Ann. For. Sci. 58 (2001) 853–859

Original article

Influence of browsing cessation on *Picea sitchensis* radial growth

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(Received 15 September 2000; accepted 18 January 2001)

Abstract – *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 precising 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.

***Picea sitchensis* / radial growth / browsing / modeling / black-tailed deer**

Résumé – Influence de l'arrêt de l'abroutissement sur la croissance radiale de *Picea sitchensis.* *Picea sitchensis* est un composant majeur tant au niveau écologique qu'au niveau économique des forêts pluviales et tempérées de l'Amérique du Nord. Sur l'archipel Haida Gwaii, qui est recouvert par une forêt des plus productive de Colombie Britannique (Canada), c'est une essence à forte valeur commerciale. La présente étude vise à préciser les conséquences de l'abroutissement par le cerf à queue noire sur la croissance des individus au cours de la régénération. Sur la base de séries d'épaisseurs de cernes, un modèle empirique de croissance radiale est construit. Il décrit l'effet de l'abroutissement et de la suppression de celui-ci lorsque les individus parviennent à dépasser la limite supérieure d'abroutissement. La prise en compte de l'impact du cerf sur la croissance radiale et de la limite supérieure d'abroutissement dans l'élaboration des modèles prédictifs de croissance en hauteur s'avère intéressante pour comparer les modèles de croissance de différentes espèces abrouties et en déduire des conséquences sur la dynamique forestière.

***Picea sitchensis* / croissance radiale / abroutissement / modélisation / cerf à queue noire**

1. INTRODUCTION

Herbivores were introduced in the early 20th century in several places of the world for game hunting [25]. Due to many habitats favourable to their development and/or due to the lack of predator, populations attained sufficient densities to exert significant impact on native vegetation and animal populations [16, 34]. Haida Gwaii archipelago is a fair example because among the eleven

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introduced species occurs the black-tailed deer (*Odocoileus hemionus sitchensis* Merriam) whose activities became dominant such as disturbing ecosystem functioning [10, 14, 26].

Introduced in the North of the archipelago in 1901, 1912 and 1925, black-tailed deer were not long to settle the whole archipelago. Single phytophagus after endemic caribou (*Rangifer dawsoni* Seton) became extinct in the 1920's [6] deers make up with forest exploitation major disturbance altering forest ecosystem dynamic. Browsing pressure exerted by deer has radically affected the structure and the function of understory hindering natural regeneration and impoverishing primary or secondary forest ecosystems [2, 10, 11, 17, 18, 19, 26, 28].

With regard to flora, deer are responsible of a severe impoverishing of understory [3, 28] in which numerous endemic species are located [23, 33]. This combined with structural site modifications is a major concern disturbing also fauna, particularly birds communities which decrease under introduced predators pressure [14, 17].

With regard to forest development, through browsing exerted on seedlings and saplings, fraying scars and bark stripping [20, 21] on older trees, deer induce high mortality rate, delay in recruitment [9, 35], wood depreciation and tree composition forest changes [1, 12]. Between the three main tree species in the study area, unequal deer browsing pressure among species results in the absence of *Thuja plicata* D. Don ex Lamb. regeneration and a sharp modification of *Picea sitchensis* (Bong.) Carrière recruitment whereas *Tsuga heterophylla* (Raf.) Sarg. seedlings and saplings are more often not eaten. Pojar and Banner (1984) concluded that the severe impacts of continued overbrowsing include the probable elimination of *Thuja plicata* as commercial timber species on Haida Gwaii and increasing damage to *Picea sitchensis* and *Tsuga heterophylla* especially in recent plantations. Changes concerning wood industry are quite noticeable and will become important in the future. So far, their main consequences are a deliberate decrease of annual timber volume in order to compensate the longer time necessary for re-establishment from expensive plantation with protected saplings [15].

The richness displayed by insular ecosystems such as those of Haida Gwaii is huge in terms of flora endemism, birds communities and timber quality produced; therefore understory browsing by deer induces far-reaching effects on biodiversity [23, 33], landscape and economy [24]. A five-year pluridisciplinary project "Forest ecology, forest renewal and introduced species in Haida Gwaii, Queen Charlotte Islands" carried out by the Research Group on Introduced Species aims at understanding the biological effects of species introduced in the forests of Haida Gwaii. This project focuses on the interactions between vegetation, introduced animals and it also investigates changes in the biodiversity and ecology of protected and harvested forests.

Because *Picea sitchensis* is an outstanding timber species in coastal British Columbia especially in Haida Gwaii archipelago where it covers 21% of the timber harvesting landbase [5], the present study aims at precising deer browsing consequences on growth regeneration of *Picea sitchensis*. Using ring-width series in order to evidence particular growth patterns, we aim at building an empirical model that describes impacts of browsing and cessation of browsing pressure on young tree growth. 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.

2. MATERIALS AND METHODS

2.1. Area characteristics

The Haida Gwaii archipelago (53° N, 132° W) situated on the Pacific coast (British Columbia, Canada) is composed of more than 150 islands (*figure 1*). Sampling was focused on Laskeek Bay islands, located in the eastern side of the archipelago which corresponds to the Coastal Western Hemlock Zone, wet Hypermaritime sub-zone [4]. At low elevation, old-growth forests consist of a mixture of *Tsuga heterophylla* the dominant species, *Thuja plicata* often codominant and *Picea sitchensis* of which regeneration depends on windthrow. The understory is composed of shrubs as *Gaultheria shallon* Pursh, *Vaccinium parvifolium* Smith in Rees, grasses, mosses and lichens [3].

2.2. Deer in British Columbia

On coastal British Columbia, black-tailed deer inhabits a variety of serial stages from recent clear-cut areas to old-growth forests. Type of habitat used depends largely on season and climate. Browsed species and their proportion evolve according to seasons and deer frequentation of sites [13]. Old-growth Western hemlock-Sitka spruce forests provide important habitat for black-tailed deer

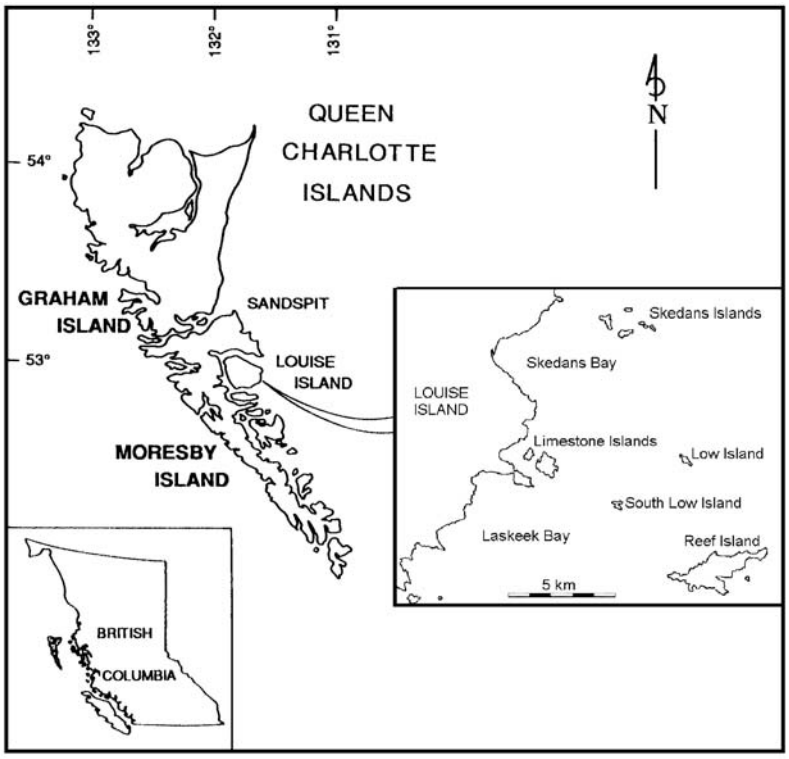

Figure 1. Haida Gwaii archipelago and Laskeek Bay islands.

whereas even-aged second-growth forests produce enough forage for the deer only during the 30 years following the felling [37] due to the canopy closure. On small islands (less than 300 ha) where the study is carried out and which are totally covered by primary forest, deer preferentially uses coastal range and windthrows. Those areas are privileged foraging sites because deer can find there an abundant and pioneer vegetation with better nutritive values than understory species [32]. In that areas, plant availability for deer foraging is low and mostly represented by *Gaultheria shallon* and *Vaccinium parvifolium* in shoreline, regeneration of *Picea sitchensis* and grass in windthrow.

2.3. *Picea sitchensis*

Picea sitchensis is a major component of North America north temperate coastal rain forest. Large, commonly to 70 m tall, it grows in pure or mixed stands often on moist well drained sites such as alluvial floodplains, marine terraces, headlands and old logs [27]. It is a shade-intolerant, submontane to montane evergreen conifer occurring in hypermaritime to maritime mesothermal climates on nitrogen-rich soils. Its occurrence increases with increasing latitude and precipitation and decreases with increasing elevation and continentality. It forms pure open-canopy stands along the outer-coast on sites affected by ocean spray and in advanced stages of primary succession on floodplains. *Picea sitchensis* is usually associated with *Tsuga heterophylla* or *Thuja plicata* in stands that have some of the highest growth rates in North America [24].

Picea sitchensis is a valuable commercial species. On Haida Gwaii, a mild climate, high rainfall, lack of summer drought and few diseases combine to give this archipelago some of Canada most productive forest lands. The Haida Gwaii land base contributed over 3% of British Columbia annual timber harvest, with Sitka spruce as one component of this harvest [24].

2.4. Sampling

Sampling is focused on individuals directly affected by disturbance [34]. Browsing induces on severely browsed spruces a shrubby port under the browsing limit; once saplings have overcome the browsing limit they dis-

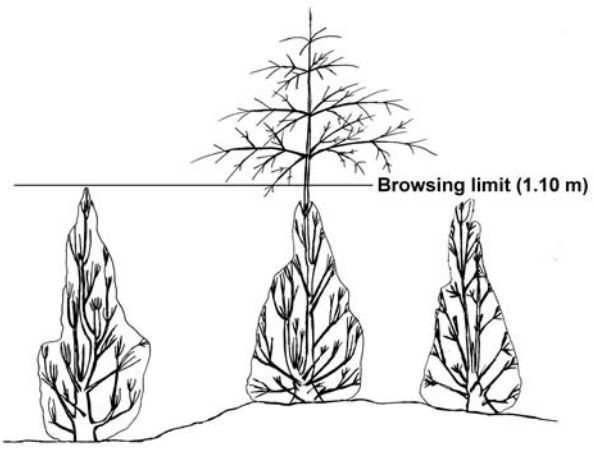

Figure 2. Architecture of still severly browsed spruces (below browsing limit) and of escaped spruces.

play a regular port above it (*figure 2*). Escaped individuals were collected in two windthrows of the coastal coniferous forest, on ecologically homogeneous and comparable islands. A first windthrow is located at Limestone Island (49 ha) and a second is located at Reef Island (249 ha). Both islands are characterized by a density of 0.30 deer/ha. No shrub layer, no ground vegetation, browsing limit occurring at 1.10 m and palatable species confined to inaccessible areas indicate a very heavy pressure according to the table completed by Reimoser et al. (1999). Sampling consisted in collecting at the bottom of each tree cores by means of a Swedish increment borer or stem cross sections taken when it was not possible to core them due to their small diameter. Coring was repeated until pith was reached for each tree. 37 spruces were sampled at Limestone Island; 4 spruces were sampled at Reef Island.

2.5. Method

Once cores or sections were sanded, two radii were measured (1/100 mm) along a radial file of cells using Eklund measuring device and ring-width series were crossdated. The average value of each ring was calculated in order to obtain a mean chronology for each tree according to dendrochronology methods [30, 31]. The particular radial growth pattern due to browsing evidenced in a previous study [36] was observed. This pattern is characterized by narrow ring widths followed by a sharp positive growth change occurring when herbivore

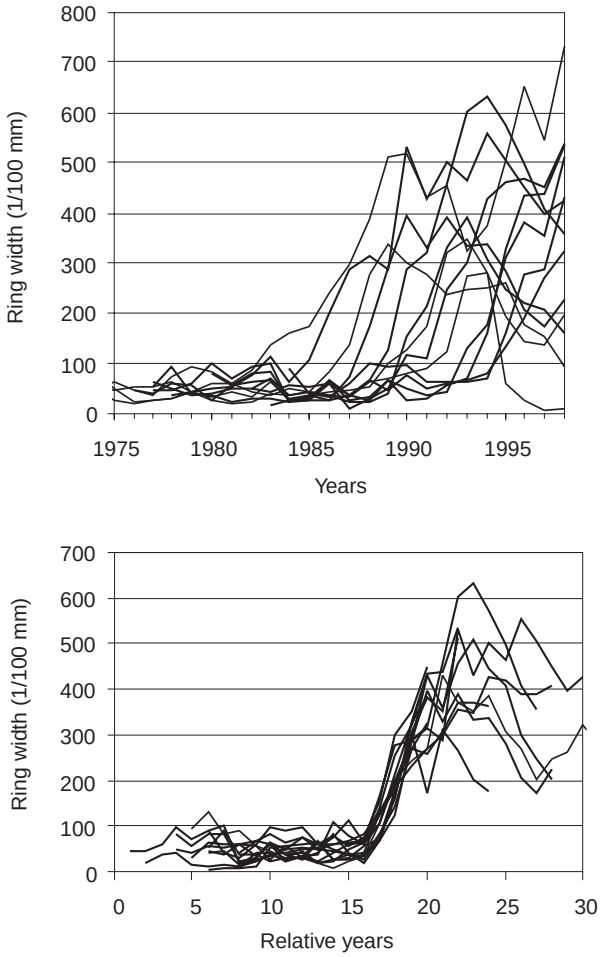

Figure 3. Above. Individuals ring-width curves synchronised according to years. Below. Individuals ring-width curves synchronised according to their abrupt growth change.

pressure stops (*figure 3*). Then each tree curve was synchronized with others according to its abrupt growth change. Standardizing of individuals ring-width series consisted in dividing each by its standard deviation. Then, median, 5th and 95th percentiles were calculated from those indexed ring series. Modelling of median, 5th and 95th percentiles was carried out by means of least squares method using sigmoid function identified on individuals radial growth curves.

$$50\text{th percentile} = 0.3 + \left(\frac{2.2}{1 + e^{(-1.2x + 4)}} \right)$$

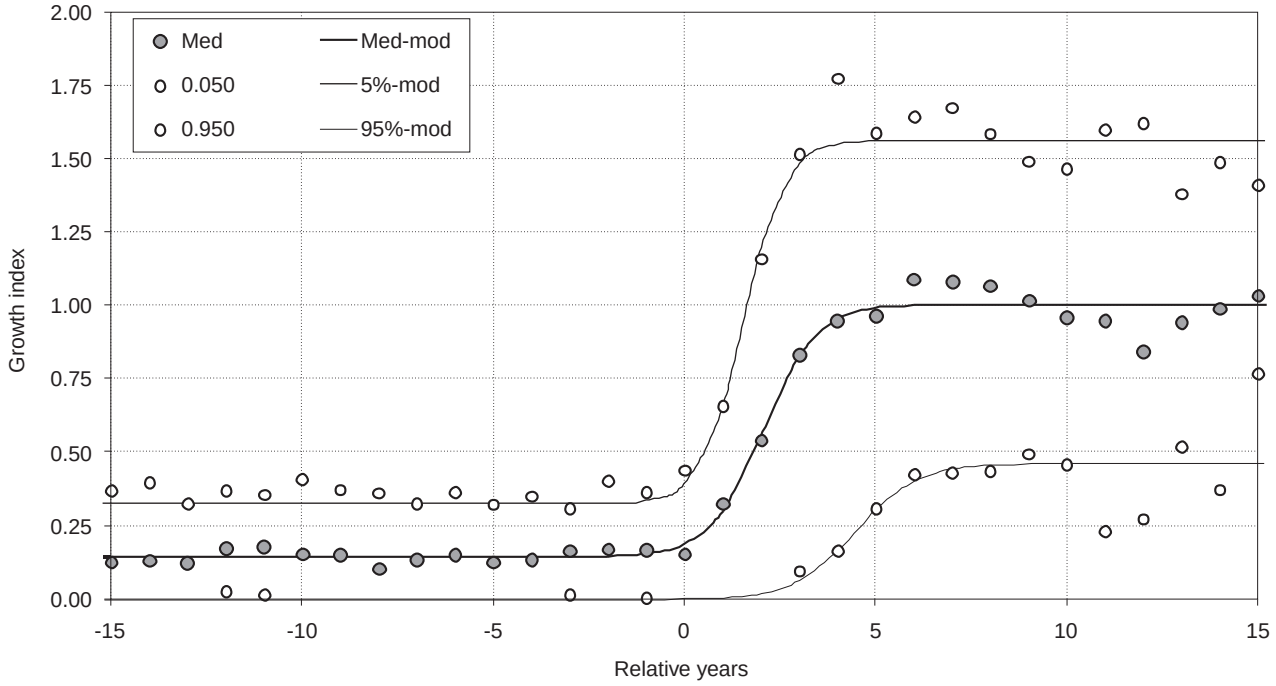

Figure 4. Radial growth model including browsing stage and escaped stage.

3. RESULTS

Ring width variations and differences between 5th and 95th percentiles are very low during the browsing period indicating that browsing exerts a severe impact (*figure 4*). Annual radial growth varies from a mean index equal to 0.14 during the browsing period to 1.0 when browsing stops: growth is multiplied per 7 within only 5 years. During browsing period, mean ring width is equal to 0.49 mm (σ = 0.06); then, it reaches 3.55 mm (σ = 0.50) when browsing ceases (Mann-Whitney test, t = 20.76; $p \leq 0.001$). Afterwards growth stays stable and common annual ring-widths variations are higher than during the browsing period which seems to evidence a higher sensitivity to interannual climate variations. Coefficients of determination are equal to 0.99 (median), 0.78 (5th percentile) and 0.95 (95th percentile).

4. DISCUSSION

Picea sitchensis is not heavily browsed when alternative food sources are available. Usually *Thuja plicata* is the preferred species for deers but even when it is present, little browsing occurs on *Picea sitchensis*. Coates et al. (1985) studied the effect of deer browsing in Haida Gwaii and found few browsing losses on *Picea sitchensis* or *Tsuga heterophylla* but heavily losses on *Thuja plicata*. But given that *Thuja plicata* is gradually eliminated by deer browsing, damages to *Picea sitchensis* and *Tsuga heterophylla* regeneration are expected to increase. As a result, systems of forest management involving small clear-cuts, shelterwood or selection will probably be ruled out by the intense browsing that occurs in all conifer regeneration in small cleared areas of Haida Gwaii forests [26]. Presently, due to growth delay in regenerating harvested areas, an annual allowable timbering reduction is being made in management acts (Tree Farm Licence 24) to overcome losses due to browsing [7]. For example, Vila et al. [35] showed that spruce saplings which are being browsed usually take more than 13 years to reach 1.10 m high, the browsing height above which growth gets undisturbed, while this height is attained within only 5 years for deer-protected saplings [9]. Therefore browsing pressure exerted by deer delays saplings recruitment up to 8 years when deer density is 0.30 deer/ha.

Height-age models are used in forestry to assess height from age and site-index. Height reflects the potential production of a site. A curve is generated by the

model for each site index [22] but problems occur as far as age is concerned. Either one considers age from the bottom or from a given height on the trunk. In the present study, breast height age (1.30 m) is more appropriate than age at the bottom because height growth below breast is largely disturbed by browsing. On Haida Gwaii where browsing limit occurs at 1.10 m high [36], breast height seems convenient but for areas under other ungulates browsing pressure, this level could be too low [7]. Generally, age determined at a given height should be preferred because underneath it is often influenced by competition with understory or other non-site factors [8]. Age allowance should not be neglected as a single small age error could lead to larger error in fertility index. In addition, the smaller the age and the higher the fertility, the higher the error.

Ring-widths analysis can provide information on the trees capacity (i) to stand browsing and on its temporal variation and (ii) to escape deer teeth. In the present study *Picea sitchensis* capability to survive and grow at a high rate, once escaped, reveals some resistance to browsing that does not occur in all tree species [7]. For instance, *Thuya plicata* is less resistant either because its seedlings are heavily browsed or because a much larger amount of foliage is browsed than for spruce; a large reduction of foliage induces a high mortality rate. As far as spruce is concerned, damages occur on young shoots during spring flush after winter consumption of other ligneous plants by deer [26]. Browsing results in ablation of young shoots of which only basal needles remain; previous years shoots are not browsed because thorny ligneous needles cause a physical defense.

5. CONCLUSION

Deer impact on ring series is characterized by a high growth reduction (8-year delay between impacted and non impacted saplings) and by very narrow rings which are followed by a positive growth change when herbivore pressure stops [36]. Present on all trees, browsed in the past and now escaped, this pattern can be modeled showing the homogeneity of tree response facing the disturbance. In next studies carried out by the Research Group on Introduced Species, two other browsed species (*Thuja plicata* and *Tsuga heterophylla*) will be analyzed in the same way in order to determine their growth pattern under browsing pressure to understand variations in regeneration dynamics susceptible to modify timber economy.

So far, growth of browsed saplings had never been modeled meanwhile it appears necessary to take into account accurately height growth only above the browsing limit otherwise the height-age model does not reflect growth potential supplied by the habitat but browsing pressure exerted at the site.

Developing such an investigation is not only fundamental in describing adequately growth patterns and therefore comparing specific responses to browsing and understanding interactions dynamic but also in setting forward predictive approaches of a sustainable management of temperate forests submitted to increasing browsing by wild ungulates.

Acknowledgments: The pluridisciplinary project is funded by the Forest Renewal British Columbia (FRBC), South Moresby Forest Replacement Account (SMFRA), International Program for Scientific Cooperation (PICS 489, France – Canada). Significant funding and logistic support are also provided by the Archipelago Management Board (Parks Canada), Laskeek Bay Conservation Society, Canadian Wildlife Service, Ministry of Forests and the CNRS in France.

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