Ungulate browsing in winter reduces the growth of *Fraxinus* and *Acer* saplings in subsequent unbrowsed years

Andrea D. Kupferschmid · Harald Bugmann

Abstract Browsing by ungulates has become a hotly debated issue in many European mountain forests in the past century. *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. are broadleaved tree species that are preferentially browsed by roe deer (*Capreolus capreolus*) in central Europe. We analyzed growth data from shaded saplings of both tree species to quantify the extent to which height growth after game browsing is reduced in subsequent, unbrowsed years in forest stands.

Sixty saplings of *F. excelsior* and *A. pseudoplatanus* from forest stands at Albisriederberg (Switzerland) were available to us that had been dissected into pieces that then were split in the middle for counting tree rings and assessing ungulate damage. We fitted the von Bertalanffy growth equation to these height growth data and included a reduction factor for winter browsing.

Both tree species showed significantly reduced height growth in unbrowsed years after one to several browsing events in winter, and this effect increased with the number of browsing events. Saplings with a high growth rate showed a higher growth reduction. After winter browsing, height growth of *A. pseudoplatanus* saplings was less affected in unbrowsed years than that of *F. excelsior* saplings.

We conclude that browsed saplings of these species in forest stands are not able to compensate browsing-induced height loss, but that height differences between browsed and unbrowsed saplings probably increase over time. A comparison between our analysis and the parameters estimated using equations published by Eiberle for predicting age at 130 cm height suggests that our parameter values are rather conservative estimates of the growth reduction effect after winter browsing. Neither *F. excelsior* nor *A. pseudoplatanus* show a distinct pattern in browsing-induced growth reduction with respect to soil moisture, nutrient level, and altitude. We thus conclude that our results are likely to be valid for a wide range of forested sites.

Keywords Ash · Growth rates · Herbivory · Maple · Tree regeneration · Von Bertalanffy growth equation

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Introduction

Browsing by ungulates has become a major hazard for tree regeneration in many temperate as well as boreal forests in the past century (e.g., Coté et al. 2004; Gill 1992b; Putman 1996). Several factors are involved; among others, the number of ungulates has increased strongly and is likely to continue to do so in the future (e.g., Breitenmoser 1998; Caudullo et al. 2003; Rooney and Waller 2003), in particular, in the absence

of predators (cf. Breitenmoser 1998; Coté et al. 2004). *Acer pseudoplatanus* and *Fraxinus excelsior* are deciduous broadleaved tree species that are often preferentially browsed by red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and chamois (*Rupicapra rupicapra*) in central Europe (e.g., Ammer 1996; Brändli 1996; Eiberle and Bucher 1989). Browsing by ungulates has therefore been reported to cause growth delays (Eiberle 1985a, b; Pépin et al. 2006) or even a loss of preferentially browsed species in forest stands (Brändli 1996; Gill and Beardall 2001).

Particularly, growth delays have been reported for *A. pseudoplatanus* and *F. excelsior* saplings based on a comparison of the age of unbrowsed saplings to that of browsed saplings of the same height in forest stands (Eiberle 1985a, b; Rettich 1985). In these investigations, the stems of saplings with a height of 130 cm were split vertically to determine the sapling age by counting the tree rings, and to count the number of all damage that were due to ungulates. Based on these data, linear equations to predict age at height 130 cm (A_{130}) from the total number of shoot browsing events (V_{130}) were calculated (where a and b are parameters):

$$A_{130} = a + b * V_{130} \qquad (1)$$

This study resulted in a higher age the more often a sapling was browsed (Eiberle 1985a, b; Eiberle and Nigg 1987; Rettich 1985). These results were then used to determine "tolerable browsing intensities" (e.g., a maximum of 23% of the saplings of either species can be browsed per year without long-term regeneration failure, cf. Eiberle 1985a, b); these data are still used in Switzerland today, e.g., as a base for negotiations between foresters and hunters to stipulate shooting quotas (for an English summary of the method to calculate browsing intensities, see Berwert-Lopes 1996).

However, this approach has considerable shortcomings, as saplings typically grow some years before they are browsed the first time, and they usually also have unbrowsed years following the browsing event(s) in which they may be able to catch up in height to some degree. Therefore, rather a "height delay" than a "growth delay" was reported in these experiments, and an accurate analysis of height increments based on these detailed data is still missing.

By contrast, an increase of the height increment was measured in several investigations after (repeated) simulated browsing between late autumn and budburst in spring (cf. Krefting et al. (1966) for *A. spicatum*, Canham et al. (1994) for *F. americana* and *A. rubrum*, and Eiberle (1978) for *F. excelsior* and *A. pseudoplatanus*) or after sheep grazing (cf. Hester et al. (1996) for *F. excelsior*). According to these studies, sapling height 2–10 growing season after the cessation of clipping was similar to the height of control saplings (Canham et al. 1994; Eiberle 1978) or even significantly greater, i.e., over-compensation occurred (Eiberle 1978). The reaction was more pronounced, the higher the simulated browsing intensity was (Eiberle 1978; Hester et al. 1996; Krefting et al. 1966). Common to all these investigations was that saplings grew in open sites without strong nutrient limitations.

As the growth of tree saplings is light-dependent (e.g., Ammer 1996; Harmer 1999), it is likely that saplings react differently to tissue loss due to browsing if grown in full light (open sites) versus in shade (closed forest stands). An interaction between light conditions and response after browsing has been reported for example for *Sorbus aucuparia* (Bergman 2001) and *Abies alba* (Häsler et al. 2008). For *Acer rubrum* and *F. americana*, however, there was no significant interaction term between light level and clipped/unclipped for height or height increment, but for new shoot biomass and starch root reserves (Canham et al. 1994). Yet, little is known about the height growth in the years after a browsing event of individual saplings of both *A. pseudoplatanus* and *F. excelsior* growing in forest stands.

For forest management applications or for simulating the effects of browsing on forest succession in near-natural or primeval forests, sapling response to browsing under shaded conditions should, however, also be known, and we therefore focus on shaded saplings here. The objectives of this study were (i) to determine to which extent height growth of browsed *Acer pseudoplatanus* and *Fraxinus excelsior* saplings is influenced in subsequent, unbrowsed years in forest stands (i.e., under shaded conditions), and (ii) how widely generalizeable this growth reaction is.

To this end, we re-analyze data on sapling age and browsing events collected by Rettich (1985) in forest stands. We investigate individual height increments in unbrowsed years after a browsing event and compare these to the height growth of saplings of the same height that have never been browsed, and to height

growth data from years prior to the first browsing event of browsed saplings. As we thus focus on the comparison of height increments of browsed saplings prior to browsing with height increments of saplings after browsing, we ensure that the patterns observed were due to browsing damage and not to variables that may be confounded with browser preferences, i.e., with other differences between individuals that could have driven different growth patterns of never browsed versus browsed saplings.

Unfortunately, individual sapling data including annual height increments and the single browsing years for these two species were available only for one site (cf. Rettich 1985). We therefore evaluate how the relationship between browsing damage and growth is likely to vary with elevation and soil moisture/nitrogen levels by additionally re-analyzing data from a variety of sites published by Eiberle (1985a, b) in the form of parameters for Eq. 1.

Methods

Study site

Rettich (1985) sampled saplings of both *Fraxinus excelsior* and *Acer pseudoplatanus* on Albisriederberg in the Research forest of ETH Zürich, southwest of Zürich (47°21′30″–22′30″ N and 8°28′–29′45″ E). The forest lies between 470 and 850 m a.s.l. on acid brown soils. The estimated mean annual precipitation is 1,200 mm and the estimated mean annual temperature is 7°C. These forest stands belong to the *Galio odorati-Fagetum typicum* and *Aro-Fagetum* associations; structurally, they originate from coppice with standards (so-called "Mittelwälder") that were transformed into high forests with a standing volume of ca. 300 m³/ha. At least 5% of the number of understory trees were *F. excelsior* and *A. pseudoplatanus* (Rettich 1985). The area is part of a wildlife sanctuary with a high number of roe deer (*Capreolus caprolus* L.). The interannual variation in browsing intensities was small and not correlated with tree growth rates. A detailed description of the site can be found in Rettich (1985).

Sampling design

Sixty naturally regenerated saplings (no sprouts) of *Fraxinus excelsior* and 60 of *Acer pseudoplatanus*

with a height of about 125–130 cm were cut at their base in spring 1985. The saplings to be sampled were determined using a regular grid with 80 m between the intersection points of the grid, where for each intersection point the nearest (distance <25 m) sapling of both species was chosen. A subjective choice of vigorously growing saplings was therefore avoided, and the sampled saplings typically grew in at least partly shaded conditions and not under full light (Rettich 1985).

All saplings were dissected into pieces of 5 cm length in order to count the tree rings. The resulting pieces were split in the middle and all ungulate damage were noted and dated back to the corresponding year. Along the split-up stems, marks of shoot browsing can be detected even if they are not visible from the outside of the stem any more, in particular by tracing the darker heartwood (cf. schematic view in Fig. 1 and detailed descriptions in Eiberle and Nigg 1984; Mlinsek 1969). Only terminal shoot damage but not twig and leaf browsing can be detected using this method. The assessment of bud browsing versus damage due to frost, insect, mice, and birds is difficult to impossible, but it is reasonable to assume that such damage were rare in the study area.

The following definitions were used for the re-analysis of these data: Spring browsing = sapling had been browsed on their shoots and continued to grow in the same growing season; winter browsing = sapling was browsed after the end of a growing season.

Data analysis

To analyze sapling growth, we utilized the von Bertalanffy growth equation, although there are many other growth equations that could have been used
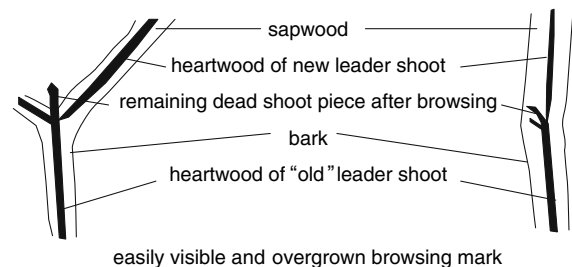

Fig. 1 Schematic diagram of vertically split sapling stems that can be used to determine past shoot browsing events

(Zeide 1993). This choice was made because (i) the equation has been used successfully in forestry for simulating growth of saplings up to old trees (e.g., Colbert et al. 2004; Rammig et al. 2007; Vanclay 1994), (ii) it has a biologically motivated base (von Bertalanffy 1957; Zeide 1993), and (iii) it has only two parameters (cf. Eq. 2, contrast to Chapman-Richards that has three parameters). The integral form of this equation for height at age A (H_A) as a function of sapling age (A, i.e., the time), a growth rate parameter (g) and maximum tree height (H_{max}, i.e., the asymptote as $A \to \infty$) is (cf. Zeide 1993, Table 1):

$$H_A = H_{max} * \left(1 - e^{(-g*A)}\right)^3 \qquad (2)$$

The differential form for height increment (Δh) is:

$$\Delta h = 3 * H_{max} * g * e^{(-g*A)} * \left(1 - e^{(-g*A)}\right)^2 \qquad (3)$$

Alternatively, after decomposition this can be expressed as (cf. Zeide 1993, Table 1):

$$\Delta h = 3 * g * \left(H_{max}^{1/3} * H_A^{2/3} - H_A\right) \qquad (4)$$

As the scope of our work was to analyze the growth reduction effect of browsing, the growth parameter g in Eq. 4 was substituted by $\frac{g}{(vW*W)+1}$ in the case of winter shoot browsing, resulting in

$$\Delta h = 3 * \frac{g}{(vW * W) + 1} * \left(H_{max}^{1/3} * H_A^{2/3} - H_A\right) \qquad (5)$$

In the case of spring shoot browsing, g was substituted by $\frac{g}{(vS*S)+1}$, and when both spring and winter shoot browsing occurred by $\frac{g}{(vW*W)+(vS*S)+1}$. The

variables W and S denote the sum of winter (W) and spring (S) browsing events per sapling, and vW and vS are reduction parameters. Note that W and S stand for the sum of browsing events up to a certain age, and not the total sum of winter or spring browsing events during the total life span of a sapling. For example, if a sapling was browsed at the end of its second and fifth year, W was 0 at age 1, 1 at ages 2–4, and 2 at age 5.

To examine whether saplings grew less or even more after a browsing event, non-linear mixed-effects models (part of the nlme package (Pinheiro et al. 2005) of the software R 2.2.0 (R Development Core Team 2005)) were fitted for height increment in unbrowsed years as the response variable. Thereby all saplings were included as being unbrowsed up to the first browsing event (i.e., they were included in Figs. 2a and 3a). If a sapling had been browsed on the shoot of year x, height increment in the year x was excluded from this analysis, and from the year $x + 1$ until the next browsing event, it was defined as once browsed (i.e., included in Figs. 2b and 3b). In the case of a first browsing event in winter, we thus included in our analysis the first growing season after the browsing event. In the case of a first browsing event in spring or summer, we however excluded from our analysis the first reaction of the sapling during the growing season in which it had been browsed (i.e., year x), knowing that the sapling continued to grow until the end of the growing season and probably compensated partially or fully for the height loss. However, as we do not know the amount of tissue lost due to browsing and the exact time of browsing, we decided to focus on the unbrowsed years subsequent to browsing.

Table 1 Overview of the sample of the 60 *Acer pseudoplatanus* and 60 *Fraxinus excelsior* saplings

Species	0x		W															S		S + W	
	(N_{never})		1x		2x		3x		4x		5x		>5x		≥1x		1x		2–12x	
	N_t	N_i	N_t	N_i	N_t	N_i	N_t	N_i	N_t	N_i	N_t	N_i	N_t	N_i	N_t	N_t	N_i	N_t	N_i
Acer	41(4)	102(22)	27	54	18	27	12	24	6	11	3	5	3	7	43	2	4	5	8
Fraxinus	42(4)	94(17)	22	54	9	11	4	5	6	11	4	6	2	2	38	0	0	7	9

"0x" = trees which have been never browsed or have unbrowsed height increments prior to the first browsing event. W = winter browsing, where "1x" = trees that have had a browsing event during winter and in the subsequent year(s) have unbrowsed height increments; "2x" = trees that have been browsed twice and in the subsequent year(s) have unbrowsed height increments. "3x" – ">5x" = analogous to "1x" but 3x till >5x browsed. "≥1x" = all trees that have been browsed at least once in winter and that have unbrowsed year(s) afterwards. S = browsing in spring or summer with unbrowsed year(s) afterwards. $S + W$ = browsing in spring/summer and in the same year in winter with unbrowsed height increments in the subsequent year(s). N_t = numbers of tree saplings that had at least one unbrowsed year after 0–12 browsing events, N_i = number of unbrowsed height increments after 0–12 browsing events

Equation 5 with height as the explanatory variable was used in the analysis, thus fitting g, vW, and vS as fixed parameters, and g additionally as a random parameter with individual saplings as the grouping factor. This was done separately for each tree species, with 40 m as the maximum height parameter (H_{max}) for *F. excelsior* and 35 m for *A. pseudoplatanus* (cf. Brzeziecki and Kienast 1994). As most of these saplings were exactly 125 cm tall, this led to abnormalities in the distribution of the residuals and we therefore excluded from our analysis the last measured height increment of each sapling. The fit of the growth models was evaluated by verifying the

distribution of the residuals and by using the AIC criterion with a likelihood ratio test.

Comparison with data from Eiberle

As we wanted to know how widely applicable the g, vW, and vS parameters are, we compared our results with data from Eiberle derived from a variety of sites at differing altitudes and differing soil moisture and nutrient levels. Eiberle published equations for *A. pseudoplatanus* (Eiberle 1985a) and *F. excelsior* (Eiberle 1985b) from several sites to predict age at
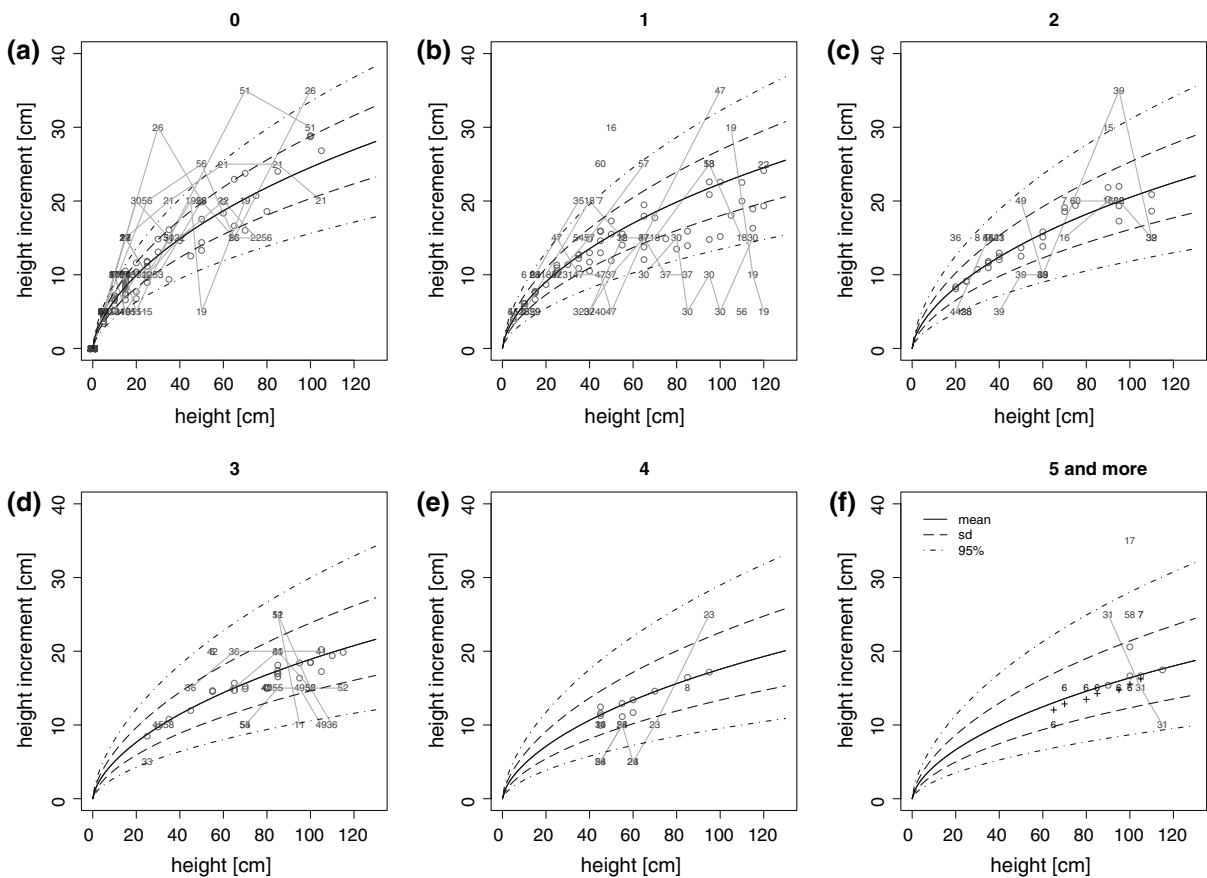

Fig. 2 Variability of observed unbrowsed height increments (gray numbers aligned with gray lines) and fitted height increments (open black circles) versus observed height of individual *Acer pseudoplatanus* saplings. Each panel shows the results for saplings in unbrowsed years after having been browsed 0–5 and more times in winter (cf. panel titles). In Table 1 the number of trees and number of height increments included in each panel is listed. In the last panel, observed unbrowsed height increments of the saplings that were browsed more than 5 times are shown with black numbers indicating

their number of browsing events (rather than tree numbers) and with black crosses their fitted height increments (analog to the open black circles). Black lines represent estimates based on Eq. 5, combining (i) the upper 95% confidence interval of the mean of the parameter g with the lower 95% confidence interval of the mean of the browsing reduction parameter vW, and vice versa (labeled 95%), (ii) the means of g and vW (labeled mean), and (iii) the means plus/minus the square root of the sum of the variances of the fixed and the random g, and the standard deviation of the fixed vW (labeled SD)
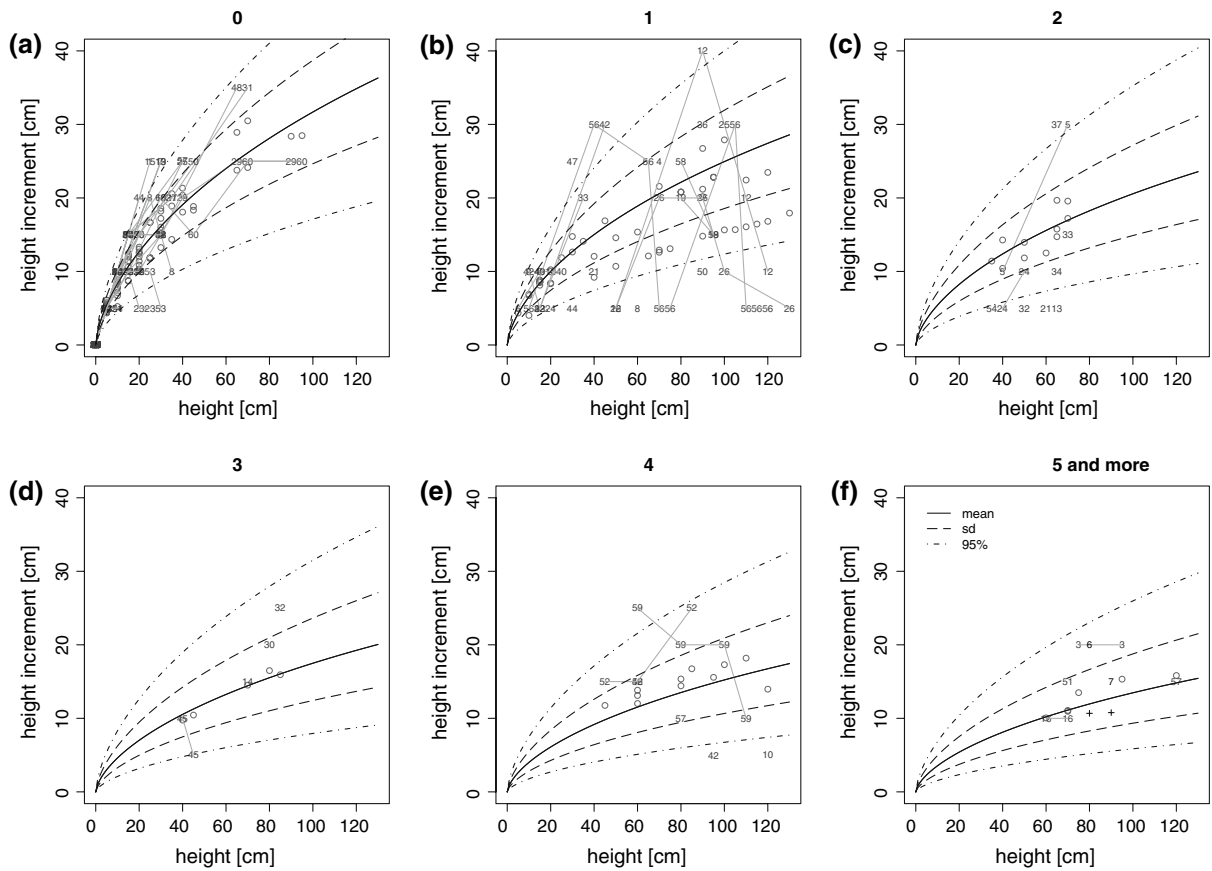
Fig. 3 Variability of observed unbrowsed height increments (gray numbers aligned with gray lines) and fitted height increments (open black circles) versus observed height of individual *Fraxinus excelsior* saplings. Each panel shows the results for saplings in unbrowsed years after having been browsed 0–5 and more times in winter (cf. panel titles). In Table 1 the number of trees and number of height increments included in each panel is listed. For details, see Fig. 2

height 130 cm (A_{130}) as a linear function (cf. Eq. 1) of the total number of all winter and spring browsing events (V_{130}). Note that Eiberle's V_{130} values do not account for the distribution of browsing events throughout the sapling's lifespan, but rather treat the browsing events as if they all occurred simultaneously at germination. Thus, it neglects the fact that saplings often grew some years without having been browsed. Returning to our example sapling that was browsed at the end of its second and fifth year, resulting in a value for W of zero at age 1, one at ages 2–4, and two at age 5 (including the years 1, 3, and 4 in the analysis of unbrowsed years), this would have been simply integrated in Eq. 1 with $V_{130} = 2$. Furthermore, no information about the season of the browsing event is available, thus only a browsing reduction parameter v instead of vW and vS can be obtained.

Based on Eq. 2, height increment (Δh) of an unbrowsed sapling can be calculated as

$$
\begin{aligned}
\Delta h &= H_A - H_{A-1} \\
&= H_{\max} * \left[\left(1 - e^{(-g*A)} \right)^3 - \left(1 - e^{(-g*(A-1))} \right)^3 \right]
\end{aligned}
\tag{6}
$$

and therefore the age at a given height (A_H) is given by

$$
A_H = \frac{\ln\left(1 - \left(\frac{H_A}{H_{\max}} \right)^{1/3} \right)}{-g}
\tag{7}
$$

By combining Eq. 7 for A_{130} (i.e., $H_A = 130$ cm) with Eq. 1 and assuming that $V_{130} = 0$, we solved for the growth rate parameter g:

$$g = -1 * \left(\frac{\ln\left(1 - \left(\frac{130}{H_{\max}} \right)^{1/3} \right)}{a} \right) \quad (8)$$

The growth rate parameter g can be substituted in case of browsing by $\frac{g}{(v*V_{130})+1}$; by combining Eqs. 7 and 1, this results in the following equation for the browsing reduction parameter v:

$$v = \frac{-g * (a + b)}{\ln\left(1 - \left(\frac{130}{H_{\max}} \right)^{1/3} \right)} - 1 \quad (9)$$

To compare the effect of using V_{130} instead of W, we first calculated for Albisriederberg (cf. section "Study site") the parameters g and v based on the parameters a and b from Rettich (1985) using Eqs. 8 and 9. Second, we calculated these parameters for saplings that have also grown in Albisriederberg but under different soil moisture and nitrogen levels (cf. Eiberle 1985a, b). From the forest stands I–IV on Albisriederberg, there is an increasing soil moisture level and increasing nitrogen availability (cf. Table 3). *Fagus sylvatica* has its optimum in Albisriederberg III, *Acer pseudoplatanus*, and *Fraxinus excelsior* both in Albisriederberg IV, which contain stands of the association *Aceri–Fraxinetum*. Third, we calculated these parameters for saplings that have grown in forest stands along an elevational gradient in the Northern Swiss Pre-Alps (cf. Table 3).

Results

In Albisriederberg, only four *Acer pseudoplatanus* and four *Fraxinus excelsior* saplings had never been browsed (Table 1). All the other *A. pseudoplatanus* and *F. excelsior* saplings had been browsed 1–12 times in winter or in spring. Nevertheless, 41 of the *A. pseudoplatanus* and 42 of the *F. excelsior* saplings grew for some years before they were browsed the first time (cf. column "0x" in Table 1), resulting in 102 and 94 height increment records of unbrowsed trees for the two species, respectively. Unbrowsed growing years after 1–7 browsing events in winter were frequent (cf. W: "1x" − ">5x" in Table 1), and these data were thus used in the analysis. By contrast, only two *A. pseudoplatanus* saplings had been browsed once in spring without being browsed in

the same or in the following winter (cf. "S" in Table 1). A combination of browsing in winter and in spring of the next year (or vice versa) was frequent, but browsing in the same year in spring and in winter combined with unbrowsed years thereafter was rare (cf. $S + W$ in Table 1). This implies that no statements can be made about height increment in unbrowsed years following spring browsing for *F. excelsior* and *A. pseudoplatanus* saplings based on these data.

Acer pseudoplatanus

Mean observed height increment was 12.0 ± 8.0 cm for *A. pseudoplatanus* saplings that had never been browsed or for unbrowsed years of winter-browsed saplings. The observed height increments were between 5 and 35 cm (Fig. 2a), except for one sapling with an exceptionally large height increment of 60 cm (this sapling was eliminated from the analysis because the value is likely to be erroneous). A clear tendency toward lower height increment in unbrowsed years after winter browsing (Fig. 2b–f) compared to unbrowsed saplings can be seen (Fig. 2 a). However, trees that were browsed frequently in later years did not have higher or lower relative height increments before their first browsing event compared to rarely or never browsed trees.

The mean growth development was simulated well with Eq. 5 including winter browsing (mean fitted height increment $= 11.7 \pm 6.5$ cm; cf. open circles in Fig. 2). Furthermore a likelihood ratio test comparing our modified model (cf. Eq. 5 with $\frac{g}{(vW*W)+1}$) to the original von Bertalanffy equation (cf. Eq. 4 with only g as parameter) indicated that our model should be preferred (L ratio $= 18.0$, $P < 0.0001$). Winter browsing reduced height increment in the following years, as calculations resulted in a vW of about 0.10 (cf. Table 2). Thus, the growth rate of once browsed *A. pseudoplatanus* saplings is about 9% lower, and that of twice browsed saplings 17% lower than the growth rate of unbrowsed saplings.

A positive correlation (0.75) between the g and vW parameters was found (Table 2), indicating that the larger the height increment of a sapling, the larger the relative growth reduction after the browsing event. However, multiplying vW with g so that saplings with a large g would have a higher browsing reduction

Table 2 Estimation of (i) the growth parameter g and (ii) the browsing reduction parameter vW of the modified von Bertalanffy equation (Eq. 5) for *Acer pseudoplatanus* and *Fraxinus excelsior*

Species	Parameter	Lower	Mean	SD	Upper
Acer	g	0.03	0.04	0.00	0.04
Fraxinus	g	0.04	0.04	0.00	0.05
Acer	SD(g)	0.00	0.01		0.01
Fraxinus	SD(g)	0.01	0.01		0.01
Acer	vW	0.04	0.10	0.03	0.16
Fraxinus	vW	0.16	0.27	0.06	0.38
Acer	σ	4.80	5.30		5.87
Fraxinus	σ	5.37	6.05		6.82
Acer	corr g-vW		0.75		
Fraxinus	corr g-vW		0.64		

The lower and upper 95% confidence intervals, together with the mean and standard deviation (SD) are shown for the fixed parameter g, the random parameter g (SD(g)), the fixed parameter vW and the residual standard deviation σ (= within-group standard error). Significance was always ≤ 0.0001. The last two lines show the correlation coefficients between the parameters g and vW

than saplings with a lower g did not result in better model performance; AIC was even higher by 0.3 (this was implemented by substituting $\frac{g}{(vW*W)+1}$ in Eq. 5 by $\frac{g}{(g*vW*W)+1}$). Furthermore, no trend could be detected that the reduction of growth in the year after browsing would be larger than in the second or third year after browsing (cf. Fig. 2; by using gray lines, the growth of individual saplings in the years after a browsing event can be followed).

Due to the positive correlation between the parameters g and vW, the fitted height increments are very close to the mean (Fig. 2, circles). However, the variability in observed height growth was estimated well by combining the upper 95% confidence interval of the mean of the parameter g with the corresponding lower value for vW, and vice versa (Fig. 2, dotted lines). Moreover, the residual standard deviation (σ) of the model was rather small (cf. Table 2). Nevertheless, there were some remarkable deviations from modeled growth rates. Particularly, some large saplings that had been browsed only once grew more slowly in unbrowsed years after browsing than estimated by our Eq. 5 (cf. Fig. 2b; height increment of saplings below the dotted line), and a few saplings grew faster than modeled.

Fraxinus excelsior

Similar results as for *Acer pseudoplatanus* were found for *Fraxinus excelsior* saplings (Fig. 3). The pooled sample of *F. excelsior* saplings that had never been browsed and the winter-browsed saplings in unbrowsed years had a mean observed height increment of 12.1 ± 8.9 cm and a mean fitted height increment of 11.8 ± 6.8 cm. Winter browsing reduced height increment of *F. excelsior* in the subsequent years more strongly than of *A. pseudoplatanus* saplings ($vW = 0.27$ vs. 0.10; cf. Table 2). Thus, the growth rate of once browsed *F. excelsior* saplings is 21% smaller, and that of twice browsed saplings is 35% smaller than the growth rate of unbrowsed saplings. Furthermore, a likelihood ratio test comparing the modified model (Eq. 5 with $\frac{g}{(vW*W)+1}$) to the original von Bertalanffy equation (Eq. 4 with only g as parameter) indicated that our model should be preferred (L ratio $= 44.03$, $P < 0.0001$).

A positive correlation (0.64) between the g and vW parameters was found. Again, multiplying vW with g, so that saplings with a large g have a higher browsing reduction than saplings with a lower g (i.e., implemented by substituting $\frac{g}{(vW*W)+1}$ in Eq. 5 by $\frac{g}{(g*vW*W)+1}$) did not result in better model performance (AIC even higher by 3.4). In addition, no trend could be found that the reduction of growth in the year after browsing would be larger than in the second or third year after browsing (cf. Fig. 3; by using gray lines, the growth of individual saplings in the years after a browsing event can be followed).

As for *Acer pseudoplatanus*, the variability in observed height growth was estimated well when combining the upper 95% confidence interval of the mean of the parameter g with the corresponding lower value of vW, and vice versa (Fig. 3), except for some very slowly growing, once browsed *F. excelsior* saplings (Fig. 3b).

Comparison with data from Eiberle

Using the total sum of browsing events of a sapling up to 130 cm height (V_{130}), we calculated the growth parameter g (cf. Eq. 8) and the browsing reduction parameter v (cf. Eq. 9) of the von Bertalanffy equation. We did this first for the saplings in

Albisriederberg (uppermost line of each species in Table 3, and Fig. 4; location A). For both species, the resulting value of g (Table 3) was almost twice as high as when it was calculated based on the height increment data (cf. Eq. 5; Table 2), while v (Table 3) was always smaller than vW (Table 2; cf. Fig. 4).

Second, we calculated g and v for sites at Albisriederberg that differ in soil moisture (Table 3; A I–IV) and several other sites at higher altitudes (cf. Table 3). Again, g was always larger and typically almost twice as high (Table 3) as when it was calculated with Eq. 5 for our site at Albisriederberg (Table 2 and Fig. 4). In contrast, v was more variable (Table 3); for *Acer pseudoplatanus*, v was typically similar or larger than vW, and for *Fraxinus excelsior* it was typically smaller (cf. Tables 2 and 3; cf. Fig. 4). Neither *F. excelsior* nor *A. pseudoplatanus* showed a pronounced response in g and v to soil moisture/nitrogen level, apart that for *A. pseudoplatanus* saplings the browsing reduction parameter v was higher on poorer (cf. A I–II, Table 3) than on richer sites (cf. A III–IV, Table 3). Third, neither for g nor for v could we find a trend towards lower g and higher v at higher altitudes (Fig. 4, Table 3).

Discussion

Growth reduction and tree species

Both *Acer pseudoplatanus* and *Fraxinus excelsior* showed significantly reduced height growth in un-browsed years after one to several winter browsing events. The more frequently a tree sapling was browsed in winter, the smaller was its subsequent height increment (cf. Figs. 2 and 3). However, the browsing reduction parameter integrated in the von Bertalanffy growth equation—vW—of *A. pseudoplatanus* was 2–3 times lower than that of *F. excelsior* saplings (e.g., mean values of 0.10 vs. 0.27, cf. Table 2). Thus, *A. pseudoplatanus* saplings are hindered by browsing events less severely than *F. excelsior* saplings at this site. As the saplings of both species have similar growth rates (e.g., mean $g = 0.04$, cf. Table 2), and perhaps *F. excelsior* has even somewhat smaller ones (cf. Table 3), it is surprising that Eiberle postulated for the sites at Albisriederberg (A I–IV) the same "tolerable browsing intensities" for the two species (23%, cf. Eiberle

1985a, b), and for more elevated sites (cf. Table 3) even higher ones for *F. excelsior* saplings (35% for ash and 30% for maple saplings, cf. Eiberle and Nigg 1987).

Although both *A. pseudoplatanus* and *F. excelsior* are classified as competitor species ("C" strategy in Grime's C-S-R triangle, see Brzeziecki and Kienast 1994), they differ somewhat in their ecological properties or life history traits (Brzeziecki and Kienast 1994). *F. excelsior* is less shade tolerant, less frost and drought resistant and prefers wetter sites than *A. pseudoplatanus* (Brzeziecki and Kienast 1994). This might explain the higher growth reduction after browsing events of *F. excelsior* (as will be discussed in the following section).

Some individuals of both species studied here were able to survive up to 11–12 browsing events. Frequent, repeated browsing on individual broad-leaved trees occurred not only at our study sites, but it has also been reported by many other authors (cf. review by Gill 1992a) and has been confirmed in enclosure experiments (Moore et al. 2000; Pépin et al. 2006). Bergman (2001) found for *Sorbus aucuparia* saplings, a higher mortality due to browsing in clear-cut areas than in old-growth forests in Sweden, regardless of the higher growth rate in the clear-cut areas. In forest stands, growth and probably also quality reduction (e.g., multi-trunking), therefore, may be a more serious consequence of ungulate browsing for broadleaved trees than direct mortality.

Growth reduction and stress status

Light, nutrient, and water availability are key resources for tree regeneration. Generally, three main hypotheses are invoked for explaining the response to browsing under low versus high resource levels: (i) plants are more likely to compensate herbivory loss under high resource conditions ('continuum of response' model, Maschinski and Whitham 1989); (ii) plants are typically able to compensate herbivory under low resource conditions but not under high resource conditions ('growth rate' model Hilbert et al. 1981); and (iii) the response is curvilinear, with minimum compensation at both ends of the gradient and a maximum at an intermediate point (model by Osterheld and McNaughton 1991).

Table 3 Site characteristics, values of the growth rate parameter g and of the browsing reduction parameter v estimated using Eqs. 8 and 9 for *Acer pseudoplatanus* and *Fraxinus excelsior* saplings

Species	Site	Assoc.	Trees	SM	N	Bedrock + soil	Elevation	P	a	b	g	v
Acer	A	Galio odorati-Fagetum typicum + Aro-Fagetum	Fs	m	g	Brown soil	470–850	1	7.712	0.479	0.053	0.062
	A I	Molinio-Pinetum silvestris	Qp Fs Ps	d	p	Morainic, limestone	500–820	2	5.406	1.230	0.075	0.227
	A II	Carici albae-Fagetum typicum	Fs Qp Sa	d–m	p–g	Sandstone + marl	500–820	2	5.274	1.001	0.077	0.190
	A III	Galio odorati-Fagetum typicum	Fs	m	g	Brown soil	500–820	2	6.181	0.611	0.066	0.099
	A IV	Aro-Fagetum +	Fs Fe Ag	w	r	Clay	500–820	2	5.579	0.649	0.073	0.116
		Aceri-Fraxinetum	Ap Fe Ag	w–o								
	Buchs	Cardamino-Fagetum tilietosum	Fs Tc	d–m	p–g	Limestone	790–820	4	4.671	0.942	0.087	0.202
	Wartau	Galio odorati-Fagetum typicum	Fs	m	g	Limestone	860–920	4	3.341	0.990	0.121	0.296
	Buchserhochwald	Abieti-Fagetum typicum	Aa Fs	d–m	p–g	Limestone	1280–1310	4	5.891	0.690	0.069	0.117
	Total										0.074	0.149
Fraxinus	A	Galio odorati-Fagetum typicum + Aro-Fagetum	Fs	m	g	Brown soil	470–850	1	6.244	0.629	0.062	0.101
	A I	Molinio-Pinetum silvestris	Qp Fs Ps	d	p	Morainic, limestone	500–820	3	5.664	1.098	0.068	0.194
	A II	Carici albae-Fagetum typicum	Fs Qp	d–m	p–g	Sandstone + marl	500–820	3	5.757	1.028	0.067	0.179
	A III	Galio odorati-Fagetum typicum	Fs	m	g	Brown soil	500–820	3	5.737	0.896	0.067	0.156
	A IV	Aro-Fagetum +	Fs Fe Ag	w	r	Clay	500–820	3	4.849	1.046	0.079	0.216
		Aceri-Fraxinetum	Ap Fe Ag	w–o								
	Buchs	Cardamino-Fagetum tilietosum	Fs Tc	d–m	p–g	Limestone	790–820	4	4.899	0.583	0.078	0.119
	Gams	Cardamino-Fagetum typicum	Fs	d–m	p–g	Flysch	800–820	4	1.855	1.030	0.207	0.555
	Wartau	Milio-Fagetum	Fs Aa	m	g	Limestone	860–920	4	3.363	0.622	0.114	0.185
	Haslen	Cardamino-Fagetum typicum	Fs	d–m	p–g	Sandstone + marl	1000–1060	4	3.809	0.953	0.101	0.250
	Total										0.078	0.195

'Albisriederberg' (A) is used to denote those sites from which the Rettich (1985) data were taken from (cf. section "Study sites"); 'Albisriederberg I' to 'Albisriederberg IV' (A I–A IV) is used to denote other sites at Albisriederberg (cf. Eiberle 1985a, b). "Assoc." denotes the vegetation association (after Keller et al. 1998). "Tree" denotes the dominant tree species in the overstorey, where Fs = *Fagus sylvatica*, Qp = *Quercus petraea*, Ps = *Pinus sylvestris*, Ap = *Acer pseudoplatanus*, Fe = *Fraxinus excelsior*, Ag = *Alnus glutinosa*, Tc = *Tilia cordata*, Sa = *Sorbus aria*, Aa = *Abies alba*. "SM" denotes soil moisture, where d = dry, m = moist, w = wet, and o = oversaturated. "N" indicates nutrient availability, where p = poor, g = good and r = rich. "Bedrock + soil" denotes available information on bedrock and soil types. "Elevation": elevation of the sites in meters above sea level. Parameters a and b are the parameters of Eq. 1, and were obtained from the following publications ("*P*"): 1 = Rettich (1985), 2 = Eiberle (1985a), 3 = Eiberle (1985b) and 4 = original data provided by Heinz Nigg, used in Eiberle and Nigg (1987). "Tot": the median of the parameters a and b were calculated per species, and then g and v were estimated
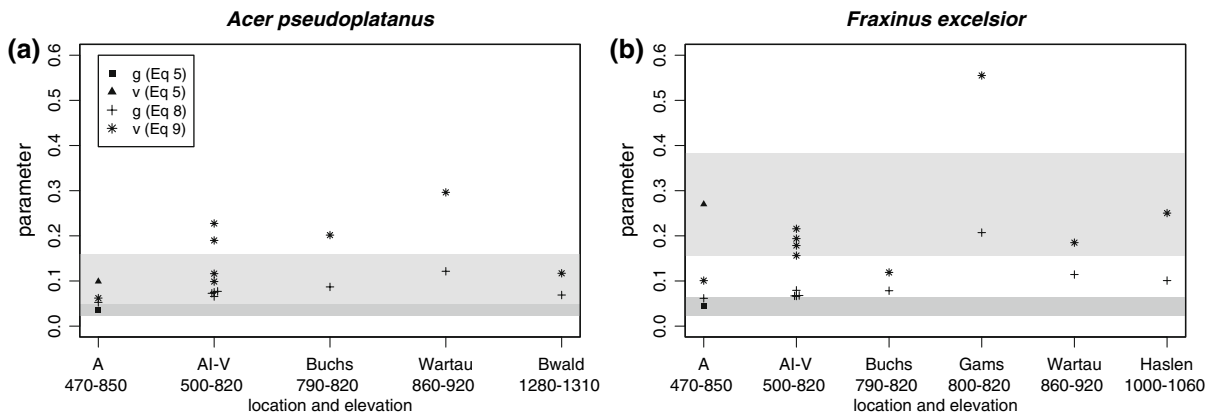
Fig. 4 Growth rate g and browsing reduction parameter v of the von Bertalanffy growth equation for the different sites shown in Table 3. Filled symbols at site A represent the average of the parameters g and vW estimated using Eq. 5 directly based on the sapling data, and the gray areas indicate their 95% confidence intervals (cf. Table 2). The crosses and asterisks represent the g and v parameters, respectively, estimated using data from Eiberle (Eq. 1) and Eqs. 8 and 9. The intervals shown below the site names denote elevation in meters above sea level. For additional details and abbreviations of the sites, see Table 3

Hypotheses (i) and (iii) are supported first by the different reaction of saplings in open compared to closed stands. Saplings that were used in simulated browsing experiments usually grew in open sites and have compensated height loss, due to larger height increments in unbrowsed years after the browsing event (cf. Canham et al. 1994; Eiberle 1978). These saplings were growing under high resource levels and therefore were stressed to a low extent only, e.g., by competition with other tree saplings. In contrast, in the closed forest stands that were used here, the light demanding *A. pseudoplatanus* and *F. excelsior* saplings were highly stressed due to shading (even though they grew under moderate to good supply of nutrients and water). Therefore, they had reduced height increments in unbrowsed years after browsing, i.e., they were unable to compensate the browsing-induced height loss. Harmer (1999) also found in his clipping experiment that the more shaded the clipped *A. pseudoplatanus* and *F. excelsior* saplings were (full light, 30, 60, and 80% shade), the lower the shoot numbers and their dry weight. A possible explanation for this is that shaded saplings had lower reserve pools (cf. Canham et al. 1994 for *F. americana*).

In addition, the fact that the growth reduction parameters v for *A. pseudoplatanus* saplings at Albisriederberg were higher on poorer and drier (cf. A I–II, Table 3) compared to richer and wetter locations (cf. A III–IV, Table 3) lends further support

to these hypotheses. Early spring growth of *A. pseudoplatanus* seems to depend strongly on N remobilization from roots and shoots, but it is independent of current N supply (Millard and Proe 1991). As winter browsing removes shoots and thus some of the stored N, less N is available for early spring growth. In nutrient poor sites, the subsequent rapid root N uptake for shoot and leaf growth may not be able to fully compensate for this initial growth restriction, and thus saplings on poorer sites were more stressed than the ones on richer sites and therefore suffered a higher growth reduction after browsing.

Hypothesis (ii) (Hilbert et al. 1981) was supported by Hawkes and Sullivan (2001) who found in their meta-analysis that woody plants were typically able to compensate biomass after herbivory under low but not under high resource conditions. Similarly, our site Albisriederberg (Table 2 and A in Table 3) and the moist to wet sites Albisriederberg III and IV (A III–IV in Table 3) were more convenient for *F. excelsior* than for *A. pseudoplatanus* saplings. Hence, the fact that higher browsing reduction parameters v were calculated for ash also supports this hypothesis.

In addition, this hypothesis is further supported by our finding that the growth rate g and the browsing reduction parameter vW were correlated positively, indicating that the larger the height increment, the larger the impact of ungulate browsing. This correlation was found for individual saplings on

Albisriederberg (Table 2) but apparently also across different sites (cf. Table 3, positive correlation between the g and v parameters). That is, slowly growing saplings are less inhibited by browsing than well growing saplings (as postulated by Hilbert et al. 1981). However, the well growing saplings may still have larger height increments in absolute terms than the slowly growing saplings.

Inconsistent with all three hypotheses, however, is our finding that neither for the growth rate parameter g nor for the browsing reduction parameter v, a trend toward lower g and lower or higher v at higher altitudes could be found (Fig. 4, Table 3). Normally, tree saplings of a given species are assumed to be stressed somewhat more in higher altitudes than in the lowlands (as long as moisture is not limiting), and this should be visible, e.g., via lower growth rates in mountain forests. From the data of Eiberle, however, no such trend was evident. In addition, *F. excelsior* showed no clear response in the values of the parameters g and v to soil moisture (cf. Table 3, Albisriederberg I–IV).

Generality of the results

For both species at Albisriederberg, the growth parameter g calculated based on the equations by Eiberle (Eq. 8) was almost twice as high as when it was calculated based on the height increment data (Eq. 5). This result together with the few observed values above the 95% confidence interval of the means in Fig. 2a indicate that when the von Bertalanffy equation is used directly for the original data (as we did with Eq. 5), the growth potential of unbrowsed saplings tends to be slightly underestimated. Underestimation of the growth of small saplings when fitting the von Bertalanffy growth equation has already been reported elsewhere (e.g., for *Picea abies* and *Larix decidua*, Rammig et al. 2007).

However, ignoring the time of browsing as done by Eiberle when calculating the age at a sapling height of 130 cm (A_{130}) based on Eq. 1 is likely to strongly underestimate the effect of browsing in unbrowsed years after browsing, i.e., the browsing reduction parameter v (calculated based on Eq. 9). This is due to the fact that saplings often grew well for some years before being browsed for the first

time, whereas in the Eiberle analysis the total number of browsing events (V_{130}) is treated as if they all occurred simultaneously at germination. Therefore, it is preferable to analyze the reduction due to browsing based on W, i.e., the sum of browsing events up to a certain age (see section "Methods"). Due to the fact that v was often higher than the 95% confidence interval of the mean of the parameter vW (cf. Fig. 4, in particular for *A. pseudoplatanus*), we conclude that our vW parameters are rather conservative estimates of the growth reduction effect in unbrowsed years after browsing.

Besides the browsing reduction parameter v of *A. pseudoplatanus* at different soil moisture/nutrient levels (A I–IV, see section "Growth reduction and stress status"), no unequivocal trends in the values of the growth rate parameter g and the browsing reduction parameter v were found along the gradients of altitude and soil moisture/nutrients for *F. excelsior* and *A. pseudoplatanus* (Fig. 4 and Table 3). We thus conclude that the growth reduction identified here for unbrowsed years following browsing is likely to be valid for a wide range of forested sites; this has already been asserted by Eiberle (1985a, b) and Eiberle and Nigg (1987).

Limitations and research perspectives

In this study, we analyzed only unbrowsed years before or after browsing, but not the browsing year itself. To correctly simulate sapling growth in a model of forest development, one should thus estimate the height loss due to winter browsing itself, and for spring and summer browsing, the height loss and the length of the new shoot produced in that year, respectively. Unfortunately, we were not able to analyze this because height loss is not known in retrospective data. The only workaround would be to nearly continuously observe the saplings over the growing seasons until they attain a height at which they are beyond the reach of ungulates in order to identify the exact amount and timing of browsing.

The reaction of individual saplings of *A. pseudoplatanus* and *F. excelsior* to ungulate browsing was highly variable in our data at Albisriederberg (Figs. 2 and 3) and no single current model (hypothesis (i)–(iii)) could account for the found responses (cf. section "Growth reduction and stress status"). By

combining the upper 95% confidence interval of the mean of the parameter *g* with the corresponding lower value of *vW*, and vice versa (Figs. 2 and 3; in spite of the positive correlation between *g* and *vW*) we still were able to catch this high variability in height increments for both studied tree species. However, several factors that could have helped to constrain the variability in the observed data were not fully considered here, but they have been shown in other studies to strongly influence the browsing response; these factors include (i) plant size at the moment of browsing, (ii) local site conditions such as nutrient, water and light availability, (iii) timing (within the year) and recurrence (frequency) of browsing, (iv) amount and type of tissue eaten, (v) the period over which growth is considered, and (vi) other stress factors such as competition with ground vegetation (cf. reviews by Danell et al. 1994; Gill 1992a; Hester et al. 2006; Hilbert et al. 1981; Nykänen and Koricheva 2006; Whitham et al. 1991). This long list supports that there is no single coherent response of woody plants to herbivory by ungulates. Hence, it stresses the necessity for better understanding the effects of combined factors in order to be able to integrate them into current models of the browsing reaction.

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