

Browsing regime and growth response of *Abies alba* saplings planted along light gradients

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Abstract Silver fir is a highly desirable species in European mountain forests from a management and conservation point of view, but it is also highly palatable for ungulates. We planted *Abies alba* saplings along natural light gradients to explore under natural browsing: (1) the light conditions under which saplings grow best in the absence of browsing; (2) when and by which ungulate species which saplings are browsed; and (3) under which conditions saplings react most vigorously to browsing. The experiment was carried out in a Swiss forest using four fenced plots each containing about 30 saplings planted in 2001, which were between 17 and 100 cm tall in 2009. For half of the saplings, browsing was allowed and filmed from April 2009 to January 2010. Saplings grew better with more light (13 % rather than 10 % canopy openness). Browsing was not a single event per sapling but a continuous process during the winter months. Almost all saplings exposed to browsing suffered heavy browsing by chamois and red deer, but no roe deer browsing was observed. The remainder of the browsed shoots were longer and contained more buds under 13 % canopy openness. The browsing-induced height differences between browsed and

unbrowsed trees increased over time under all light conditions, and almost no diameter growth was measured in the years after browsing. In cases with severe browsing, management aimed at letting in more light does not lead to a substantially better tolerance of browsing. We thus recommend integrating the “feeding strength” in the assessment of browsing.

Keywords Ungulate browsing · Herbivory · Silver fir · Natural regeneration · Canopy openness

Introduction

Browsing by ungulates such as deer and chamois is one of many biotic factors that affect tree establishment, growth and mortality. Tree saplings are part of the normal food of ungulate species such as red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.) (cf. Gebert and Verheyden-Tixier 2001; Tixier and Duncan 1996; Klötzli 1965; Cornelis et al. 1999; Onderscheka et al. 1989). European silver fir, *Abies alba* Miller, is among the most palatable tree species for ungulates in Europe (cf. Gill 1992; Klötzli 1965; Kupferschmid and Brang 2010). At the same time, *A. alba* is particularly valued in mountain protection forests because of its deep rooting system, which makes it less susceptible to storm damage, and because it is also less susceptible to beetle infestations than *Picea abies* (L.) Karst (Frehner et al. 2005).

Abies alba saplings, like many other species, grow better under good light conditions (Grassi and Bagnaresi 2001; Dobrowolska 2008). Such a pattern has also been found along light gradients from closed forest stands to wind-throw gaps, but height growth seems to already peak at

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light levels with 10 % canopy openness (Kupferschmid et al. 2013, 2014). Other studies have found that higher light levels, e.g. >50 % of above canopy light (Stancioiu and O'Hara 2006), 30 % of canopy openness (Kučeravá et al. 2013) or 18 % of open-field intensity (Robakowski et al. 2003), even negatively influence the height increment of *A. alba* saplings. Thus, low light levels can still result in strong growth in this shade-tolerant tree species, and many authors recommend regenerating firs under moderately shaded conditions (e.g. Kučeravá et al. 2013; Muscolo et al. 2010).

Nevertheless, *A. alba* has declined in abundance and distribution since about 1200 BP, primarily due to increases in human activities, including deforestation, forest burning and commercial forestry, as well as browsing by domestic and wild ungulates (Diaci et al. 2010; Feurdean and Willis 2008). In recent decades, failure in natural *A. alba* regeneration has often been blamed on ungulate (over)abundance, at least for larger height classes (cf. Weber 1967). This was attributed to selective browsing by ungulates (Klopčič et al. 2010) and the sensitivity of *A. alba* to the loss of its terminal shoot (cf. Senn and Suter 2003).

Clipping experiments showed a great variability in the response of *A. alba* saplings after terminal shoot reduction in winter, ranging from substantially decreased to increased tree height (Eiberle 1978; Häsler et al. 2008). In Kupferschmid and Bugmann' (2013) experiment, this variability was attributed to sapling vitality: fast-growing (dominant) saplings overcompensated for the height loss by "flagging up" a twig, while slow-growing (suppressed) saplings under moderate artificial shading showed reduced height. Furthermore, the timing of clipping also had considerable impact on the response and thus on the height of the trees at the end of the experiment (see Kupferschmid and Bugmann 2013). Summer browsing was found to have the most negative effect (Vandenberghe et al. 2008). Repeated clipping also had a negative impact (Ayres et al. 2004; Eiberle 1978).

How *A. alba* saplings react along natural light gradients to natural ungulate browsing is not clear. Under dark canopy conditions (less than about 10 % canopy openness), small *A. alba* saplings did often not respond in the first year after browsing, but flagging occurred along the whole light gradient and led to height compensation (Kupferschmid et al. 2014). By comparing individual *A. alba* saplings in fenced vs. unfenced plots, Ammer (1996) found that, in unfenced plots, browsing reduced height under good light conditions, but not in shaded plots, and that height growth was not reduced by browsing on either site. Szymura et al. (2007) reported that the height increment of *A. alba* saplings was not correlated with light conditions and attributed this to the indirect effect of continuous browsing, which

leads to higher *A. alba* mortality in more shaded places. However, in other studies, browsing-induced mortality on small *A. alba* saplings was not only higher under dark canopy conditions but also in small gaps than under moderately shaded conditions (i.e. 10–14 % canopy openness, Kupferschmid et al. 2014; Kolly and Kupferschmid 2014).

Independent of light, the fastest growing *A. alba* saplings were browsed most strongly, leading to the paradoxical situation that the height growth of unbrowsed, suppressed saplings was still less than the overall height growth of browsed saplings (Kupferschmid et al. 2013). Häsler and Senn (2012) found that ungulates preferentially browsed *A. alba* saplings with long needles. Thus, it appears that the vitality of *A. alba* saplings has a double effect: on the one hand, sapling vitality influences the probability of being browsed (dominant rather than suppressed, cf. Plant Vigour Hypothesis by Price 1991), and on the other hand, sapling reaction to browsing is strongly influenced by vitality (cf. Kupferschmid and Bugmann 2013).

It is therefore not clear whether *A. alba* saplings can offset the height loss caused by natural browsing by specific responses and compensate fully, or whether the height difference remains or even increases over time. An experiment with natural browsing along natural light gradients but with even-aged planted saplings of known height would thus help to disentangle the impacts of ungulates, i.e. the selection of specific saplings by ungulates and the resilience of individual saplings after browsing.

We set up an experiment with even-aged planted *A. alba* saplings along natural light gradients around the light intensity at which height growth was found to peak and mortality was low, i.e. under moderately shaded conditions between 10 and 14 % canopy openness. The specific objectives were to analyse: (1) the light conditions under which saplings grow best in the absence of browsing, (2) when and by which ungulate species which saplings are browsed and (3) under which conditions saplings react most vigorously to browsing.

Methods

Site

The mountain forest "Altenbann" (coordinates 46°59'00"/9°05'07") is located on a hillslope above Schwanden, Canton Glarus (Switzerland), at about 995–1,020 m a.s.l. It faces north-east and has an inclination of 12–25°. A soil profile close to the experimental location revealed a humid cambisol (with a slight tendency towards an umbric regosol) with Verrucano bedrock (not limestone). The humus

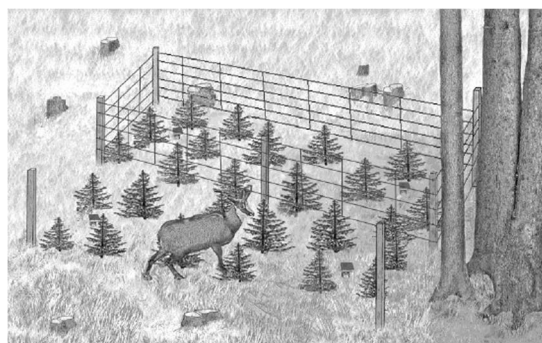
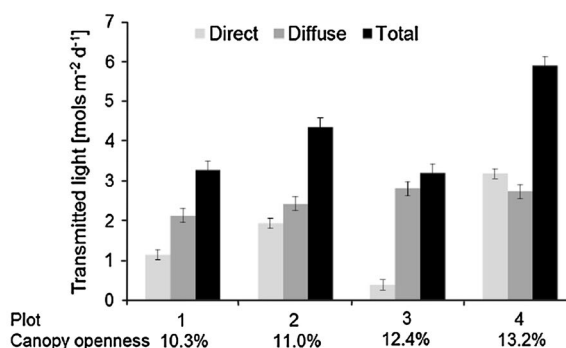


Fig. 1 Schematic representation of one plot used in the experiment during the opening time with a temporary fence between the control part and the part that was opened for browsing in 2009. Locations of temperature measurements and of “external” photographs are



indicated with the wooden constructions to which the iButtons were attached. *Right panel* mean resulting direct or indirect transmitted light and standard deviation over the whole year in the four plots

form is moder, the clay content about 10 % and the soil thus rather porous. There was no sign of waterlogging, and the water storage capacity amounts to only 7.8 mm as far as 24 cm soil depth and 84.7 mm as far as 100 cm soil depth, due to the low proportion of fine material between the stones. Thus, in spite of 1,600 mm precipitation per year (measured in Elm, distance ca. 6 km, MeteoSchweiz 1998–2010), drought in the topsoil is a considerable risk.

Since 1548, the forest has been a part of the wildlife sanctuary “Freiberg Kärf”, which covers an area of 102 km² with currently about 680 chamois, 173 red deer and 143 roe deer (counted in 1997, cf. Müller and Zopfi 1999). In recent years, there has been focused hunting to fight the infectious keratoconjunctivitis affecting chamois and to reduce the high ungulate-caused impact on tree regeneration (*personal communication*, F. Luchsinger, wildlife warden).

Tree plantation

In 2001, approximately 30–40 three-year-old *Abies alba* seedlings were planted in four fenced plots each measuring 5 m × 5 m. The provenance of the seeds was Chur Känzeli (a north-facing site at about 1,200 m a.s.l.). All fenced plots were placed so that just outside one side there were 1–3 large spruce trees (*Picea abies*). Some of the planted *A. alba* seedlings were thus under the canopy, some on the canopy edge and some in a gap (Fig. 1).

In July 2009, we took five fish-eye photographs 85 cm above the soil surface, four of them between the three most peripheral saplings towards each corner of the fenced plot and one at the centre of each plot (Fig. 1). We converted the pictures into black-and-white using the program Side Look (Nobis 2005) and calculated the canopy openness (i.e. the percentage of open sky seen from beneath a forest canopy given the additional influence of topographic shading) with the Gap Light Analyzer (GLA) software

(Cary Institute of Ecosystem Studies 1999). We also used GLA to estimate the diffuse and direct light for the entire year. The four fenced plots represent a light gradient from 10.3 % on to 13.2 % canopy openness (Fig. 1). As other differences, such as competition from tree roots or ground vegetation, may exist within each plot, we measured the distance to the nearest large spruce tree for every *A. alba* sapling as a proxy of such effects.

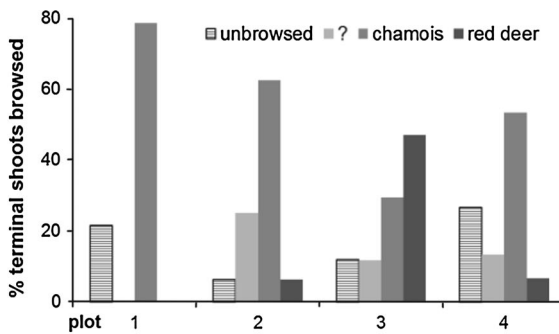
From fall 2008 to fall 2011, the air temperature 5 cm above the soil surface was measured using temperature loggers (DS1921G-F5#, Thermochron® iButton, Maxim Integrated). To protect the loggers from direct sunlight, they were wrapped in aluminium foil and placed under a small wooden shelter (Fig. 1). The mean annual temperature was 6.2–6.9 °C. Snow covered the site from about mid-November to March/April. Assuming that a constant daily temperature of zero indicates the presence of sufficiently deep snow cover to insulate the soil from the atmosphere, we estimated there were 110 days with deep snow cover in the winter 2008/09, 77 in 2009/10 and 60 in 2010/11. Furthermore, the annual degree-day sum (using a threshold temperature of 5 °C) varied between 1,220 and 1,460 °C day.

As a measure for tree vitality, we analysed the concentration of elements in needles. In early July 2012, we harvested one twig of the third uppermost whorl from three control *A. alba* saplings out of each fenced plot. The needles from the years 2011 and 2012 were oven-dried separately at 65 °C to constant weight, weighed to an accuracy of 0.001 g and chemically analysed in the laboratory (method described in Kupferschmid et al. 2013).

At the beginning of the experiment in fall 2008, all *A. alba* saplings were measured to determine their height (H_{2008}), all height increments since they were planted on the site (e.g. g_{2008}), the total length of all side shoots and the length of all shoots formed in 2008. In addition, we counted the number of buds on the terminal shoot formed in 2008.



Fig. 2 Browsing by ungulates: Left panel: process of browsing; *Abies alba* sapling in plot 3 at 14 October 2009, after the fence had been opened, chamois browsing on December 15 and 17, and red deer browsing on January 7 and 9, when red deer finally browsed the terminal shoot of this sapling. The fence was closed on 12 January



2010, and in fall 2010, the sapling was dead due to the combination of thrashing and heavy browsing (cf. Kupferschmid and Wasem 2014). *Right panel* reconstruction based on game camera movies of the ungulate species that caused the terminal shoot loss in the four plot parts that were opened for browsing in winter 2009/2010

Browsing experiment

Half of each fenced plot was opened on 16 April 2009 to allow chamois, roe and red deer to browse naturally (Fig. 1). Browsing activity was monitored by two infrared video-capable game cameras (Moultrie GameSpy I-60) per plot. We opened the fences shortly after snowmelt on 13 April 2009 when only a few *A. alba* saplings were still covered by snow, but observed practically no side shoot and absolutely no terminal shoot browsing until 2 July 2009. We therefore decided to close the fences in early July 2009, so that all the shoots that had formed in 2009 could be measured. In addition, we measured stem diameter at the root collar (DRC, 2 cm above the soil surface) to an accuracy of 1 mm.

On 14 October 2009, we reopened half of each fenced plot and closed them again on 12 January 2010, by which time most of the terminal shoots of the saplings had been browsed (e.g. Fig. 2). Again, browsing activity was monitored by two infrared game cameras per plot. In spring 2010 prior to the beginning of bud elongation, we measured tree height (Res_H₂₀₀₉), the length of the remaining terminal (Res_g) and of all 2009 shoots (Res_s) and counted the buds on the remaining piece of the terminal shoot and in the top whorl (bud). In fall 2010 and 2011, we remeasured all tree heights and shoot lengths. In addition, DRC was measured in 2011. We counted the number of terminal shoots (multiple terminal leaders) and determined the type of the highest terminal shoot after browsing, i.e. three reaction types were distinguished: (1) flagging up a twig, (2) new bud or shoot out of the remaining section of the terminal shoot or out of a twig whorl and (3) no reaction. In one plot (plot 4), a mature spruce had fallen in winter 2010/2011, so that 11 of the 16 control firs of that plot were browsed as well (but fortunately not the previously browsed firs).

Statistical analysis

To analyse the data, we adopted an a priori parsimonious model selection and inference using information-theoretic criteria (cf. Stauffer 2008). This involved grouping the explanatory variables into light (canopy openness, diffuse light and direct light), height (H₂₀₀₈–H₂₀₁₁ and Res_H₂₀₀₉) and diameter (DRC₂₀₀₉ and DRC₂₀₁₁). Of each group, we included only one variable in any given statistical model, so as not to overfit the models with correlated variables. As only the mean and standard deviation of the light measurements per plot was calculated (cf. Fig. 1), we could not include the variable “plot” and light-related variables at the same time. Nevertheless, to capture some plot-dependent variability, we included the interaction term between the minimum distance to the nearest large spruce tree and the plot.

We fitted linear regression models using the “lm” procedure of the statistical software package R (version 2.15.0, R Development Core Team 2011). Variables and interactions with insignificant coefficients were removed from the model. The best candidate models were selected using the lowest Akaike’s Information Criterion (AIC), together with the highest AIC weights, i.e. scaled likelihoods for the models, calculated according to the R package “MuMIn” (method analogue chapter 5 in Stauffer 2008). All numeric response and explanatory variables were transformed using Tukey’s first aid transformations, i.e. log₁₀ for measured data and square root for counted data (Mosteller and Tukey 1977).

Results

Preface on mortality

In fall 2008, 108 *A. alba* saplings were still alive and six had been died (five of the latter were in plot 2). In autumn 2009,

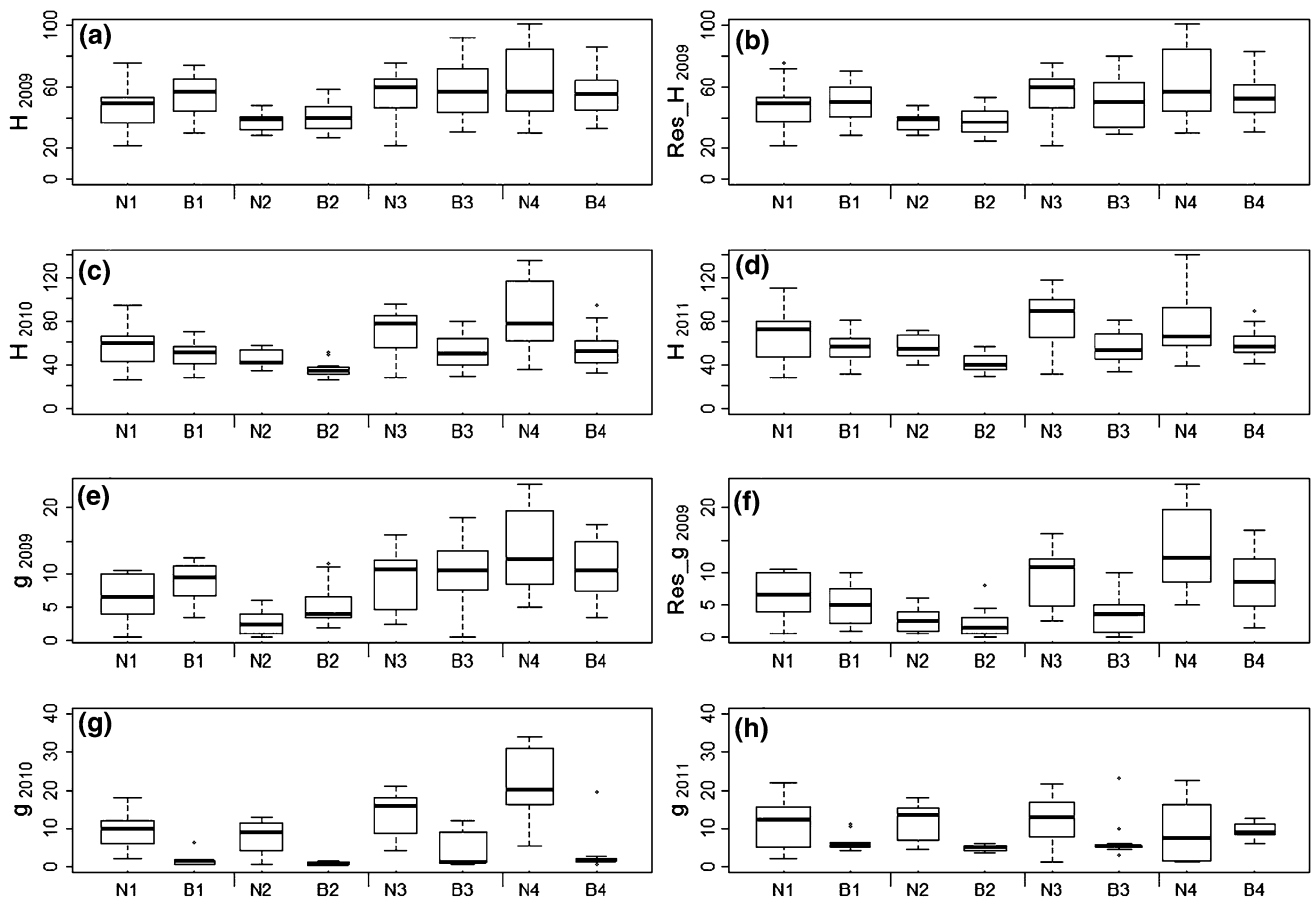


Fig. 3 Height and growth prior to and after ungulate browsing on planted *Abies alba* saplings. “N” refers to no browsing (i.e. the control trees), “B” to terminal shoot browsing in the winter 2009/2010 and the number to the plots 1–4. **a** Height in fall 2009 before browsing (H_{2009} [cm]), **b** height directly after browsing in winter 2009/2010 (Res_H_{2009} [cm]), **c** height one vegetation season after browsing in fall 2010 (H_{2010} [cm]), **d** height in fall 2011 (H_{2011}

[cm]), **e** terminal shoot growth in fall 2009 before browsing (g_{2009} [cm]), **f** residual 2009 terminal shoot length after browsing in winter 2009/2010 (Res_g_{2009} [cm]), **g** terminal shoot growth in 2010 (g_{2010} [cm]), **h** terminal shoot growth in 2011 (g_{2011} [cm]). Note that in plot 4 some browsing occurred in winter 2010/2011 on previously unbrowsed trees as a result of a fallen spruce tree; this explains the low values in N4 in 3d and particularly in 3h compared to 3c and 3g

two more saplings were dead, one of them in plot 2, and the other had been removed by workers as it was damage when the fence was repaired. The fungus *Phomopsis* was isolated on the six *A. alba* saplings in plot 2 that died naturally, and on one sapling, *Mollisia* was also found but no traces of the fungus *Armillaria* or *Heterobasidion*. *Phomopsis* could have played a role in the trees’ mortality, although it is usually only lethal if other stress factors are operating, i.e. it is a weak parasite after frost or drought. During the experimental period, mortality caused by chamois and red deer amounted to 4.7 %, i.e. two saplings due to browsing and three after additional red deer fraying who thrashed the trees with their antlers (Fig. 2 and Kupferschmid and Wasem 2014).

Under which light conditions do *Abies alba* saplings grow best in the absence of browsing?

The *A. alba* saplings were all planted in 2001, and thus of the same age. Nevertheless, their height increment and

height eight growing seasons after planting varied greatly within and between the plots. In fall 2009, when the fences were reopened, the 106 *A. alba* saplings that were still alive were between 17 and 100 cm tall (Fig. 3a).

Within the small range of site openness in the study (cf. Fig. 1), it seems the more light available, the better the *A. alba* saplings grew prior to browsing, and the larger and thicker (DRC) they were in autumn 2009 (Fig. 3a, e; Table 1). The models for height and height increment in 2009 prior to browsing were slightly better if percentage site openness was used as a predictor variable (e.g. AIC – 378.10 for H_{2009} , cf. Table 1) compared to those with only direct light (AIC – 372.28) or diffuse light (AIC – 373.81). Including the interaction term between the minimum distance to the nearest large spruce tree and the plot improved some, but not all models (cf. Table 1).

The needles from the unbrowsed control saplings in the fenced plot 4 that received the most light (cf. Fig. 1) were by far the heaviest (0.5 g per 100 needles compared to

Table 1 Results of linear regression models for *Abies alba* saplings before browsing: height in fall 2009 (H_{2009}), terminal shoot growth of the years 2008 (g_{2008}) and 2009 (g_{2009}) and diameter at root collar in 2009 (DRC_{2009})

	H_{2009}^a		g_{2008}^a		g_{2009}^a		DRC_{2009}^a	
Intercept	-0.401 ± 0.102	***	-2.800 ± 0.370	***	-5.075 ± 2.321	*	-2.918 ± 0.561	***
Canopy openness ^a	0.416 ± 0.093	***	1.053 ± 0.336	**	3.936 ± 2.219	.	1.486 ± 0.536	**
Min.distance ^a -plot 4		ns		ns	-0.110 ± 0.263	ns	0.034 ± 0.064	ns
Min.distance ^a -plot 3		ns		ns	-0.280 ± 0.231	ns	0.049 ± 0.056	ns
Min.distance ^a -plot 2		ns		ns	-0.376 ± 0.200	.	0.164 ± 0.048	***
Min.distance ^a -plot 1		ns		ns	0.150 ± 0.253	ns	0.119 ± 0.061	.
H_{2008}^a	1.017 ± 0.029	***	1.519 ± 0.156	***	1.079 ± 0.250	***	0.867 ± 0.060	***
Adjusted R^2	0.926		0.695		0.345		0.738	
AIC	-378.10		-106.30		67.59		-233.42	

The number of observations in the analyses was 106

Significance code: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, “.” tendency with $p \leq 0.1$ and ns not significant

^a Log transformed

0.31–0.38 in needles from saplings in fenced plots 1–3). Two-year-old needles from the *A. alba* saplings in the fenced plot 4 also contained proportionally more nitrogen (1.78 % of dry weight compared to 1.43–1.58 % in fenced plots 1–3). Little magnesium (Mg) was found in the needles from the saplings in the fenced plots 2 and 4 (0.05–0.06 %) compared to saplings in the fenced plots 1 and 3 (0.09–0.11 %), and little calcium (Ca: 0.18 %) and zinc (Zn: 17.13 ppm) in one-year-old needles from the saplings in the fenced plot 4 (additional data are given in Online Resource ESM_1).

When and by which ungulate species are which *Abies alba* saplings browsed?

No terminal shoots were browsed in spring and summer 2009 on the 62 *A. alba* saplings accessible to browsing during that time. The chamois and roe deer that triggered the game camera ate either *Rubus* sp. or *Vaccinium myrtillus* growing between the *A. alba* saplings (Kupferschmid and Wasem 2014), or they just sniffed the *A. alba* saplings. Only very occasionally were 14 trees browsed on a 2009 lateral shoot.

In fall 2009, after the first snowfall, browsing by chamois and red deer began first on the current-year lateral shoots, then on older lateral shoots and only later on the terminal shoots (see movies in Kupferschmid and Wasem 2014). This sequence occurred although many twigs had first to be dug out of the snow by the animals (Kupferschmid and Wasem 2014). Importantly, browsing on each sapling was not a single event. Rather, chamois (mostly an adult female with three kids) browsed during the day and a red deer during the night. This pattern continued for weeks (cf. Fig. 2 and the movie in Kupferschmid and Wasem 2014).

Based on photos and movies obtained with the game cameras, we reconstructed which ungulate species had browsed the terminal shoots of which *A. alba* saplings (Fig. 2). The browsers of some *A. alba* saplings could not be identified (cf. ? in Fig. 2) as the game cameras have a short-time delay between the detection of an animal and the beginning of the recording, and there is a minimum delay of 1 min between two consecutive films. No roe deer was observed browsing on shoots of the *A. alba* saplings. Chamois browsed the most terminal shoots except in plot 3, where red deer browse was more frequent (cf. Fig. 2). Ten *A. alba* saplings that were accessible to browsing after part of fence had been opened were not browsed, and these saplings are included in the unbrowsed trees in the statistical analysis. More than only the last terminal shoot was browsed on just four trees.

The remaining lengths of all 2009 shoots were significantly greater, the larger the tree had been prior to browsing ($\log_{10}(\text{Res}_s) = 0.457 \pm 0.031 \times \log_{10}(H_{2009})$, AIC = 36.02), and thus the greater the site openness ($\log_{10}(\text{Res}_s) = 0.727 \pm 0.05 \times \log_{10}(\text{canopy openness})$, AIC = 36.98). The remaining terminal shoot section was longer, the larger the tree had been prior to browsing, and also if it had been browsed by an “unknown” animal (Res_g in Table 2). The taller the tree was prior to browsing, the more buds remained after browsing on the residual terminal shoot sections and on the lateral shoots of the uppermost whorl (Fig. 4a; Table 2).

Which *Abies alba* saplings react best after browsing?

Of the surviving *A. alba* saplings, only one browsed sapling in plot 4 failed to form a new terminal shoot by the end of the second growing season after browsing. All other saplings reacted by producing a new shoot either out of the

Table 2 Results of linear regression models for browsed *Abies alba* saplings

	Res_g ^a	Bud ^b	g ^a ₂₀₁₀	g ^a ₂₀₁₁	H ^a ₂₀₁₀	H ^a ₂₀₁₁	
Intercept	−32.241 ± 39.546	ns	−3.197 ± 1.320	−1.211 ± 0.550	−0.189 ± 0.145	0.331 ± 0.076	***
Canopy openness ^a		ns					ns
Min.distance ^a -plot 4	−0.738 ± 12.320	ns	2.999 ± 1.236	1.248 ± 0.498	0.242 ± 0.132		ns
Min.distance ^a -plot 3	−74.932 ± 15.582	***	ns	ns	ns	ns	ns
Min.distance ^a -plot 2	−67.198 ± 15.859	***	ns	ns	ns	ns	ns
Min.distance ^a -plot 1	−25.74 ± 14.799	.	ns	ns	ns	ns	ns
H2009 ^a	51.39 ± 21.217	*	***				ns
Res_H2009 ^a				ns	0.171 ± 0.066	0.416 ± 0.018	***
Bud ^b			0.283 ± 0.075	***	ns	ns	***
Ungulate species: chamois	11.979 ± 8.894	ns	ns	ns	ns	ns	ns
Ungulate species: unknown	26.983 ± 9.688	**	ns	ns	ns	ns	ns
Adjusted R ²	0.630	0.370	0.319	0.563	0.934	0.885	ns
AIC	381.96	185.54	32.54	−48.29	−165.51	−149.53	

Remaining lengths of 2009 terminal shoot in percentage of 2009 terminal shoot (Res_g), buds in the whorl 2008/2009 and on the remnant of the 2009 terminal shoot (Bud), terminal shoot length in 2010 (g₂₀₁₀) and 2011 (g₂₀₁₁), sapling height in different years (H_{year}) and remaining height after 2009/2010 browsing (Res_H₂₀₀₉). Dead trees and the tree that formed no new terminal shoot were omitted. The number of observations in the analyses was 44. Reference for “ungulate species” is red deer browsing

Significance code: *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$, “.” tendency with $p \leq 0.1$ and ns not significant

^a Log transformed

^b Log transformed after adding 0.00001 due to occurrence of zero values

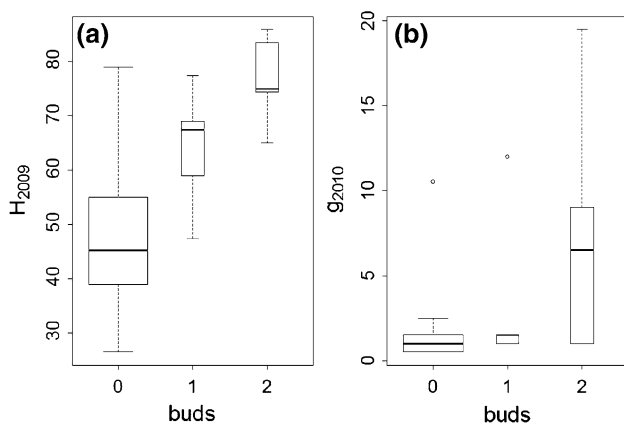


Fig. 4 Relationship between buds on the remaining piece of 2009 terminal shoot after browsing in winter 2009/2010 and **a** the tree height in fall 2009 before browsing (H_{2009} [cm]), and **b** the terminal shoot growth 2010 after browsing (g_{2010} [cm])

uppermost whorl or out of the section of the terminal shoot remaining after the 2009/2010 browsing. That is, no flagging occurred.

Browsed *A. alba* saplings grew better in the first growing season after browsing (g_{2010}) if they had more light and more buds remaining on the residual section of the 2009 terminal shoot (bud), regardless of their height (Table 2; Fig. 4b, excluding all the dead saplings and the sapling that had not yet reacted). In the second growing season after browsing, the browsed saplings grew better the more light they had and the taller they had been after browsing (g_{2011} in Table 2). This applied regardless of which ungulate species had browsed, how many buds had remained on the 2009 terminal shoot piece or whether the new shoot came out of the whorl or distally out of the remaining section of the 2009 terminal shoot. The height of the browsed saplings one growing season after browsing (H_{2010}) was greater the more light was available and the larger the tree had been after browsing. The height two seasons after browsing (H_{2011}) even depended on sapling height alone (Table 2).

Comparing the height in 2010 and 2011 of all living *A. alba* saplings, the browsed saplings were shorter than unbrowsed ones (Table 3; Fig. 3c, d). This also applied to the height increments of 2010 and 2011 (Table 3, Fig. 3g, h). *A. alba* saplings that had been browsed on their terminal shoot were not even able to partially compensate, i.e. even 2 years after browsing they did not achieve the same terminal shoot length as unbrowsed saplings (Fig. 3h). Thus, browsing-induced height differences increased greatly over time (compare Fig. 3b with 3d).

Stem diameter at the root collar (DRC) in 2011 was smaller for browsed than unbrowsed *A. alba* saplings, but larger the longer the distance to the nearest large spruce

Table 3 Results of the linear regression models of all surviving *Abies alba* saplings

	H_{2010}^a	H_{2011}^a	g_{2010}^a	g_{2011}^a	DRC_{2011}^a	DRC_{2011}^a
Intercept	−0.311 ± 0.084	0.219 ± 0.070	−3.841 ± 0.780	−0.556 ± 0.242	−0.348 ± 0.112	−0.396 ± 0.115
Terminal shoot browsed	−0.098 ± 0.007	−0.118 ± 0.011	−0.878 ± 0.061	−0.269 ± 0.039	−0.088 ± 0.018	−0.097 ± 0.018
Canopy openness ^a	0.406 ± 0.081		2.683 ± 0.745			
Min.distance ^a -plot 4		0.057 ± 0.030		0.386 ± 0.106	0.147 ± 0.047	0.147 ± 0.049
Min.distance ^a -plot 3		0.112 ± 0.032		0.307 ± 0.112	0.222 ± 0.054	0.226 ± 0.050
Min.distance ^a -plot 2		0.065 ± 0.030		0.299 ± 0.105	0.0230 ± 0.053	0.236 ± 0.055
Min.distance ^a -plot 1		0.036 ± 0.029		0.169 ± 0.100	0.058 ± 0.050	0.060 ± 0.051
Res. H_{2009}^a	0.986 ± 0.024	0.948 ± 0.041	1.190 ± 0.218	0.881 ± 0.144	0.907 ± 0.065	0.915 ± 0.067
Adjusted R^2	0.958	0.889	0.729	0.504	0.721	0.716
N	104	88	100	87	104	104
AIC	−406.25	271.28	51.13	−51.60	−199.54	−193.15

Sapling height in 2010 (H_{2010}) and 2011 (H_{2011}), terminal shoot growth in 2010 (g_{2010}) and 2011 (g_{2011}), remaining height after 2009/2010 browsing ($Res.H_{2009}$), diameter at root collar in 2011 (DRC_{2011}) and DRC increment calculated as DRC_{2011} minus DRC_{2009} (DRCg). Trees that formed no new terminal shoot were omitted in the analyses of terminal shoots. The control trees in plot 4 that had been browsed in winter 2010/2011 were omitted from the analyses of H_{2011} and g_{2011}

N is the number of observations in the analyses

Significance code: *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; “.” tendency with $p \leq 0.1$ and ns not significant

^a Log transformed

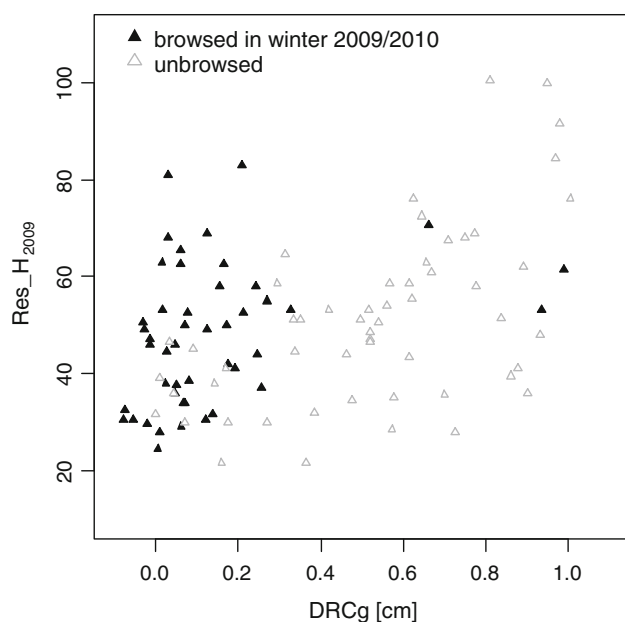


Fig. 5 Relationship between the tree height in spring 2010 after browsing in winter 2009/2010 (Res_H_{2009} [cm]) and the increment in diameter at the root collar (DRC_g), calculated as DRC_{2011} minus DRC_{2009} for browsed and unbrowsed *Abies alba* saplings

tree and the taller the sapling was after browsing (Table 3). Browsed trees grew hardly at all in diameter. Therefore, diameter growth from 2009 to 2011 (DRC_g) was much lower for browsed than unbrowsed saplings (Fig. 5; Table 3).

About three quarters of the browsed saplings became forked or had multiple leaders. In total, 11 saplings had one terminal shoot, 20 two and 15 three terminal shoots after browsing, while only one unbrowsed sapling became forked.

Discussion

Under which light conditions do *Abies alba* saplings grow best in the absence of browsing?

We had planted the *A. alba* saplings along natural light gradients around the light intensity at which height growth was found to peak, i.e. 10–14 % canopy openness (Kupferschmid et al. 2013, 2014). Height growth and needle weight were generally better the more light was available. However, the variability in height was large and the shade-tolerant *A. alba* saplings grew relatively well with little light, with the exception perhaps of plot 2 (cf. Fig. 3).

Naturally grown, i.e. unfertilised *A. alba* saplings, can most likely be considered healthy if their needle elements exceed the concentrations specified in guidelines regarding

the desirable nutrient concentrations for Christmas plantations of *A. alba* (Mutch 2000) or other *Abies* saplings (Hart et al. 2012). Indeed, this was the case for all elements except magnesium in the needles of saplings in the fenced plots 2 and 4 and for Ca and Zn in the fenced plot 4, where the values were slightly below the recommended values. Magnesium concentrations of *A. alba* saplings on other sites in Switzerland were found to be similar to those in our fenced plots 1 and 3 (Kupferschmid et al. 2013). As magnesium is important for photosynthesis, this could explain the relatively low growth rates in our plot 2, but the growth rate in plot 4, which had the most available light, was the highest.

Among the planted saplings in the four plots (ca. 100 m²), only six *A. alba* saplings naturally established from 2001 to 2012. In addition, there was a high mortality of saplings due to weak parasitic fungi, particularly in plot 2. This raises the question whether soil-related limitations might be responsible for low establishment, low growth and high mortality (cf. discussion in Paluch 2005). The soil data clearly revealed a higher potential drought risk in the upper soil horizon than at other Swiss sites that feature abundant *A. alba* regeneration (Kupferschmid et al. 2013). Fir establishment was found to be positively influenced by air humidity (Gabellini and Screm 1968), and edaphic conditions could result in the elimination of superficially rooted seedlings (Tan and Bruckert 1992). Shielding from wind has also been found to enhance fir establishment (Weber 1967). As our site is located in the northern Pre-Alps of Switzerland, strong warm-dry downslope winds (foehn) are frequent and may sometimes dry out the upper soil horizon. In addition, the humus form of the study site is a moder and pH was low. Neither of these factors are conducive to fir regeneration (Priewasser et al. 2013; Ignesti and Paci 1990).

To conclude, fir saplings under moderate light levels grew better with 13 % than with 10 % canopy openness, but vitality, as measured through element concentration of elements in the needles, did not tend to be enhanced.

When are *Abies alba* saplings browsed?

Eight years after planting, we exposed half of the *A. alba* saplings to natural ungulate browsing. Surprisingly, no browsing occurred in spring before budburst and during the first growing season, but only after the first snow cover in the winter. Although this may have been a coincidence, the following factors may have played a role:

1. Snow melt in spring in 2009 took place very rapidly as temperatures were unusually high, thus many chamois may have moved immediately to higher regions and were not present near the experimental site.

2. Chamois browsed on *A. alba* regeneration mostly during winter (cf. the four plots in 2009/2010 and the plot 4 in 2010/2011).
3. Red deer were apparently not in the area during spring and summer and the few roe deer present showed no interest in *A. alba* but preferred to browse on black- and blueberry bushes (Kupferschmid and Wasem 2014).
4. Human disturbance may have deterred the ungulates, as all saplings were checked weekly for browsing, sometimes with accompanying dogs (belonging to the rangers).

However, in a study in some windthrow areas in Switzerland, coniferous saplings (*Abies alba* and *Picea abies*) were selected in both summer and winter and browsed according to availability in spring (Moser et al. 2006). There, *Rubus* spp. was also consumed mostly by roe deer (Moser et al. 2006). Analysing the content of roe deer rumen, winter feeding on coniferous saplings was more frequent than feeding during the growing season, but bits of coniferous tissue were found in their rumen in every season (Tixier and Duncan 1996; Cornelis et al. 1999). The same was found for red deer and chamois (Onderscheka et al. 1989). According to Häslér and Senn (2012), *A. alba* consumption by red and roe deer continuously decreased from winter to spring until fall, unlike for chamois, where it was at one site highest in summer. In contrast, other studies have found *A. alba* saplings tend to be browsed during certain periods only, for example: only in winter (September to April) by chamois in the Spanish Pyrenees (Garcia-Gonzalez and Cuartas 1996), or before bud break of *A. alba* (Saint-Andrieux et al. 1999 cited in Pépin et al. 2006). In another study, roe deer were found to prefer *A. alba* saplings in May, but browsing was frequent from January until May (Klötzli 1965). Places with early snow melt appear to be more prone to chamois browsing (Kupferschmid and Bugmann 2005). Odermatt and Wasem (2008) repeatedly observed that browsing took preferentially place between snowmelt and the beginning of bud elongation in spring, which is exactly the time when we opened the fences.

Based on our results, we conclude that terminal shoot browsing on *A. alba* saplings occurs mostly during periods of little snow in winter, but not or at least less often during the growing season.

Which ungulate species browse *Abies alba* saplings?

Only chamois and red deer browsed the terminal shoots of the *A. alba* saplings in our experiment. Roe deer probably avoid sites where red deer are present.

Browsing by red deer tends to be more intensive than by chamois. Shipley et al. (1999) found that the diameter at

which the shoots were bitten off was clearly smaller for roe deer than for red deer and moose (*Alces alces*). Chamois's body size and feeding behaviour are more similar to those of roe than to those of red deer. Therefore, larger bites from red deer than from chamois could be expected. However, roe deer seem to often consume only the buds of *A. alba* saplings (Kupferschmid et al. 2013), whereas chamois browse large parts of the terminal and lateral shoots, if they are repeatedly browsing on the same tree (as in our experiment). Red deer are even more likely to browse large parts or whole shoots, which leads to greater "feeding strength" and thus heavier impact on the saplings.

Which *Abies alba* saplings are browsed?

Ungulates probably choose trees as a food patch according to morphological features (Iason et al. 1996). Larger saplings with a large crown volume are more likely to be browsed by deer (Häslér and Senn 2012; Kupferschmid et al. 2013; Iason et al. 1996). They are typically browsed for longer periods with more offtake than smaller or less bushy saplings (Iason et al. 1996; Danell et al. 1994). Thus, ungulates consume more tissue from larger saplings (Shipley et al. 1999). In our study, the remaining length of the current years' terminal shoot was larger, the taller the saplings had been prior to browsing (Table 2). Thus, larger *A. alba* saplings remained larger even after heavy browsing.

Which *Abies alba* saplings react best after browsing?

We found that the *A. alba* regeneration in our study could not even partially compensate for the height loss caused by browsing. The *A. alba* saplings that had been browsed on their terminal shoot did not have the same height increment as unbrowsed trees even 2 years after browsing, and thus the browsing-induced height difference became even larger over time (Fig. 3). Similarly, the growth in stem diameter appears to be strongly reduced by heavy browsing (Fig. 5). No compensation has also been found for *A. alba* saplings after heavy and repeated clipping (Eiberle 1978; Ayres et al. 2004).

Flagging up a side shoot to form a new leader shoot was the best reaction for an *A. alba* sapling to ensure future growth in clipping experiments, in particular when growing in full sun (Häslér et al. 2008). This led to overcompensation in the most vigorously growing trees (Kupferschmid and Bugmann 2013). *Pinus sylvestris* saplings that had been clipped directly below the uppermost whorl typically reacted by flagging and thus lost only about the equivalent of one annual height increment, while saplings where all current shoots of the second uppermost whorl had been additionally clipped reacted with distal epicormic shoots

and lost the equivalent of two annual height increments (Långström and Hellqvist 1992). Not a single tree in our experiment was able to react by flagging up an existing shoot, probably because all annual shoots of the upper whorls had been browsed (e.g. Fig. 2).

This suggests that the amount of tissue eaten, i.e. “feeding strength”, is at least as important for the reaction of *A. alba* saplings to browsing as site or environmental conditions.

The intensive browsing of saplings at our study site meant that they lost most of their reserves, as coniferous evergreen species store the greater part of the nutrients in the most recent needle generations (Chapin et al. 1980; Millard et al. 2001). In addition, the majority of nitrogen for leaf growth in spring is usually mobilised from the reserves (cf. Millard 1995). Hence, the *A. alba* saplings in the present experiment first had to produce new adventitious buds in the first year (mostly on the uppermost bud whorl) using their small amount of residual reserves. We therefore detected almost no height and diameter increment after browsing. Typically, it took another year for the saplings to produce a real new terminal shoot. This finding was confirmed at three other sites in Switzerland, where half of the *A. alba* saplings produced only a new terminal bud in the first year (Kupferschmid et al. 2013). Thus, our results affirm that *A. alba* tend to react with delay to leader shoot lost (Osterloher and Wiechmann 1993), at least after intensive browsing.

Abies alba saplings reacted to browsing by producing a new shoot in the first year only if buds were already present on the residual section of the terminal shoot. If more light was available, more buds remained on the residual section of the terminal shoot and in the uppermost whorl (cf. our study and Kupferschmid and Bugmann 2013). Thus, the saplings had more options to react with shoots out of regular lateral buds (Häsler et al. 2008), and the terminal shoot increments after browsing were larger. Nevertheless, the inability of *A. alba* saplings to compensate for height loss was independent of light in our study, in contrast to in clipping experiments. In general, it is assumed that sapling response depends on the type of tissue removed and less on the total biomass lost (Baraza et al. 2007). For example, for *Acer saccharum*, clipping promoted the elongation of regular lateral buds into new leader shoots of the same length (i.e. partial height compensation due to equal growth) if the clipping of leader shoots included several lateral buds. No such compensation occurred, however, if only a very small fraction or almost all of the annual leader shoot was removed (Metzger 1977).

Thus, the availability of intact twigs and the amount and distribution of buds along the leader shoot play a crucial role in determining the compensation capacity of tree saplings after browsing.

Irrespective of light availability, approximately 75 % of all *A. alba* saplings browsed in our experiment formed several new leader shoots. Multi-trunking due to the loss of apical dominance has often been reported (Mitscherlich and Weise 1982; Bergquist et al. 2003; Långström and Hellqvist 1992). For forest management, the development of multi-trunking is probably an as serious consequence of browsing as delayed and reduced height growth (Welch et al. 1992).

Conclusion

Browsing by chamois and red deer on tree saplings such as *Abies alba* is part of natural ecosystem dynamics. “Feeding strength”—i.e. the amount of tissue ungulates eat such as terminal buds, part(s) of the annual terminal shoot, the entire whole annual shoot or the drastic curtailment of much more than just the annual shoots—appears to vary with the browsing species (roe deer < chamois < red deer) and site conditions (e.g. Gill 1992). Typically, the more severe the browsing (or clipping) was, the smaller the height increment, the larger the difference in height between browsed and unbrowsed trees, the lower the aboveground biomass (cf. Tables 2, 3, and e.g. Canham et al. 1994; Edenius et al. 1993; Kristöfel and Pollanschütz 1995; Crouch 1966; Chaar et al. 1997) and the lower the seed production (e.g. Bergström and Danell 1987). Neither heavily browsed nor suppressed and “moderately” browsed saplings are probably able to compensate for height loss caused by (artificial) browsing (cf. this study but see also Kupferschmid and Bugmann 2013). Therefore, we recommend integrating a measure of “feeding strength” into the assessment of browsing. An additional measure of tree vigour would strongly enhance the value of such assessments. As *A. alba* is very shade-tolerant, managing for more light alone is unlikely to lead to a substantially better reaction. On the contrary, *A. alba* saplings have many competitive advantages under somewhat shaded conditions (Paluch 2005), i.e. under little more than 10 % site openness (see our study or Kupferschmid et al. 2013, 2014; Szymura et al. 2007).

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