Available online at www.sciencedirect.com

SCIENCE DIRECT

Forest Ecology and Management 181 (2003) 139–150

Forest Ecology and Management

www.elsevier.com/locate/foreco

Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps

Renzo Motta*

Dep. Agroselviter, Via Leonardo da Vinci 44, I-10095 Grugliasco (TO), Italy

Received 1 November 2001; received in revised form 10 June 2002; accepted 20 August 2002

Abstract

A new approach for studying browsing impact on the regeneration of rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) is presented. This approach can be a useful, complementary tool to damage surveys because it helps to identify possible underestimation of damage in cases where the most palatable species are likely to have completely disappeared due to browsing. The impact of wild ungulates on the height structures of the populations of these two species was studied at four sites in the Trentino area (Italy). The recorded height structures (affected by ungulate browsing) were compared with predicted structures and then residuals were calculated from power function models. The residuals of the most palatable species (rowan) showed that in all study sites there is a decrease in regeneration individuals in the height classes most affected by browsing. Indeed, the greater the density of wild ungulates, the greater the decrease, and in the site with the highest density (Paneveggio), there is a total absence of rowan individuals with a height between 100 and 160 cm. On the contrary, among the Norway spruce we did not observe a high number of residuals in the height classes affected by browsing. In order to better define the temporal dimensions of the browsing, a dendroecological study was conducted. Abrupt growth releases in the tree rings indicate exactly when the leader of a single tree escapes from intense browsing. An abrupt growth release chronology for each site and each species was thus constructed and the differences, in terms of the length and intensity of browsing, were evidenced. The dendroecological study did not show particular differences in the temporal distribution of abrupt growth releases in the Norway spruce, whereas it did show a significant difference for the rowan between the first three study sites and the Paneveggio site. After 1985, no further releases from suppression were observed in Paneveggio and we can therefore hypothesize that following that date, the browsing was so intense that it prevented any rowan individuals from growing beyond browsing height. The fact is that in Paneveggio, the impact from wild ungulates is splitting the rowan population in two: one part established and grew above browsing height before the recent wild ungulate population increase, while the second is made up of those trees that established after the wild ungulate population explosion and which at the time of measurement had either not yet reached browsing height or had been kept suppressed in the lower vegetation layers by browsing.

Keywords: Height structure; Browsing; Norway spruce; Rowan; Residuals; Abrupt growth releases

1. Introduction

Ungulate browsing can strongly influence the structure, composition, growth and succession of forest

* Tel.: +39-011-6708640; fax: +39-011-6708734.
E-mail address: rmotta.selv@iol.it (R. Motta).

0378-1127/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0378-1127(03)00128-2

stands as a result of the intensity and the selectivity of damage (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Risenhoover and Maass, 1987; Brandner et al., 1990; McLaren and Peterson, 1994a). It can compromise regeneration processes, both in cultivated forests and in natural or old growth forests. In cultivated forests, wild ungulates can reduce or compromise the profitability of wood production in artificially regenerated forests as well as in forests where close-to-nature silviculture has been applied. In the latter, ungulates can compromise natural regeneration and render silvicultural treatments inefficient or even useless (Bernhart, 1988; Ammer, 1996; Motta, 1999). In old growth forests, ungulate impact can compromise regeneration processes and biodiversity (Abrams et al., 1996; Linder et al., 1997).

Mountain forests are more vulnerable to damage than lowland forests to ungulate damage (Eiberle and Nigg, 1987; Ott, 1991; Motta, 1996). In these forests, regeneration is only possible every few years as it is linked to climate and seed production (Mencuccini et al., 1995); as a consequence, natural regeneration is divided into cohorts with a few years of distance between each one. At the upper-mountain and subalpine levels, the early growth of trees is very slow and young trees need an average period of 20–60 years (varying among diverse sites and species) to reach a height of 150 cm (Motta, 1996). This means that the trees are inevitably exposed to browsing for a long period and therefore just a few years of ungulate overpopulation, or a few severe winters when animal populations are concentrated in a limited area, are enough to endanger a recruitment process of decades.

Ungulates damage forest regeneration in three main ways: fraying (limited to deer species), bark stripping, and browsing (Gill, 1992a). Previous studies (Motta, 1996; Motta, 1999) have shown that fraying damage in the Italian Alps only occurs with a high incidence in the deer rutting range and in the event of exceptional deer densities, while bark stripping is limited to emergency winter foraging and only takes place with high red deer densities and during winters when deep snowcover restricts the range of animal movement. Letality rates (dead/damaged trees) are low for bark stripping, and though they are higher for fraying, they are almost always associated with a low overall incidence of damage. The letality rates for browsing are null or very low when ungulate density is low; they can, however, reach very high levels (also associated with a high incidence) in the most palatable species when ungulate density is high.

Ungulate browsing does not affect all species of trees throughout the forest in equal measure, but rather exhibits a marked preference for the most palatable species. Altered species composition due to selective foraging is a general feature of plant-ungulate interaction that extends across the temperate and boreal forests (Augustine and McNaughton, 1998). It is generally accepted that the incidence and intensity of browsing are causally associated with ungulate density (Tilghman, 1989; Maizeret and Ballon, 1990; Welch et al., 1991; Augustine and McNaughton, 1998), although ungulate density estimates are often imprecise no matter what method is used and no matter how competent wildlife managers are. Browsing takes place in a defined range of tree height from approximately 0 to 300 cm, depending on the ungulate species involved (Gill, 1992a).

Wild ungulate impact on forest regeneration is a relatively recent problem in the Italian Alps because, except for sporadic cases, the exponential increase of the ungulate population has largely occurred over the past 2–3 decades. For this reason there is a lack of long-term studies in the field and thus the effects of ungulate overpopulation are still relatively unknown.

In the last 10 years, some forest damage surveys have been carried out in the Italian Alps (Motta, 1999) and, in particular, in the Parks of the Autonomous Province of Trento (Motta and Franzoi, 1997; Armani and Franzoi, 1998).

Thanks to these surveys, important information has been collected about the incidence, type, selectivity and spatial distribution of ungulate damage. In addition, some general features common to all of the areas studied were observed and recorded. In terms of the incidence of damage in relation to ungulate density, an increase in damage was linked to an increase in ungulate density. A similar pattern was observed for most of the forest species, though an anomalous situation among some of the most palatable species was noted: indeed in some highly palatable species a stable value or an actual reduction in the incidence of damage was observed with increases in ungulate density. Based on these findings, we hypothesized that there was some underestimation of damage in the most browsed species and that this underestimation could be related to the intensity of browsing (Gill, 1992a). A high intensity in browsing could mean in effect that some individuals were completely browsed or had been kept suppressed in lower vegetation layers (and therefore not considered in the study figures); we also hypothesized that the length of time that the ungulates have been affecting forest regeneration could be related to the phenomenon of underestimation. In addition, we noted that the non-browsed individuals were those situated in "safe sites" (Harper, 1977), which provide them with protection from ungulate browsing. Therefore, it may well be that a simple measurement of browsing incidence alone can give rise to an underestimation of browsing impact.

There are two principal questions to be addressed: (1) how can the cumulative effect of past browsing be measured? (2) if some saplings have been completely browsed, is it possible to date the beginning of the period of intense browsing that produced their disappearance?

In order to answer these questions, we investigated two species: rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.). The former is common in montane and sub-alpine forests in the Alps. It is an edaphically unspecialized light-demanding pioneer species (partially shade tolerant during seed germination and juvenile stages) which colonizes clearings following natural and anthropogenic disturbances, although it rarely forms pure populations (Kullman, 1986; Zerbe, 2000). The Norway spruce, on the other hand, is one of the most widespread and important species in the Alps. It is commonly found in montane and sub-alpine forests and may be considered a shade tolerant late seral species.

The rowan is highly attractive to wild ungulates and consequently is much browsed (Ahlén, 1975; Miller et al., 1982; Szukiel, 1986; Eiberle and Bucher, 1989). Indeed, inventories of wild ungulate damage in various areas of the Italian Alps show that the rowan is generally the species most subject to browsing, and the incidence of browsing of the terminal leader shoot varies from 12.6 to 86.8% during regeneration.

On the contrary, the Norway spruce is among the least preferred species and is browsed only when more palatable species have been depleted or when there are no other species available. Inventories of wild ungulate damage in various areas in the Italian Alps show browsing damage in the terminal leader shoot whose incidence varies from 0.0 to 33.8% (Motta, 1999).

As an indicator of the cumulative effects of past browsing, we analyzed the height structure of the two species. Browsing damage influences many structural parameters of a forest stand, e.g. age, size and height structures. Among these structural parameters, height structure has proven particularly efficient for evaluating ungulate browsing impact. Browsing reduces vertical growth and, when sustained, it can prevent vertical development of the saplings by keeping them for decades in a non-reproducing state at a height vulnerable to browsing (Thomson et al., 1992; McLaren and Janke, 1996; Motta and Puppo, 2001).

It is possible to precisely define the height range of browsing for each specific ungulate species (Gill, 1992a) and then to subsequently identify which trees are potentially vulnerable to browsing and which have reached a height that puts them out of browsing danger (Gill, 1992b).

In order to investigate the temporal aspect, tree rings can be used to analyze the suppression effect of browsing (McLaren and Peterson, 1994b; Vila and Guibal, 2001; Vila et al., 2001; Chouinard and Filion, 2001). If the suppression is a result of browsing, then the release corresponds to the leader's reaching a height that is above browsing height. If the browsing is intense and prolonged, then the trees are either kept at a constant height which is low enough to be reached by browsing ungulates or else they are completely browsed and/or die.

Therefore, the aims of the present study were:

- to measure the incidence of wild ungulate browsing on the rowan and Norway spruce leader shoots in four study areas situated at the sub-alpine level with varying densities of wild ungulate populations;
- to record the actual height structures of the rowan and the Norway spruce populations and to quantify the impact of wild ungulates on these structures by evaluating the differences between the theoretical and actual structures under different wild ungulate densities;
- to reconstruct the impact of wild ungulate populations on the growth of young trees in recent decades by means of a dendroecological analysis.

2. Materials and methods

2.1. Site descriptions

The study was conducted in four sites situated in the sub-alpine belt at an altitude range varying between 1620 and 1820 m a.s.l. The sites are representative of the most typical sub-alpine forests of the Trentino area and are dominated by Norway spruce. The first site (PAN) is located in the Paneveggio Forest in the municipalities of Predazzo and Siror. The second site (SMA) is located in the S. Martino forest (municipality of S. Martino di Castrozza). Both forests are owned by the Province of Trento and are part of the Paneveggio–Pale di S. Martino Provincial Park. The third site (ADA) is located in the municipality of Madonna di Campiglio (Adamello) and the fourth (BRE) is located in the municipality of Pinzolo (Brenta), both of which are located in the Adamello–Brenta Provincial Park. The four sites are comparable with respect to altitude, tree density and growing stock (ranging between 250 and 300 m^3/ha). According to their Forest Management Plans, the sites have developed without silvicultural influence for several decades. The stand structures are generally mono-layered with a few small gaps. In the Paneveggio and S. Martino sites, the forests are made up almost exclusively of Norway spruce. In the Adamello–Brenta area, while the Norway spruce is the dominant species, it coexists with other sub-alpine conifers.

The ungulates present at the sites are red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.). The four sites show different ungulate densities (Table 1): red deer were re-introduced to the Paneveggio forest in the early 1960s whereas they have appeared more recently in the S. Martino and in the Adamello–Brenta forests; roe deer and chamois have always been present in all of the sites studied. The total number of all wild ungulates species has increased sharply in recent years (Armani and Franzoi, 1998).

The impact of the wild ungulates on forest regeneration was analyzed in a previous study by means of a systematic inventory of the damage caused by wild ungulates to forest species in the four sites (Motta and Franzoi, 1997; Armani and Franzoi, 1998). The purpose of these damage inventories was to describe the damage status of the studied areas: type of damage, quantity, forest species selectivity, and spatial distribution. In these inventories, "browsing damage" was defined only as the removal of the terminal leader, because this type of damage negatively influences both the future of the individual (there is a positive correlation between average height increment loss and mortality) (Eiberle and Nigg, 1987) and timber quality (Welch et al., 1991). Owing to the methodology adopted, the uprooting of small seedlings was not considered.

2.2. Height structures

Three transects were delineated at each site; each transect started from a small group of seed-producing rowan and ran along the contour lines of the respective hill slopes. The transects were 4 m wide, varied in length from 127 to 568 m, and were divided up in such

Table 1
Characteristics of the study sites

	Altitude (m a.s.l.)	Forest composition (dominant layer)	Ungulate density index[a] (UDI[b])
Paneveggio	1620–1760	*Picea abies* >95%	14.3
S. Martino	1740–1810	*Picea abies* >95%	6.0
Adamello	1640–1820	*Picea abies* >70%, *Abies alba*, *Larix decidua*	5.9
Brenta	1700–1780	*Picea abies* >70%, *Larix decidua*, *Abies alba*	6.8

[a] Data available for the whole area (Paneveggio, S. Martino, Adamello and Brenta, respectively) and not referred to the studied sites. The ungulate density in the Adamello and in the Brenta area is estimated from data related to municipalities only partially included in the Adamello–Brenta Park.

[b] Ungulate density index (UDI): red deer density + 1/4 chamois density + 1/5 roe deer density (all densities refer to 100 ha). This index represents the overall burden of all ungulate species present since it is not possible to identify the species responsible. Each ungulate species was taken into account using a relative weight proportional to the mean impact of a single animal on forest regeneration based on feeding requirements and the ratio of woody vegetation to total diet (Motta, 1996).

a way so as to include 200 rowan and Norway spruce individuals between 10 and 310 cm height in each transect. The minimum height was chosen in view of the fact that at a height of less than 10 cm it becomes very difficult to observe regenerating plants completely and accurately (Eiberle and Nigg, 1987); the upper height limit was chosen as it is the maximum height at which the wild ungulates were able to reach with their mouths, even in heavy snow conditions. Each Norway spruce and rowan specimen within the transects was examined for browsing damage in the terminal leader (Gill, 1992a), and its height was measured. The data from the three transects were than added up and height structures were calculated for all the individuals in each site. The power function (Hett and Loucks, 1976; Harper, 1977; Broad, 1998) is the most common equation used to characterize size structures in forest science. It is defined as:

$$y = y_0 x^{-b}$$

where y is the frequency of individuals of a given height class, x the height class and a and b are the parameters that control the slope and the shape of the curve, respectively. We used a coefficient of determination to assess the aptness-of-fit of the models. In order to reduce the site-induced wildlife influence in the modeling, one model was built using a curve fitted to all four rowan populations sampled. This model does not represent a reference curve in the absence of browsing (almost impossible to find in the Alps) because it includes the "average" effects of browsing in the four sites. The power function assumes a constant recruitment rate but allows for a changing mortality rate with age (Ågren and Zackrisson, 1990; Szeicz and MacDonald, 1995). Actually, at the sub-alpine level, forest regeneration does not occur every year but rather in cohorts every few years (at least for the Norway spruce). This pattern is accentuated in the age structure, although size and age structures are influenced not only by the date of establishment, but also by many other factors (e.g. light availability, nutrients, competition, etc.). Thus saplings that have the same date of germination may show a different growth rate, resulting in a continuous distribution among size and height classes for seedlings and saplings (Motta and Puppo, 2001). Deviations of the actual structures from the modeled structure may reflect a changing pattern of recruitment/survival over time and were calculated using residuals (Kaennel and Schweingruber, 1995). The residuals represent the noise of the system as well as any signal not accounted for by functional relationships (Fritts, 1976), and were used to highlight how and where the data measured were incoherent with the model. The residuals were calculated by subtracting predicted height frequencies (using the power function) from observed height frequencies after log-transformation. A value of 1 was added to each class frequency before log-transformation so as to be able to take empty classes into account (Ågren and Zackrisson, 1990).

2.3. Abrupt growth releases

An increment core was extracted at a height of 40 cm from 15 saplings of each species in each transect with a height >310 and <500 cm (a total of 45 saplings for each species and each site). All the cores were fixed to wooden supports and smoothed with a razor blade or by sanding until optimal surface resolution allowed annual rings to be measured. Ring-width was measured to within 0.01 mm and data were collected and stored using the LINTAB device and the TSAP package (Rinn, 1996). Due to multiple factors such as age, disturbance from browsing and heterogeneous growth, it was possible to cross-date only 40% of the chronologies. There were no missing rings in any of the cross-dated chronologies. Both the rowan and the Norway spruce produce distinct rings and therefore the accuracy of the ring count is high. Abrupt growth releases in radial growth (releases from suppression) were identified in all of the cores. We defined an abrupt growth release as a sudden increase in ring-width >166% relative to the previous 4 years (Schweingruber et al., 1990). Data from the three transects in each site were pooled, and an abrupt growth release chronology was constructed for each site.

3. Results

3.1. Incidence of browsing in the terminal leader

The ungulate population densities observed in the four sites are shown in Table 1. The incidence of ungulate damage observed in the transects was higher than that recorded in previous forest damage inventories covering the total surface area of the two parks (Motta and Franzoi, 1997; Armani and Franzoi, 1998; Table 2).

Table 2
Tree densities and browsing incidence in the terminal leader (BITL) at the study sites

	Norway spruce density (m^3/ha)	BITL[a] Norway spruce forest surveys (%)	BITL[a] Norway spruce study sites (%)	Rowan density (m^3/ha)	BITL[a] rowan forest surveys (%)	BITL[a] rowan study sites (%)
Paneveggio	3250	16	25	1430	45	52
S. Martino	2890	12	17	2924	50	58
Adamello	2416	10	16	1820	42	55
Brenta	2680	11	19	1166	51	60

[a] The browsing incidence is for regeneration between 10 and 150 cm height.

Damage was not uniformly distributed over all height classes, but rather concentrated in those at the browsing height of the wild ungulates present in the area, i.e. between 20 and 200 cm above ground level (Fig. 1).

3.2. Height structures

Height distributions of both species at all four sites showed a reverse J-shape (Fig. 2).

Table 3
Coefficient of determination for power function models fitted to the height structure data by linear regression of log-transformed data

	Norway spruce	Rowan
Paneveggio	0.98	0.56
S. Martino	0.97	0.84
Adamello	0.98	0.89
Brenta	0.98	0.93

The data were analyzed by height classes.

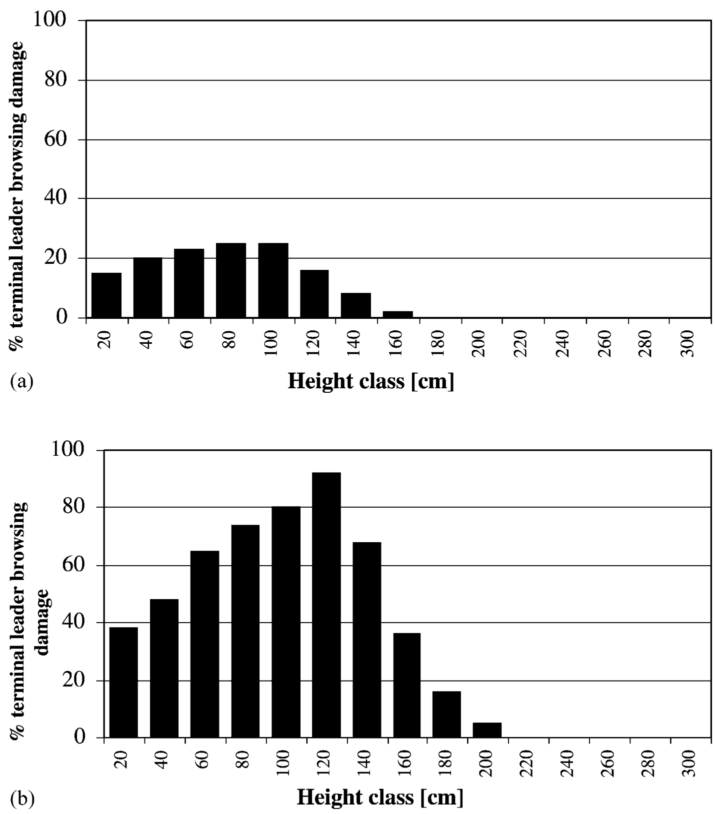


Fig. 1. Frequency of browsing damage incidence in the terminal leader by height class for Norway spruce (a) and for rowan (b).

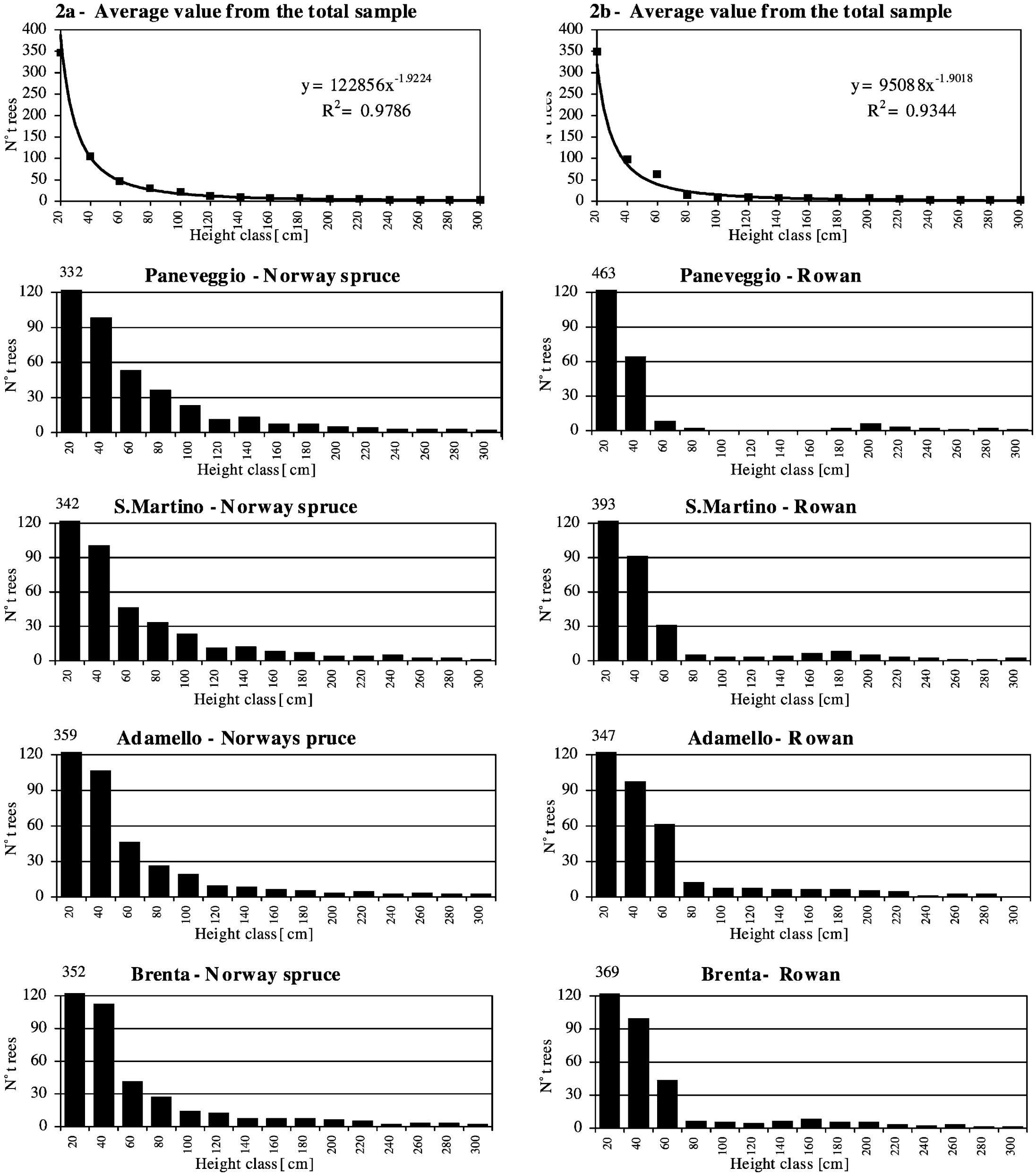


Fig. 2. Height structures of the total of the four Norway spruce populations (a) and of the four rowan populations (b). For the total sample the regression equation for the power function is given with its coefficient of determination.

For the Norway spruce, the power function model accounts for over 97% of the total variance of height structures at all four sites. For the rowan, the model accounts for over 84% of the total variance of height structures at the SMA, ADA and BRE sites, but for only 56% at the PAN site (Table 3) where no rowan individuals were found.

The Norway spruce residuals are very small and have a random distribution (Fig. 3a). On the contrary, in the rowan, the distribution of the residuals

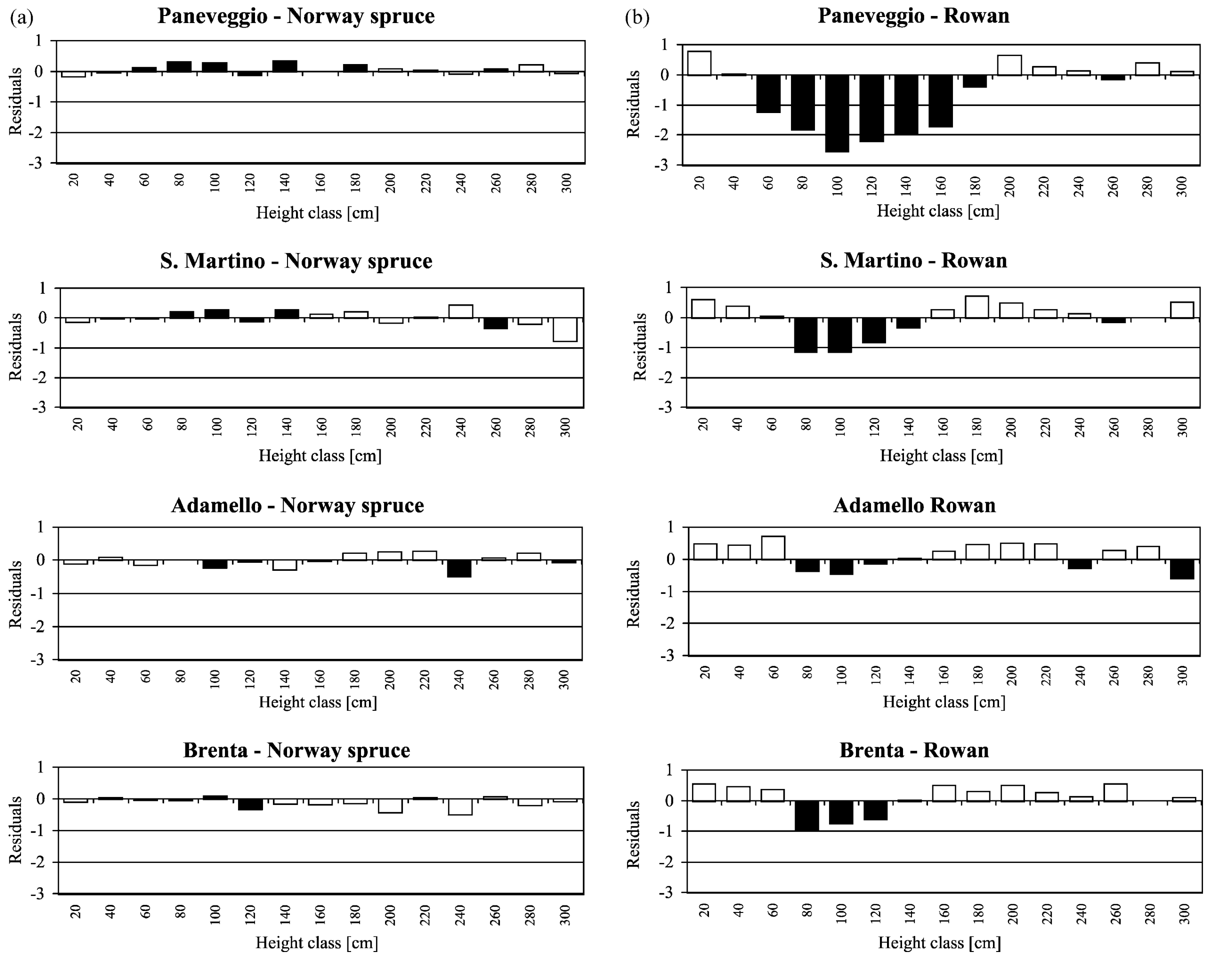


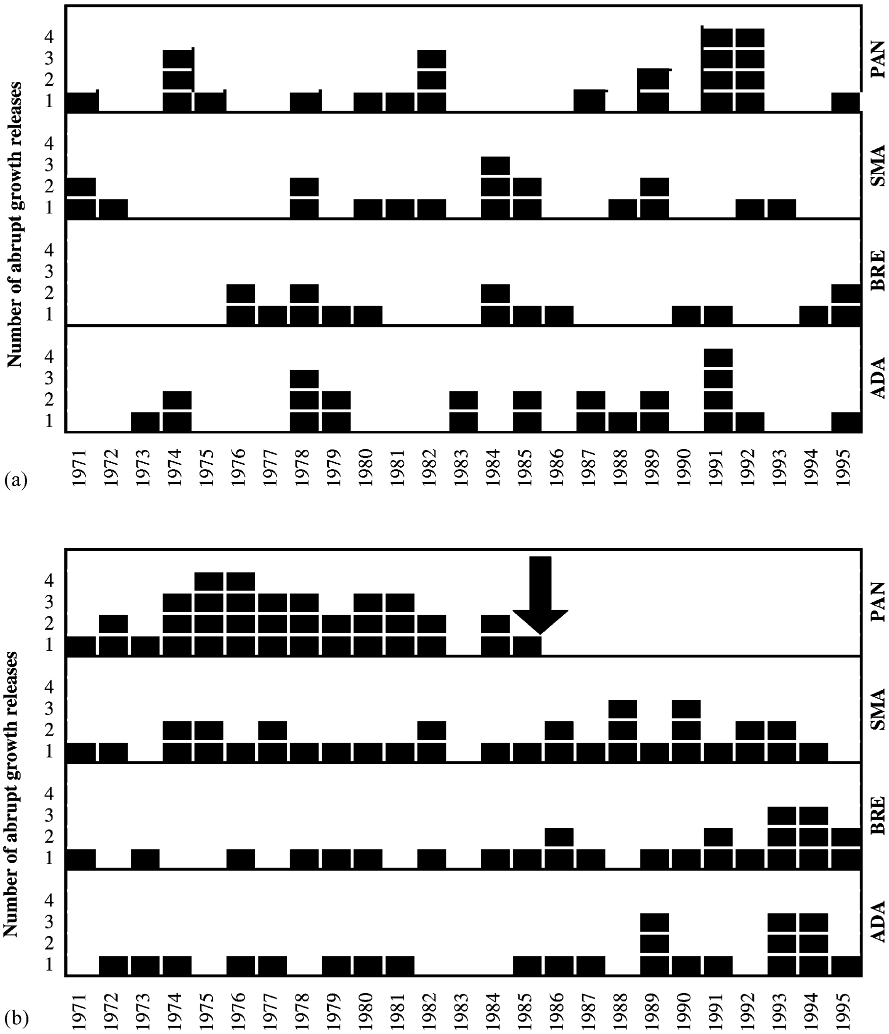
Fig. 3. Residuals, deviations of the present height structure from the modeled structure and from the power function model. Norway spruce (a) on the left and rowan (b) on the right. The residuals were calculated by subtracting predicted height frequencies (using the power function) from observed height frequencies after log-transformation. A value of 1 was added to each class frequency before log-transformation so as to be able to take empty classes into account.

is not random, and the 80–120 height classes are under-represented in all four sites (Fig. 3b). The most anomalous values were observed in the PAN site.

3.3. Abrupt growth releases

An analysis of the abrupt growth releases in the Norway spruce shows that the majority of saplings (55%) underwent a period of suppression. The releases (Fig. 4a) exhibit a distribution that is relatively continuous during recent decades, with some years that have a larger number of release events distributed randomly within the chronology.

The rowan data also show that many saplings in the study areas experienced a period of suppression (44%). As for the release chronologies (Fig. 4b), two distinct situations are observable: in the SMA, ADA and BRE sites, the releases show a distribution that is relatively continuous over time during recent decades, but with increased frequency since approximately 1988–1990. In the PAN site, on the other hand, all of the observed releases took place before 1985.



(a) (b)

Fig. 4. Abrupt growth releases chronology for the two species in the four sites. Norway spruce (a) and rowan (b). The arrow shows the end of abrupt growth release in Paneveggio that could be explained with the increase of ungulate density and browsing intensity. The level of browsing intensity inhibit the terminal leader of the rowans to grow above the height browsing range.

4. Discussion

The incidence of browsing in the terminal leader was much greater in the rowan than in the Norway spruce, as expected. In all of the areas studied and in both species, the height structures show a typical reverse J-shape. However, whereas the height structures of the Norway spruce correspond well to the theoretical model (Fig. 2a), the height structures of the rowan deviate from it (Fig. 2b). The analysis of the rowan residuals (Fig. 3b) shows that they are concentrated in the height classes within the browsing range. The residuals in the PAN site, as expected, present the greatest deviations in height structures from the theoretical model (Fig. 4b). Based on our results, I hypothesize that in the Norway spruce and rowan populations in the sites studied, deviation of the observed height structures from the theoretical model is mainly attributable to the activity of wild ungulates. A comparison between these two species, one not particularly palatable (Norway spruce) and the other very appetizing (rowan), offers some interesting insights into the impact of wild ungulates on forest regeneration. In the rowan, when an increase in ungulate density with a consequent increase in browsing incidence and intensity occurs (Gill, 1992a), the number of individuals in the highly browsed height classes decreases. In the present study, it is particularly evident that the ungulate impact in the PAN site corresponds to a total lack of rowan saplings in the 100–160 cm height class. This absence may be due either to the complete consumption or death of individuals, or to the constant browsing of the part of the tree that is outside the protective limits of grassy and shrubby vegetation (and of snow in winter).

As far as the abrupt growth release data are concerned, there is an important ecological difference in the behavior of the two species: the rowan is a pioneer, shade intolerant early seral species (partially shade tolerant during seed germination and juvenile stages), while the Norway spruce is a shade tolerant late seral species. The presence of trees that show abrupt growth releases among the Norway spruce is very common in sub-alpine forests (Schütz, 1969; Piussi, 1976) and the cause of this is difficult to link to one precise factor (i.e. increased availability of light or cessation of browsing) because the Norway spruce can establish under canopy cover and may remain suppressed for decades until natural or anthropogenic disturbances permit an increase in growth rate. On the contrary, the abrupt growth releases in the rowan may be linked to the cessation of wild ungulate browsing in the terminal leader (Kullman, 1986; Sperens, 1997; Zerbe, 2000). At any rate, it is not possible to establish a direct cause–effect relationship for each abrupt growth release and the dendroecological analysis may involve some unavoidable subjectivity, as is often the case in studies dealing with past disturbances in forest stands.

The analysis of the abrupt growth releases in the Norway spruce shows that the releases are randomly distributed over recent decades. Certain years with a high incidence of releases (e.g. 1991 in the PAN and ADA sites) can be linked to windthrows, but it is not possible to discriminate between the releases due to increased light availability and those due to a cessation of browsing in the terminal leader.

Regarding the release chronologies, two different and distinct situations emerge in the rowan: in the SMA, ADA and BRE sites, the releases are quite evenly distributed over past decades, with a somewhat higher frequency in recent years. On the contrary, the releases registered in the PAN sites all took place before 1985. We can hypothesize that the absence of releases in over the last 15 years in the PAN site is due to the heavy browsing of the terminal leader by wild ungulates, which prevents the leader from attaining a level above browsing height. Indeed, the impact of wild ungulates in the PAN site seems to be splitting the rowan population in two: one part established and grew above browsing height before the recent wild ungulate population increase, while the second one is made up of those trees that established after the wild ungulate population ‘‘explosion’’, and which at the time of measurement had either not yet reached browsing height or had been kept suppressed in lower vegetation layers by browsing. The starting date of this division in the PAN rowan population can be fixed at about 1985. This division, already marked, is likely to become even more pronounced over the next few years. Given that the rowan is not a long-lived species, a possible scenario is that in a few decades there will simply be no more fruit-bearing rowans in the site. Although the rowan appears to be particularly resilient to browsing, often surviving clipped to ground level (Miller et al., 1982), and has a great capacity for vegetative regeneration and survival without seedling establishment, its survival should not be entirely entrusted to these capacities alone.

5. Conclusions

Damage inventories, conducted in any manner, may underestimate browsing impact (Gill, 1992a). Browsing damage in the terminal leader acts as an important factor that limits the height growth of the forest regeneration. The ungulates browse the terminal leader, which reduces vertical growth, and in the case of sustained browsing, this can prevent vertical development, maintaining saplings for decades in a non-reproducing state and at a height vulnerable to browsing. Height structure is a useful tool for evidencing underestimation because there is a vertical damage range and most browsing occurs at an intermediate level between the ground and full reach; the most vulnerable height range varies among the different ungulates. In the areas studied, the most affected height classes are those between 80 and

140 cm. Depending on the palatability of the species and on the density of the ungulates, the importance of browsing as a limiting factor for the growth of forest regeneration may vary, but in the worst conditions, like those observed for the rowan in the PAN site, it is capable of completely obstructing the growth of the saplings.

A site's current situation in terms of regeneration density and damage also depends on the length of time that forest regeneration has been exposed to browsing. A dendroecological approach, based on the detection of abrupt growth releases, can be used to add a temporal perspective when historical data on ungulate impact on forest regeneration are scarce or completely missing.

Both height structures and abrupt growth release chronologies can be a useful complement to traditional and extensive browsing surveys (especially those associated with forest surveys) in order to evidence the impact of browsing on the population dynamics of the most palatable species and in order to detect, if present, an underestimation of ungulate impact on the forest regeneration of the most palatable species.

Acknowledgements

This study was funded by the European Union (RENFORS Project, FAIR, CT95-0420). The authors would like to thank Luigina Armani, Maria Franzoi and Barbara Garassino for their help during field sampling, and the "Paneveggio–Pale di S. Martino" and "Adamello–Brenta" Parks for having supplied data related to ungulate densities and for their collaboration during field surveys.

References

Abrams, M.D., Orwig, D.A., Dockry, M.J., 1996. Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, USA. Can. J. For. Res. 27, 994–1001.

Ågren, J., Zackrisson, O., 1990. Age and size structure of *Pinus sylvestris* populations on mires in central and northern Sweden. J. Ecol. 78, 1049–1062.

Ahlén, I., 1975. Winter habitats of Moose and Deer in relation to land use in Scandinavia. Swedish Wildlife Res. 9, 45–192.

Ammer, C., 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. For. Ecol. Manage. 88, 43–53.

Anderson, R.C., Loucks, O.L., 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. J. Appl. Ecol. 16, 855–861.

Armani, L., Franzoi, M., 1998. Foreste di montagna ed ungulati selvatici nei Parchi naturali del Trentino. Dendronatura 19, 37–48.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildlife Manage. 62, 1165–1183.

Bernhart, A., 1988. Waldentwicklung, Verjüngung und Wildverbiss im oberbayerischen Bergwald. Schweiz. Z. Forstwes. 139, 463–484.

Brandner, T.A., Peterson, R.O., Risenhoover, K.L., 1990. Balsam fir on Isle Royale: effect of moose herbivory and population density. Ecology 71, 155–164.

Broad, L.R., 1998. Allometry and growth. For. Sci. 44, 458–464.

Chouinard, A., Filion, L., 2001. Detrimental effects of white-tailed deer browsing on balsam fir growth and recruitment in a second-growth stand on Anticosti Island, Québec. Ecoscience 8, 199–210.

Eiberle, K., Bucher, H., 1989. Interdependenzen zwischen dem Verbiss verschiedener Baumarten in einem Plenterwaldgebiet. Z. Jagdwiss. 35, 235–244.

Eiberle, K., Nigg, H., 1987. Grundlagen zur Berteilung des Wildverbisses im Gebirgswald. Schweiz. Z. Forstwes. 138, 747–785.

Frelich, L.E., Lorimer, C.G., 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biol. Conserv. 34, 99–120.

Fritts, H., 1976. Tree-Rings and Climate. Academic Press, New York.

Gill, R.M.A., 1992a. A review of damage by mammals in North Temperate Forests. 1. Deer. Forestry 65, 145–169.

Gill, R.M.A., 1992b. A review of damage by mammals in North Temperate Forests. 3. Impact on trees and forests. Forestry 65, 363–388.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, Oxford.

Hett, J.M., Loucks, O.L., 1976. Age structure models of balsam fir and eastern hemlock. J. Ecol. 64, 1029–1044.

Kaennel, M., Schweingruber, F.H., 1995. Multilingual Glossary of Dendrochronology. Wsl/Fnp Birmensdorf, Paul Haupt, Berne.

Kullman, L., 1986. Temporal and spatial aspects of subalpine populations of *Sorbus aucuparia* in Sweden. Ann. Bot. Fenn. 23, 267–275.

Linder, P., Elfving, B., Zackrisson, O., 1997. Stand structure and successional trends in virgin boreal forests reserves in Sweden. For. Ecol. Manage. 98, 17–33.

Maizeret, C., Ballon, P., 1990. Analysis of causal factors behind cervid damage on the cluster pine in the landes of Gascony. Gibier Faune Sauvage 7, 275–291.

McLaren, B.E., Janke, R.A., 1996. Seedbed and canopy cover effects on balsam fir seedling establishment in Isle Royale National Park. Can. J. For. Res. 26, 782–793.

McLaren, B.E., Peterson, R.O., 1994a. Seeing the forest with the trees: using dendrochronology to investigate moose-induced changes to a forest understory. Alces 30, 77–86.

McLaren, B.E., Peterson, R.O., 1994b. Wolves, moose and tree rings on Isle Royale. Science 266, 1555–1558.

Mencuccini, M., Piussi, P., Zanzi Sulli, A., 1995. Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. For. Ecol. Manage. 76, 109–125.

Miller, G.R., Kinnaird, J.W., Cummins, R.P., 1982. Liability of saplings to browsing on a red deer range in the Scottish Highlands. J. Appl. Ecol. 19, 941–951.

Motta, R., 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. For. Ecol. Manage. 88, 93–98.

Motta, R., 1999. Wild ungulate browsing, natural regeneration and silviculture in the Italian Alps. J. Sustainable For. 8, 35–53.

Motta, R., Franzoi, M., 1997. Foreste di montagna ed ungulati selvatici nel Parco naturale di Paneveggio–Pale di S. Martino (TN). Dendronatura 18, 15–32.

Motta, R., Puppo, C., 2001. L'impatto degli ungulati selvatici sul sorbo degli uccellatori (*Sorbus aucuparia* L.) nelle foreste di montagna dei parchi provinciali del Trentino. Dendronatura 21, 43–57.

Ott, E., 1991. Verijüngungsökologische Besonderheiten im Gebirgsfichtenwald im Verleicht zur Bergswaldstufe. Schweiz. Z. Fortswes. 142 (11), 879–904.

Piussi, P., 1976. Observations sur l'âge et la croissance en diamètre de certains épicéas de haute montagne. F. Beiheft zu den Zeitschriften des Schweiz. 57, 66–73.

Rinn, F., 1996. TSAP Reference Manual. Version 3.0. Heidelberg.

Risenhoover, K.L., Maass, S.A., 1987. The influence of moose on the composition and structure of Isle Royale Forests. Can. J. For. Res. 17, 357–364.

Schütz, J.P., 1969. Etude des phénomènes de la croissance en hauteur et en diamètre du sapin (*Abies alba* Mill.) et de l'épicéa (*Picea abies* Karst.) dans deux peuplements jardinés et une forêt vierge. Supplemento alle Riviste forestali edite dalla Società Forestale, no. 114.

Schweingruber, F.H., Eckstein, D., Braker, O.U., 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8, 9–38.

Sperens, U., 1997. Long-term variation in, and effects of fertiliser on, flower, fruit and seed production in the tree *Sorbus aucuparia* (*Rosaceae*). Ecography 20, 521–534.

Szeicz, J., MacDonald, G.M., 1995. Recent white spruce dynamics at the subartic alpine treeline of north-western Canada. J. Ecol. 83, 873–885.

Szukiel, E., 1986. Ecological status of deer in the Western Sudety mountains in relation to large-scale regeneration. Sylwan 130, 49–58 (in Polish, with English abstract).

Thomson, I.D., Curran, W.J., Hancock, J.A., Butler, C.E., 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. For. Ecol. Manage. 47, 29–37.

Tilghman, N.G., 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildlife Manage. 53, 524–532.

Vila, B., Guibal, F., 2001. Assessing browsing influence in forest understory using dendrochronology on Haida Gwaii archipelago (British Columbia, Canada). Dendrocronologia 19, 139–151.

Vila, B., Keller, T., Guibal, F., 2001. Influence of browsing cessation on *Picea sitchensis* radial growth. Ann. For. Sci. 58, 853–859.

Welch, D., Staines, B.W., Scott, D., French, D.D., Catt, D.C., 1991. Leader browsing by red and roe deer on young Sitka spruce trees in Western Scotland. 1. Damage rates and incidence. Forestry 64, 61–82.

Zerbe, S., 2000. Eberesche und Birke: ein biologisch-ökologisches Kurzporträt von zwei sehr unterschiedlichen Weichlaubhölzern. For. Holz. 55, 499–502.