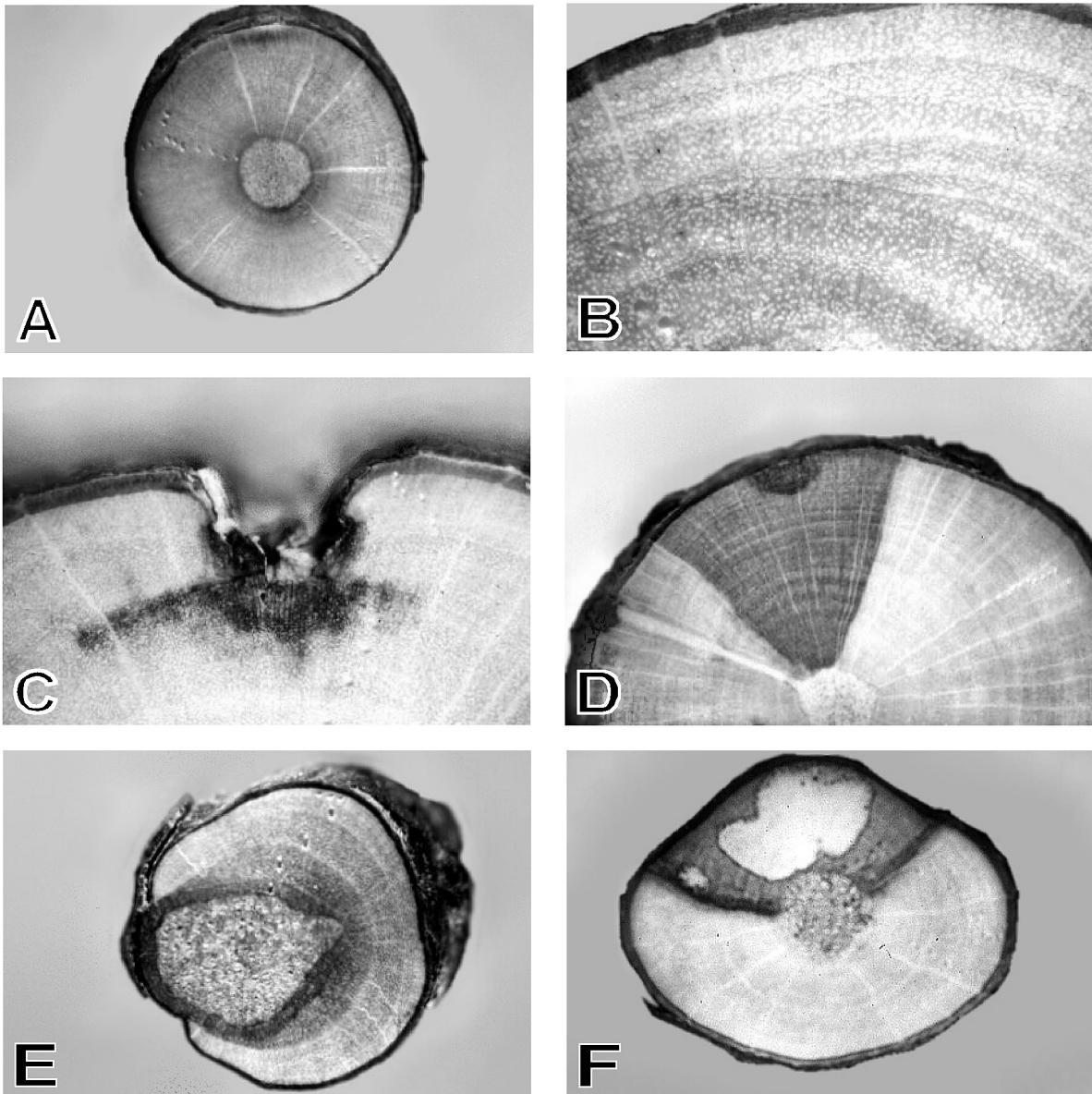
Fig. 4 - Salal photographs. Comparison between a control section (A) and affected sections. (B) wedging ring. (C) Alteration and scaring process at an injured level. (D) Brown coloration. (E) Eccentricity of pith and deformed cross-section, wedging rings. (F) Compartmentalization, alteration, fungi degradation and deformed cross-section.

pith is always distorted but this eccentricity tends to decrease;

- lobe frequencies are also different between control and affected populations for the same reasons as cambium is removed;
- pith form and position vary poorly;
- differences between affected and non affected populations are more remarkable in form section;

- wedging rings seem to be less correlated to deer pressure probably because they are linked to cambial activity failure.

Counting of these characteristics evidence large differences between these sets of individuals, all these differences varying in the same way (Tab. 2). Whatever the anatomical features are, χ^2 is always significant.
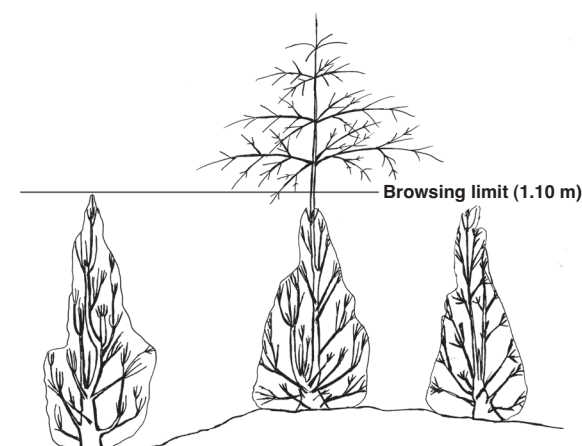
Fig. 5 - Architecture and shape of two heavily browsed spruces and one spruce which has exceeded the upper browsing limit.

Browsing height limit, ring width analysis and age of spruces

Browsed spruces have a very compact port due to intense ramification processes following repeated browsing of all buds. That occurs under the upper browsing limit which is at a height of 1.16 +/- 0.07 m and above which spruce displays a normal port (Fig. 5).

Among spruces which have exceeded the upper browsing limit, three ring width sequences are noticeable (Fig. 6.1) :
- a period of intense browsing during which ring width < 1 mm;
- a period of growth increase during which ring width varies from 1 to 8 mm throughout 5 years;
- a period during which growth stabilizes or decreases.

When terminal bud reaches 1.16 m (i.e. browsing limit), it is no longer consumed and an abrupt growth increase occurs.

All small browsed spruces show only the initial ring sequence noticeable on trees which have exceeded the upper limit of browsing: ring width <1 mm and indicates intense and continuous browsing (Fig. 6.2).

On both islands where deer densities are equal saplings which are still browsed are younger than spruces which are not browsed any more. This age difference between recruited and still browsed is statistically significant (p = 0.001). Using the abrupt growth change evidenced on escaped spruces, saplings reach the browsing limit around 13 years of age (Tab. 3).

Consequently, saplings which are being browsed usually take more than 13 years to reach 1.16 m high while this height is attained throughout only 5 years in deer free habitats.

Discussion

Browsing height limit

Our results suggest a browsing limit at a height of 1.11 +/- 0.13 m for shrubs and 1.16 +/- 0.07 m for regenerating spruces. It must be stressed that sometimes we found shrubs with broken branches of which foliage was consumed above the browsing limit. Very few salal individuals less than 1.11 m high subsist. Spruce stems which cannot be bent and thorny ligneous needles cause a physical defence which permitted spruce to subsist and grow slowly under the browsing limit. This browsing limit differs according to species palatability and presence/

Category	Observed parameter	Reef Island	Limestone Island
Small browsed spruce	Total age	13.2 +/- 7.6	12.7 +/- 2.7
Small browsed spruce	Height (m)	0.92 +/- 0.12	0.79 +/- 0.19
Escaped spruce	Total age	21.9 +/- 6.6	25.5 +/- 3.7
Escaped spruce	Height (m)	> 2.50	> 2.50
Escaped spruce	Age when they escaped	12.8 +/- 5.0	13.9 +/- 3.4
Escaped spruce	Height when they escaped	1.16 +/- 0.07	1.16 +/- 0.07

Tab. 3 - Age and height of the two sorts of browsed spruces and spruce age when they escaped to deer.
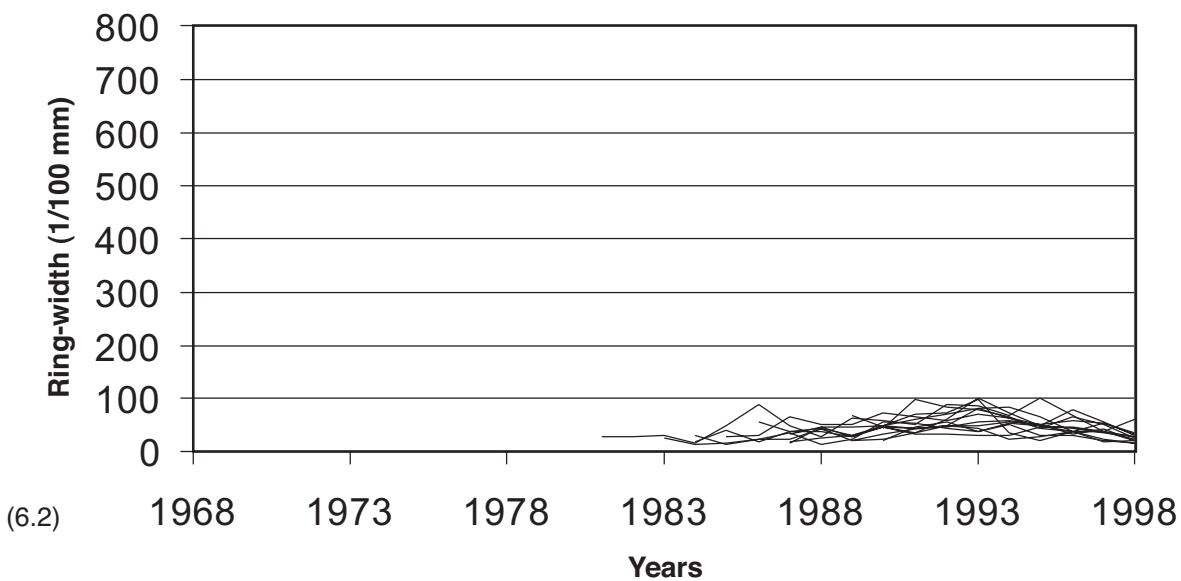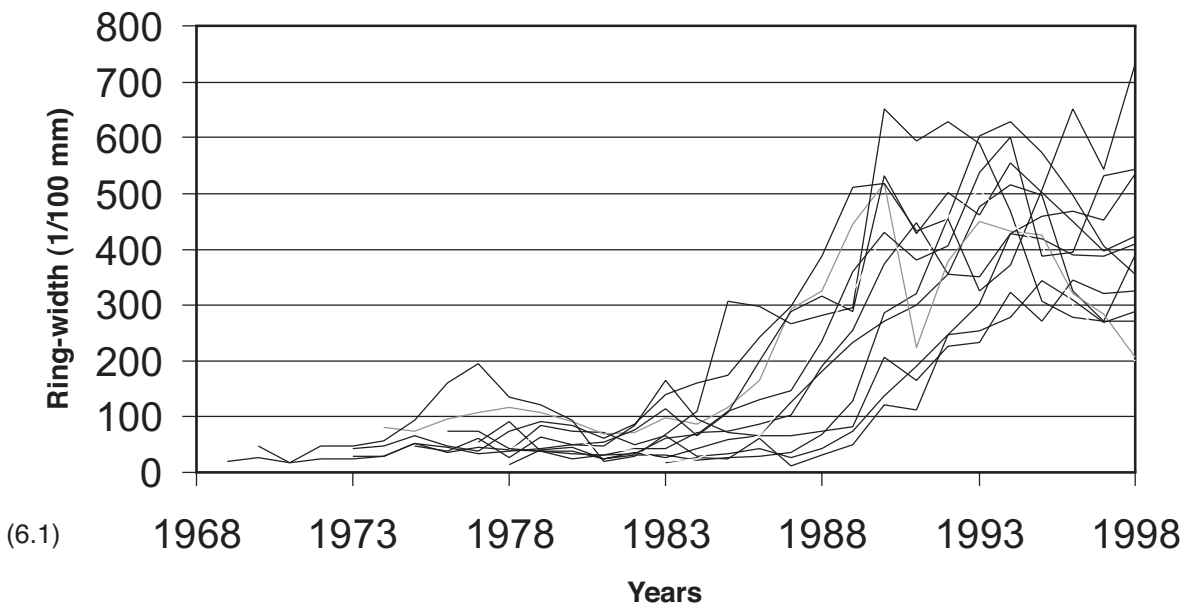
(6.1)

(6.2)

Fig. 6 - Radial growth curves of 10 spruces which have exceeded the upper browsing limit (Fig. 6.1) and of 10 heavily browsed spruces (Fig. 6.2).

absence of physical and chemical defences. Red cedar which does not show such a browsing limit because deer can bend branches to eat them is a fair example; in that case browsing limit is ca. 1.50 m.

Salal ageing

The ageing of shrub stems and the lack of stem recruitment from the stools (Pojar et al. 1980) differentiate stem age distribution between deer affected and deer free islands. On deer affected island, stems that overcome the browsing limit die without being replaced by new sprouts. On deer free islands, individuals are permanently rejuvenated by new sprouts which take over the older sprouts. This process is most noticeable for red huckleberry on deer

impacted island where most of individuals consists of few large, old decaying stems (authors observations and unpublished data). Our results confirm Pojar and Banner (1984) remark of an ongoing process that will lead to the total elimination of the shrubby understory on heavily browsed sites. These results show that studying of shrubs age structure can be powerful tools to measure past deer impact and its variation throughout time.

Salal chronologies and anatomical features

Low correlation between individual chronologies of non browsed salals may be explained by the young age, the competition and the local factors that are more important that regional climatic factors exerting little influence upon diameter growth. That could be linked to predominating endogenous factors which emphasize inter-individuals variations.

However at the scale of the individual shrub or that of ramifications, the occurrence of abrupt growth changes among ring series associated with browsing scars suggests using them as possible indicators of deer browsing. That is confirmed by the absence of anatomical scars associated with growth changes in our control sites. In the latter only few distortions and alterations occur perhaps associated to accidental breakage of small twigs.

By browsing shrubs deer creates many entrance ways for pathogens. Normally woody plants are able to develop structural and chemical boundaries in order to resist pathogen diffusion: that is the compartmentalization (Shigo 1984). Occurrence of brown coloration matching with wood alteration and bleaching matching with decaying wood are correlated to deer impact.

Pith located close to the bark indicates that a bud or a young twig was browsed and cambium was damaged. Lobes indicate that cambium was removed on one side. Pith position and form vary in the same way but less than section form which seems to be more sensitive and appropriate to assess deer impact. This is due to the fact that pith is formed before browsing impact and because cross-section form depends on cambium activity which can be altered by deer browsing. Differences between affected and non affected populations are

the largest in section form: χ^2 is highly significant (p<0.001).

Wedging rings are not always directly correlated to deer browsing. They are due to cambial activity failure which may happen even without deer pressure. Their occurrence changes in small proportions in comparison to other anatomical characteristics.

Considering that incidence and intensity of fresh signs of browsing are positively correlated to deer density (Gill 1992a) the same should apply to past browsing scars. Therefore using scar frequency and taking into account shrub mortality rate should help in reconstructing deer impact history.

Picea sitchensis*: ring width analysis and age*

Repeated browsing induces a very compact port due to intense ramification. It occurs on soft spring flush while sharp ligneous needles form efficient physical defenses throughout the rest of the year. Loosing of young needles is usually reported to be more detrimental than loosing older needles (Kulman 1971) and foliage loss is likely to be most costly during or soon after leaf expansion (Harper 1989). The rate of subsequent growth depends on damage severity (Gill 1992b). Repetitive browsing is worse than one single attack and keeps trees below browsing limit during several years (Gill 1992b). In the present study, as long as recruiting spruces are browsed, their average radial growth values is < 1 mm. When spruces cannot be reached any more by deer, a growth change is noticed, mean radial growth value is > 1 mm and it can reach 8 mm.

Because browsing reduces apical growth, it differs time when spruce escapes deer teeth. At our study sites it takes about 13 years for a young spruce to reach the height of 1.16 m necessary to isolate the apical bud from deer teeth. On the basis of the study by Coates et al. (1985) on Haida Gwaii showing that non browsed spruces need only 5 years to reach a height of 1.18 m we can conclude that deer browsing delays saplings recruitment by at least 8 years at deer densities such as those documented for the study sites.

It is far-reaching to underline that escaped trees reached the browsing limit of 1.16 m around 13

years of age whereas browsed trees smaller than the browsing limit are around 13 years old and measure less than 1.00 m (0.80 +/- 0.20 at Limestone Island and 0.90 +/- 0.10 at Reef Island). These saplings will reach the browsing limit within few years and then will be older than 13 years. This difference might be due to a recent increase in browsing pressure.

At Limestone and Reef, similar mean escaping ages and equivalent deer densities suggest a direct relationship between deer densities and their influence on growth. Eiberle (1985), Eiberle and Zehnder (1985) consider also that age of affected individuals is an efficient marker in browsing studies. The hypothesis according which mean escaping tree age would depend on deer density can therefore be advanced. In front of this problem, forestry service has decided to diminish felling intensity in order to compensate the delay in recruitment caused by disturbance (Henson 1980).

Conclusions

Deer browsing disturbs vegetation structure by removing shrub recruitment and causes delay in spruce recruitment.

Although limited by high inter-individual ring-widths variations in the salal controlled site, dendro-ecological approach can identify the effect of deer populations on salal by evidencing negative abrupt growth changes and mismatches between cross-section ring series of a same individual. In addition, anatomical characteristics analysis makes it possible to assess the effects of deer browsing on shrubs. Counting of anatomical anomalies evidences significant differences between impacted and non impacted populations. Stem geometry, pith form and eccentricity, scars, wedging rings, lobes and other various alterations are characteristics caused by deer impact. In a next stage, this study will aim at correlating anatomical characteristics frequency with browsing pressure on stems browsed at different intensities; afterwards attempts will be made to use such a calibration to assess deer populations.

Dendroecological approach seems to be most appropriate in identifying and assessing this influ-

ence throughout time taking into account spruce diameter growth and age. Pressure caused by repeated disturbances on spruce shoots induce on severely browsed saplings a very compact port whose consequences on forest management are essential. Besides influence on architecture, deer also causes a sharp radial growth decrease as evidenced by very narrow rings until sapling escapes deer teeth; then ring-widths increase. Browsing also disturbs apical growth and it delays habitat closing which implicates to take it in consideration in forest management.

Shrub age structure should make it possible to precise pressure variations exerted by herbivores throughout time. Taking into account understory age structure, traumatic anatomical characteristics and medium-frequency variations in radial growth patterns of recruited and dominant trees over a spatial scale should help know better spatial and temporal patterns of browsing effect on vegetation. Developing such an investigation is not only fundamental in understanding dynamic interactions but also to set forward predictive approaches of a sustainable management of temperate forests submitted to increasing browsing by wild ungulates.

References

Anderson RC, Loucks OL, 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadiensis* forests. Journal of Applied Ecology, 16: 855-861.

Banner A, Pojar J, Schawb JW, Trowbridge R, 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. In Scudder GGE, Gessler N (Eds.), The Outer Shores. Proceedings of the Queen Charlotte Islands First International Symposium, University of British Columbia, August

1984: 261-279.

Bordage G, Filion L, 1988. Analyse dendroécolgique d'un milieu riverain fréquenté par le castor (*Castor canadiensis*) au Mont du Lac-des-cygnes (Charlevoix, Québec). Naturaliste Canadian (Rev. Ecol. Syst.), 115: 117-124.

British Columbia Ministry of Forests, 1994. Queen Charlotte TSA timber supply analysis, B.C., Min. For., Victoria B.C

Carl GC, Guiguet CJ, 1972. Alien animals in British Columbia. Brit. Col. Prov. Mus. Handb. 14. Victoria, B.C.

Coates KD, Pollack JC, Barker JE, 1985. The effect of deer browsing on the early growth of tree conifer species in the Queen Charlottes Islands, B.C., Min. For. Research Report RR85002-PR.

Cook ER, Kairiukstis LA, 1990. Methods of dendrochronology. Applications in the environmental sciences. Kluwer Academic Press, Dordrecht.

Crawley M, 1997. Plant – herbivores dynamics. In Crawley M (Ed), Plant Ecology. Blackwell Science.

Duncan AJ, Hartley SE, Iason GR, 1998. The effect of previous browsing damage on the morphology and chemical composition of Sitka spruce (*Picea sitchensis*) saplings and on their subsequent susceptibility to browsing by red deer (*Cervus elaphus*). Forest Ecology and Management, 103: 57-67.

Eiberle K, 1985. Der wildverbiss als Forschungsproblem-dargestellt am Beispiel Bergahorns. Feld, Wald, Wasser, Schweizerische Jagdzeitung, 13: 38-44.

Eiberle K, Zehender H, 1985. Kriterien zur Beurteilung des Wildverbiss bei der weisstanne. Schei. Z. Forstwes., 136: 399-414.

Foster JB, 1989. Conservation on the Queen Charlotte Islands. In Scudder GGE, Gessler N (Eds.), The Outer Shores. Proceedings of the Queen Charlotte Islands First International Symposium, University of British Columbia, August 1984: 281-301.

Fritts HC, 1976. Tree-rings and climate. Academic Press, New York and London.

Gill RMA, 1992a. A review of damage by mammals in north temperate forests: Deer. Forestry, 65 (2): 145-169.

Gill RMA, 1992b. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry, 65 (4): 363-388.

Harper JL, 1989. The value of a leaf. Oecologia, 86: 53-58.

Haeussler S, Coates D, Mather J, 1990. Autecology of common plants in B.C.: a literature of review. Forest resource development, Agreement report 158.

Henson B, 1980. The impact of the introduced black-tailed deer of the Queen Charlottes Islands. B.C., Min. For. Report.

Hernandez MPG, Silva-Pando FJ, 1996. Grazing effects of ungulates in a Galician oak forest (northwest Spain). Forest Ecology and Management, 88: 65-70.

Huntly N, 1991. Herbivores and the dynamics of communities and ecosystems. Ann. Rev. Syst., 22: 477-503.

Kolischchkuk VG, 1990. Dendroclimatological study of prostrate woody plants. In Cook ER, Kairiukstis LA, (Eds.), Methods of dendrochronology. Applications in the environmental sciences. Kluwer Academic Press, Dordrecht: 51-55.

Kulman HM, 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol., 16: 289-329.

Mark AF, Bayliss GTS, Dickinson KJM, 1991. Monitoring the impacts of deer on vegetation condition of Secretary Island, Fiordland National Park, New Zealand : a clear case for deer control and ecological restoration. Journal of the Royal Society of New Zealand, 21 (1): 43-54.

Martin JL, 1994. The impact of red squirrel and black tailed deer on forest birds and vegetation in Laskeek Bay: a progress report. Laskeek Bay Conservation Society, Annual Scientific report, 1994, n°5, Queen Charlotte City, B.C.

Martin JL, Daufresne T, 1999. Introduced species and their impact on the forest ecosystem of Haida Gwaii. In Wiggins G (Ed), Proceedings of the cedar symposium, Canada, B.C. South Moresby Forest Replacement Account. Victoria, Canada: 69-89.

Martin JL, Brown J, Widmer-Carson L, Harfenist A, Heise K, Mercier S, 1993. The impact of introduced mammals on the vegetation and land of old-growth forest in Haida Gwaii (Queen Charlotte Islands): preliminary results. Laskeek Bay Conservation Society, Annual Scientific report, 1993, n°4, Queen Charlotte City, B.C.

Mopper S, Maschinski J, Cobb N, Whitham TG, 1991. A new look at habitat structure: consequences of herbivore – modified plant architecture. In Bell SS, McCoy ED, Mushinsky HR (Eds), Habitat structure.

Motta R, 1995. Dendroecology in ungulate forest damages: 1. Fraying scars. Dendrochronologia, 13: 33-41.

Motta R, 1996. Impact of wild ungulates on forest regeneration and tree composition of moutain forests in the Western Italian Alps. Forest Ecology and Management, 88: 93-98.

Motta R, 1997. Dendroecology in ungulate forest

damage: 2. Bark striping scars. Dendrochronologia, 15: 11-22.

Ogilvie RT, 1989. Disjunct vascular flora of Northwest Vancouver Island in relation to Queen Charlotte Islands' endemism and Pacific coastal refugia. In Scudder GGE, Gessler N (Eds), The Outer Shores. Proceedings of the Queen Charlotte Islands First International Symposium, University of British Columbia, August 1984: 127-130.

Payette S, 1987. Recent porcupine expansion at tree line: a dendroecological analysis. Canadian Journal of Zoology, 65: 551-557.

Peterson EB, Peterson NM, Weetman GF, Martin PJ, 1997. Ecology and management of Sitka spruce, emphasizing its natural range in British Columbia, U.B.C. Press, Vancouver, 336 pp.

Petrides GA, 1975. The importation of wild ungulates into Latin America with remarks on their environmental effects. Environmental Conservation, 2 (1): 137-151.

Pojar J, Banner A, 1984. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. In Meehan William R, Theodore R, Merell Jr, Thomas A, Hanley (Eds), Fish an Wildlife Relationships in Old-Growth Forests: Proceedings of a symposium held in Juneau, Alaska 12-15 April 1982. Amer. Inst. Fish. Res. Biol.

Pojar J, Lewis T, Roemer H, Wildford DJ, 1980. Relathionships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Unpubl. Rep. Brit. Col. Min. For. Smithers, B.C.

Reimoser F, Amstrong H, Suchant R, 1999. Measuring forest damage of ungulates: what should be considered? Forest Ecology and Management, 120: 47-58.

Schweingruber FH, 1988. Tree rings, Basics and applications of dendrochronology. D. Reidl. Pub. Compagny. Dordrecht, Holland.

Schweingruber FH, Eckstein D, Serre-Bachet F, Bräker OU, 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia, 8: 9-38.

Schweingruber FH, 1996. Tree Rings and Environment. Dendroecology. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscap Research. Berne, Stuttgart, Paul Haupt.

Shigo A, 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Ann. Rev. Phytopathol., 22: 189-214.

Taylor RL, 1989. Vascular plants of the Queen Charlotte Islands. In Scudder GGE, Gessler N (Eds), The Outer Shores. Proceedings of the Queen Charlotte Islands First International Symposium, University of British Columbia, August 1984: 121-126.

Veblen TT, Mermoz M, Martin C, Ramilo E, 1989. Effects of exotic deer on forest regeneration and composition in Northern Patagonia. Journal of Applied Ecology, 26: 711-724.

de Vos A, Manville RH, Van Gelder R, 1956. Introduced mammals and their influence on native biota. Zoologica: New-York Zoological Society, 41: 163-194.