

Eur J Forest Res (2013) 132:47–60
DOI 10.1007/s10342-012-0653-2

ORIGINAL PAPER

Timing, light availability and vigour determine the response of *Abies alba* saplings to leader shoot browsing

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Received: 24 January 2012 / Revised: 28 June 2012 / Accepted: 23 July 2012 / Published online: 1 September 2012
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Abstract Herbivore browsing on tree saplings is a common phenomenon that can cause damage particularly on preferred species. In this study, the combined effects of light availability and timing of browsing on the response of 9-year-old *Abies alba* saplings were tested experimentally. Leader shoot clipping was applied before budburst, shortly after budburst or in autumn on saplings grown in full light or under artificial shade. Timing of clipping, light availability and tree vigour (expressed as height and tree ring width before clipping) had an effect on the height after clipping. After clipping in autumn or before budburst, fast-growing fir saplings bent up twigs to form new leader shoots and overcompensated height loss; saplings characterised by intermediate growth rates formed new shoots out of regular visible lateral buds; and slow-growing saplings had no new shoot in the first year after clipping, such that the clipping-induced height difference even increased over time. Saplings clipped shortly after budburst elongated the remaining part of the shoot in the first year and developed shoots out of the most distal lateral buds in the second growing season, leading to complete height compensation. Multi-trunking was typical for all clipped trees. We conclude that the microscale conditions under which a tree is growing (i.e. which affect tree vigour) are highly important for determining whether the height reduction imposed by browsing is offset by overcompensation or increases over time relative to unclipped trees. This response can partly be

influenced by forest management via enhancing tree vigour via the light regime.

Keywords Clipping experiment · Herbivory · Tree regeneration · Height and radial growth · Silver fir · Simulated browsing

Introduction

Browsing by ungulates such as red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.) has become an increasing concern of managers in many temperate and boreal forests over the last century (Coté et al. 2004). Several factors are involved; among others, in many regions, the number of ungulates has increased, in particular in the absence of predators. As ungulate browsing often causes a growth delay (e.g. Gill 1992b; Danell et al. 2003; Nykänen and Koricheva 2004; Hester et al. 2006) and, in extreme cases, mortality of tree seedlings and saplings (Vandenberghe et al. 2008), browsing constitutes a significant disturbance.

Abies alba Miller (European silver fir) is among the most preferred browse species in many temperate forests of Europe (Klötzli 1965; Gill 1992a; Ammer 1996; Brändli 1996; Motta 1996; Klopčič et al. 2010). *A. alba* is an ecologically important tree species that is highly desired particularly in mountain protection forests because of its deep rooting system and its lower susceptibility to beetle infestations compared to *Picea abies* Karst. (Frehner et al. 2005). It has been reported repeatedly that *A. alba* regeneration was poor or even failed completely in the last decades, a fact that typically is attributed to ungulate browsing (Senn and Suter 2003; Diaci et al. 2010; Kucbel et al. 2010).

Communicated by G. Brazaitis.

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Only few studies have focused on the reaction of *A. alba* to natural or simulated browsing. For example, absolute height and height increment of *A. alba* saplings grown in full light were strongly reduced (10–50 %) over 10 years due to repeated (twice, 4×, 6×) leader shoot clipping before budburst and/or in autumn (Eiberle 1978). Similarly, defoliation of 50 % of the leaves of *A. alba* saplings in September and additionally in the second growing season after each flush of leaves had fully expanded (May, July) resulting in 62 % of lower leaf area, lower total biomass of buds, leaves, stems, fine and coarse roots, but 18 % of higher nitrogen content in coarse roots and stems by the end of the second growing season (Ayres et al. 2004). In addition, clipping shoots of the last 2 years in June resulted in lower biomass changes compared with unclipped fir seedlings (Vandenberghe et al. 2008). It seems that *A. alba* strongly suffers from (simulated) herbivory.

The limiting resource model of Wise and Abrahamson (2005) predicts for the case where the focal resource (e.g. light) is limiting plant growth that the tolerance to browsing (measured as plant fitness) should be higher in a high-resource environment (i.e. in full sun). In fact, higher tolerance has been found in a recent experiment by Häsler et al. (2008) where the height of *A. alba* saplings 2 years after they had been clipped before budburst was found not to differ compared to control trees in cases where the trees grew in full light, but to be smaller under artificial shade. This is not surprising, as even in the absence of browsing light is one of the most important factors influencing the growth of *A. alba* saplings (e.g. Ammer 1996; Grassi and Bagnaresi 2001; Robakowski et al. 2004; Dobrowolska 2008). Several other factors have been identified that influence the response of individual trees to ungulate shoot browsing and/or defoliation, including plant size at the time of browsing, other site factors such as nutrient and water availability, the time and recurrence of browsing, the amount and type of tissue eaten and the period over which growth is considered (cf. reviews by Hilbert et al. 1981; Whitham et al. 1991; Gill 1992b; Hawkes and Sullivan 2001; Danell et al. 2003; Nykänen and Koricheva 2004; Hester et al. 2006).

According to Whitham et al. (1991), the timing of herbivory relative to a plant's phenological stage is one of the most important factors determining its response, because it determines how much of its resources a tree loses and to what extent plant activity is reduced in subsequent resource uptake. Several authors postulated that the earlier in the growing season an ungulate impact is occurring, the less severe its effect is because the plant has a longer time to recover until the end of the growing season (Danell et al. 1994; Hester et al. 2006). Indeed, it was often found that browsing on tree saplings before budburst was less severe

than after budburst (e.g. Hjältén et al. 1993; Senn and Haukioja 1994), whereas browsing or defoliation in summer had the largest effect (e.g. Canham et al. 1994; Honkanen et al. 1994). However, *Betula pubescens* saplings clipped in August at the first sign of leaf senescence had longer leaders than bud-burst clipped saplings, and these in turn had longer leaders than unclipped trees (Millett et al. 2008). All these findings coincide with recommendations in horticulture (e.g. Pfisterer 1999).

No comparative experiments on the combination of the influence of (1) the season in which browsing occurs and (2) light availability have been conducted on *A. alba* saplings to date. The main hypotheses of the present study are as follows:

1. Fir saplings are more impaired by leader shoot browsing after budburst than in the dormant season, and shoot loss in autumn is less detrimental than before budburst.
2. Fir saplings have a higher tolerance (compensation capacity) to leader shoot browsing in full sun than under shaded conditions.
3. Fir saplings respond more efficiently to leader shoot browsing when they have a higher 'vigour' (expressed as larger height and ring width of even-aged trees).

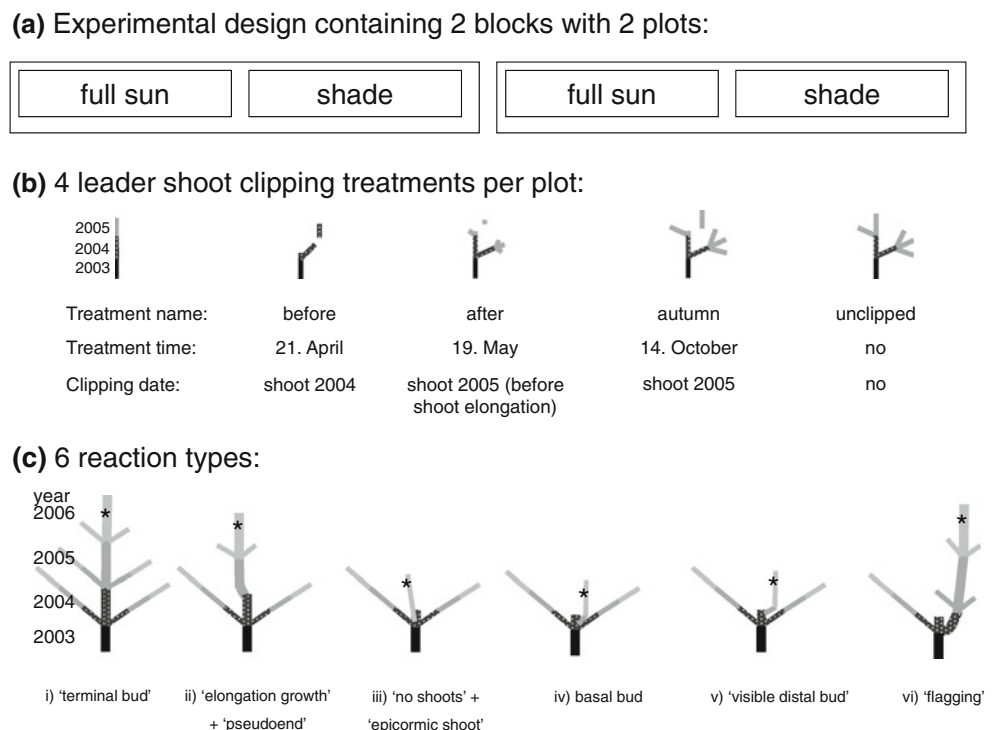
These hypotheses are addressed using even-aged *A. alba* saplings of different heights in an experimental design with two light levels and simulated leader browsing before and after budburst in spring as well as in autumn, that is, after the end of the growing season.

Materials and methods

Study site and experimental design

The simulated browsing experiment was conducted in a tree nursery field (soil pH ca. 7.2) of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) in Birmensdorf (8°26'30"E, 47°20', 50", ca. 560 m a.s.l.) near Zürich, Switzerland. In 1999, 3 years after germination, 80 *A. alba* seedlings from Beggingen (850 m a.s.l.) were planted with a planting distance of about 40 cm in 2 blocks containing 2 plots. The saplings were fertilised once at the age of four with organic NPK fertiliser (Unikorn II, Hauert, Switzerland; 20 g m⁻²). In April 2003, in one plot per block (Fig. 1a), an artificial shade was constructed with wooden slatted frames on the top and a green vertical mesh (mesh size ca. 0.5 cm, Wunderlich Ltd., Germany; 55 % transparent) on the south side. The width of the slats was 2 cm and the distance between each slat was 1 cm. For the winters 2004/2005 and 2005/2006, the slatted frame was removed from mid-December until mid-April; that is, it

Fig. 1 Schematic representation of (a) the experimental block design, (b) the clipping of the leader shoots in 2005 and (c) the possible response types after leader shoot clipping. Shoots with asterisks were sampled for fresh and dry weight analysis. Note that for the reaction types (ii) and (iii), the first term indicates the reaction after the first growing period and the second term after the second growing period



was rebuilt each time before bud elongation started. Light availability under the artificial shade was measured on 2 July 2006 between 10 and 11 am at 1.4 m above the soil surface (and above the trees) with a Quantum Sensor (Type Lambda Inst. Corp Sr. Nr. Q2326-7709, Li-185A (Li-Cor)) that measures photosynthetically active radiation (PAR). Measurements were carried out in plots with full light (100 %) and in shaded plots under the slatted frame between two slats (67 % light) and directly beneath the slats (7.7 %). This shading pattern resulted in an area-weighted light reduction of about 70 %, that is, only ca. 30 % of PAR penetrated the artificial shade, which did not alter the spectral composition of the PAR in the blue and red range (Häsler et al. 2008). No artificial watering was carried out during the experiment.

Before clipping, the 20 saplings per plot were stratified into the classes ‘small’, ‘middle’ and ‘large’ according to their height in 2004. One sapling of the class ‘small’ and two of the classes ‘middle’ and ‘large’ were then randomly assigned to one of the 4 clipping treatments, resulting in 5 saplings per plot with the same clipping treatment (i.e. in total 10 saplings per clipping time and light condition). The 4 clipping treatments were applied in 2005 as follows (cf. Fig. 1b):

- ‘before budburst’: on 21 April 2005 (= before budburst), the leader shoot of the year 2004 was clipped;

- ‘after budburst’: on 19 May 2005 (= after budburst), the new leader shoot of the year 2005 was clipped;
- ‘autumn’: on 14 October 2005, the leader shoot of the year 2005 was clipped; and
- ‘unclipped’: saplings without any clipping, that is, control trees.

Trees were clipped with pliers to a fixed length of the remaining leader shoot of ca. 4 cm (except one tree with 2 cm remaining shoot and two trees with 3 cm, due to an insufficient length of the leader shoot of the year 2005). No lateral shoots were clipped. All clipping dates were 3–4 days before full moon in order to minimise a possible lunar bias (Zürcher et al. 1998). None of the examined trees had started bud elongation on the date of clipping in April.

Field and laboratory measurements

Height of all trees was measured in autumn 2004, 2005 and 2006 and additionally in April 2005 after the clipping treatment ‘before budburst’, in May 2005 before and after the treatment ‘after budburst’ and in September 2005 before the treatment ‘autumn’. Furthermore, we measured the length of the leader shoots (i.e. shoot increment) in autumn 2004, 2005 and 2006. Since the lower 4 cm of the leader shoot remained untouched, the number of lateral

buds in these lower 4 cm and the total number of lateral buds on the leader shoots were counted as well. As the destruction of a terminal bud or shoot changes the apical dominance pattern within a tree (Bergström and Danell 1987; Bryant et al. 1991), we recorded the response type (also called ‘reiteration’) of all saplings using a relatively simple classification scheme based on the dominant new leader shoot in autumn 2005 and 2006 (Fig. 1c) and noted the number of new leaders. Bending up a lateral shoot due to the formation of compression wood on the ventral part of the twig is hereafter called ‘flagging’ (cf. vi in Fig. 1c).

Tree height after clipping was measured as the height of the dominant leader shoot (for the year 2006 marked by an asterisk (*) in Fig. 1c). Note that this does not need to be the highest point of the tree, as the tip of a lateral branch of the whorl formed in 2004 may be higher than a new small shoot out of a bud on the remaining part of the leader shoot of 2004 or 2005. When a tree had not formed a new leader shoot or had not responded by ‘flagging’ and, therefore, belonged to the response type ‘no shoot’ (iii in Fig. 1c), the height of the main stem that had been clipped was measured.

On 14 September 2006, all saplings were cut ca. 2–3 cm above the soil surface. A stem disk was taken at the sapling base to analyse tree ring width. All leader shoots of the year 2006 were cut horizontally at their base with a pruning shear except for the very small shoots of the reaction type ‘basal bud’, where a knife was used to cut parallel to the previous year’s shoot. Fresh weight of these shoots was measured right after cutting using a laboratory scale to an accuracy of 0.1 g when the shoot weighed more than 1 g, and to 0.01 g otherwise. These shoots were then placed in cross bottom paper bags and oven-dried for 116–118 h (until mass constancy) at 70 °C. An oven temperature of 70 °C was chosen to minimise the water content (remaining chemically bound water <6 %, Niemz 1993) while preventing the volatilisation of oils, fats and terpenes. Dry weight of each individual shoot was then measured to an accuracy of 1 mg.

For the measurements of tree ring width, the largest radius was marked on each stem disk, and of the two radii perpendicular to the first, the smaller one was chosen. Ring width was measured with a Lintab 5 measuring device (F. Rinn S.A., Heidelberg, Germany) with a precision of 0.01 mm. The TSAP-Win tree ring program (Rinn 2003) was used to visualise the ring width. To obtain a consistent dendrochronological data base without any missing rings, single cores were cross-dated using the averaged time series of 20 ‘well-growing’ trees as a reference. The two ring widths from each tree per year were averaged.

Statistical analysis

Linear mixed-effects models (lme, of the software R version 2.9.0, R Development Core Team 2009) allowing

for block as a random effect were used to evaluate the data. The explanatory fixed effects were light (full sun vs. shade) and clipping treatment or response type. To include a measurement for tree vigour, we included tree height in 2004 (i.e. the height before the clipping treatment initiated) and mean ring width of 2003 and 2004 (i.e. the ring width formed at a time when artificial shading was placed but clipping had not started yet).

When clipping treatment or response type had a significant effect, a pairwise comparison between group levels was performed (using pairwise t test of the software R version 2.9.0, R Development Core Team 2009) with $p < 0.05$ as the significance level. For the analyses of 2005, the data of the saplings with the treatment ‘autumn’ were included as further ‘unclipped’ trees.

Results

All *A. alba* saplings survived the one-time clipping of the leader shoot.

Light as limiting resource?

At the beginning of the clipping treatment, the 9-year-old tree saplings were mostly between 75 and 110 cm tall (cf. height of the year 2004 in Fig. 3). As expected due to the height stratification, there was no difference in height, absolute or relative shoot increment of the year 2004 between the 4 clipping treatments (Table 1), and there was no significant difference between shaded and unshaded saplings in these 3 height-related variables for 2004, either. However, there were more buds on the 2004 leader shoots for saplings growing in full sun compared with those growing under the artificial shade (Table 1). The mean tree ring widths in the years 2001 and 2002, that is, before installing the artificial shade, were not significantly different, while the mean ring widths for the years 2003 and 2004 with the artificial shade (but still without clipping) were significantly smaller than in full sun (Table 1).

Response types after clipping

All unclipped *A. alba* saplings formed single regular leader shoots, that is, response type ‘terminal bud’ (i in Fig. 1c), in the years 2005 and 2006, irrespective of light conditions (Fig. 2). In contrast, the saplings clipped ‘after budburst’ elongated the remaining leader shoots of the year 2005 and developed lateral buds, but no terminal bud until autumn 2005. The leader shoots 2006 were typically a ‘pseudoend’ shoot (ii in Fig. 1c) because it originated from one of the most distal lateral buds (Fig. 2). Only on 2 saplings that were clipped ‘after budburst’, a basal rather than the most

Table 1 Results of the linear mixed-effects models for height (cm), shoot increment (cm), lateral buds on leader shoots (numbers) and mean tree ring width (mm) before clipping the *A. alba* saplings

	df	F value			Mean (SD)		Mean (SD)			
		Intercept	Light	Treatment	Full sun	Shade	Unclipped	After	Before	Autumn
Height 2004	74	784.4***	1.1 n	0.0 n	94.3 (15.9)	90.8 (14.8)	93.2 (16.1)	92.1 (15.8)	93.2 (13.4)	91.8 (17.1)
Shoot increment 2004	74	629.8***	3.3°	0.1 n	27.9 (5.6)	25.3 (7.4)	27.1 (7.0)	26.2 (6.5)	26.1 (5.4)	26.9 (7.9)
Shoot increment/ Height 2004	74	1913.2***	3.6°	0.2 n	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)
Buds on 2004 shoot	55	207.4***	18.8***	0.1 n	6.3 (3.0)	3.4 (2.0)	5.0 (2.9)	4.7 (2.4)	NA	4.8 (3.5)
Mean tree ring width in 2003 + 2004	73	481.4***	17.3***	0.2 n	1.5 (0.5)	1.0 (0.4)	1.2 (0.5)	1.2 (0.5)	1.3 (0.8)	1.2 (0.5)
Mean tree ring width in 2001 + 2002	73	889.2***	0.0 n	0.3 n	1.5 (0.4)	1.5 (0.4)	1.5 (0.4)	1.4 (0.5)	1.5 (0.4)	1.5 (0.5)

The number of trees (*N*) is 80, apart from 79 due to a missing value in the tree ring width measurements, and except from 60 for the buds on the 2004 shoots because they were not counted for trees with clipping treatment ‘before budburst’. There was no interaction between light and clipping treatment and the interaction term was omitted from the analysis. Significance levels: n, not sign.; ° tendency with $p \leq 0.1$, *sign. at $p \leq 0.05$, **sign. at $p \leq 0.01$, ***sign. at $p \leq 0.001$

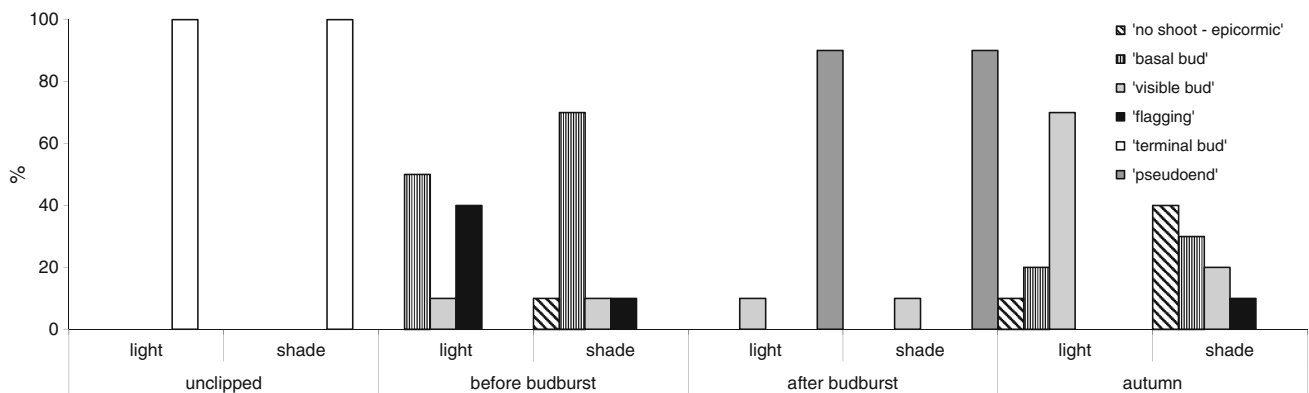


Fig. 2 Relative numbers of *A. alba* saplings with different response types (defined in Fig. 1c) grown under full light or under artificial shade

distal bud became the leader shoot in 2006; thus, these trees reacted with the response type ‘visible bud’ (*v* in Figs. 1c, 2).

Saplings with woody tissue clipped, that is, those clipped ‘before budburst’ or in ‘autumn’, showed 4 different reactions after clipping (Fig. 2): no shoot in the first year and epicormic shoots in the second year (*iii* in Fig. 1c), new shoots out of regularly formed basal buds that would have become dormant without clipping (‘basal buds’, *iv* in Fig. 1c), new shoots out of regularly formed visible distal buds (‘visible buds’, *v* in Fig. 1c), or by bending up a twig, that is, ‘flagging’ (*vi* in Fig. 1c). None of the saplings that had visible buds on the 4 cm shoot part that remained after clipping reacted with ‘no shoot’ or ‘basal buds’. A larger fraction of trees were characterised by the response type shoot out of ‘basal buds’ than out of ‘visible distal buds’, apart from saplings clipped in

‘autumn’ that were grown in full sun (Fig. 2). Many trees clipped in ‘autumn’ 2005 still had no new shoot 1 year later (Fig. 2), while only one shaded sapling that had been clipped ‘before budburst’ had no new shoot in the first year and an epicormic shoot in the second year after clipping (reaction type *iii* in Fig. 1c). In contrast, the response type ‘flagging’ occurred more often after clipping ‘before budburst’ than after clipping in ‘autumn’ and particularly often in full sun after clipping ‘before budburst’ (Figs. 2, 3).

Height, height increments and ring width after clipping

Influence of light

Shaded trees were smaller than trees grown in full light (Table 2, Figs. 4a, 5a). Similar results were found for shoot

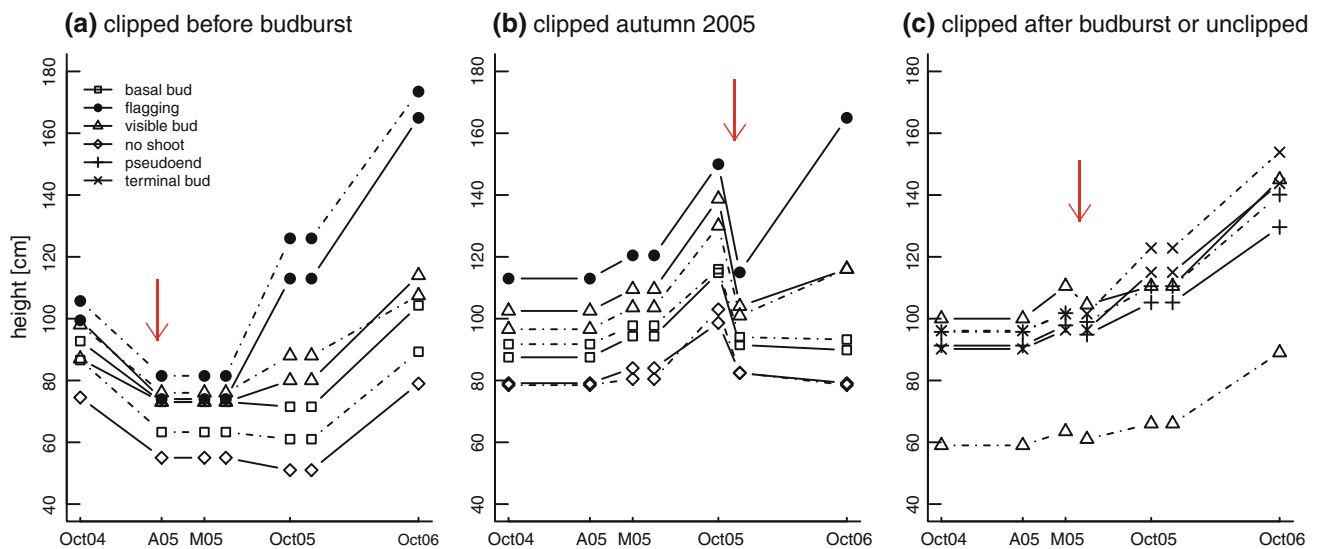


Fig. 3 Mean height for *A. alba* saplings under full sun (pointed lines) or under artificial shade (solid lines) with different reaction types (defined in Fig. 1c) to clipping in 2005 (a) before budburst, (b) in

autumn, and (c) after budburst or unclipped (control trees). The clipping date is indicated by an arrow

increments in 2005 (Fig. 4b), while shoot increments in 2006 did not differ between the light regimes (Table 2 and Fig. 5b). Tree ring widths in 2005 and 2006 were larger in sun than in shade (Table 2, Fig. 4c, 5d). There was no interaction between light and clipping treatment, and the interaction term was omitted in the analysis (cf. Table 2).

Influence of clipping treatments

There was a significant effect of clipping on height in 2005 and 2006 (Table 2). Unclipped trees were somewhat taller than trees with treatment ‘after budburst’ and significantly taller than trees with treatment ‘before budburst’ in autumn 2005 (Fig. 4a). In autumn 2006, the trees clipped in autumn 2005 were the smallest (Fig. 5a). Similar results were found for shoot increments in 2005 (Fig. 4b), while shoot increments in the year 2006 were largest for trees clipped ‘before budburst’ (Fig. 5b), which can be explained by the reaction type ‘flagging’ (see below). In contrast to height, tree ring widths in 2005 and 2006 did not differ between the clipping treatments (Table 2, Fig. 4c, 5d).

Influence of response type

In 2005, tree saplings that reacted with new shoots out of ‘basal buds’ were the smallest and had the lowest height increments and the smallest tree ring width (Fig. 4d-f). Somewhat larger were those trees that reacted with shoots out of ‘visible distal buds’, followed by trees that reacted with ‘flagging’ or with ‘terminal buds’ (Fig. 4d). Trees that were clipped ‘after budburst’ only elongated their shoots to

a length smaller than that of the ‘unclipped’ trees (with shoots out of ‘terminal buds’) but similar to that from shoots out of ‘visible buds’ (Fig. 4d).

In 2006, trees with ‘no shoot’ were similarly tall as trees with shoots out of ‘basal buds’, but significantly shorter than trees with shoots out of ‘visible buds’, and these in turn were shorter than ‘unclipped trees’ with shoots out of ‘terminal buds’ and trees clipped ‘after budburst’ with shoots out of ‘pseudoend’ buds (Fig. 5e). Finally, trees that reacted with ‘flagging’ were by far the tallest (Fig. 5e) with the largest shoot increments (Fig. 5f) in the year 2006. This can also be seen clearly in Fig. 3.

Influence of tree vigour

Tree height 2004 as measured prior to clipping had a significant positive effect on the height increments and tree ring widths in both years after clipping (cf. Table 2). The larger the trees were before clipping, the more often they reacted with ‘flagging’ or with shoots out of ‘visible buds’, and the higher they were after clipping (cf. Fig. 3).

Mean ring width of 2003 and 2004 as measured before clipping had no significant effect on the heights after clipping. Still, the AIC values (Akaike Information Criterion for a fitted parametric model, cf. R Development Core Team 2009) of the statistical models were smaller and thus better with (e.g. 599.6 for 2005) than without (607.0) ring width prior to clipping for both years. Shoot increment 2005 and tree ring widths in 2005 and 2006 were again significantly and positively affected by tree ring width before the treatments (cf. Table 2). Hence, tree vigour

Table 2 Results of the linear mixed-effects models for the first growing season after clipping ('autumn' trees are again classified as 'unclipped' trees) in autumn 2005 or for the second growing season after clipping in 2006 for the *A. alba* saplings

	<i>df</i> (<i>N</i>)	Intercept	Light	Treatment	Height 2004	Mean ring width 2003 + 2004
Height 2005	72 (79)	8739.6***	14.8***	88.5***	335.2***	2.8 n
Shoot increment 2005	72 (79)	445.4***	7.0**	65.8***	53.5***	7.7**
Shoot increment 2005/height 2004	72 (79)	288.9***	4.1*	69.9***	9.7**	7.5**
Tree ring width 2005	72 (79)	1315.7***	13.5***	2.3 n	69.2***	14.1***
Height 2006	71 (79)	5144.3***	7.4**	32.4***	196.5***	3.4°
Shoot increment 2006	71 (79)	881.2***	3.7°	41.1***	34.8***	2.7 n
Shoot increment 2006/height 2004	71 (79)	1103.8***	1.4 n	60.9***	0.1 n	0.5 n
Fresh weight/shoot increment 2006 ^a	63 (71)	995.1***	0.1 n	12.3***	45.5***	8.2**
Dry weight/shoot increment 2006 ^a	63 (71)	4172.9***	1.6 n	10.8***	49.4***	8.2**
Dry in % of fresh shoot weight 2006	63 (71)	5019.9***	16.3***	4.0*	0.0 n	0.8 n
Tree ring width 2006 ^b	71 (79)	3923.9***	26.2***	0.8 n	96.4***	4.3*
Number of new leader shoots	71 (79)	264.1***	2.6 n	16.4***	2.2 n	1.1 n

	<i>df</i> (<i>N</i>)	Intercept	Light	Reaction type	Height 2004	Mean ring width 2003 + 2004
Height 2005	69 (79)	15970.3***	35.6***	137.8***	642.7***	0.4 n
Shoot increment 2005	69 (79)	554.0***	10.9**	56.0***	56.6***	5.4*
Shoot increment 2005/Height 2004	69 (79)	306.5**	6.6*	57.4***	5.5*	5.4*
Tree ring width 2005	69 (79)	1266.6***	13.0***	2.6*	59.5***	12.5***
Height 2006	68 (79)	9597.0***	13.8***	66.6***	219.0***	1.0 n
Shoot increment 2006	68 (79)	525.4***	2.2 n	9.9***	8.9**	1.5 n
Shoot increment 2006/Height 2004	68 (79)	485.0***	0.6 n	7.0***	0.2 n	1.2 n
Fresh weight/shoot increment 2006	61 (71)	818.4***	0.8 n	15.3***	17.6***	4.5*
Dry weight/shoot increment 2006	61 (71)	1218.7***	3.0°	15.9***	20.9***	4.4*
Dry in % of fresh shoot weight 2006	61 (71)	3736.4***	15.7**	2.0°	0.6 n	0.6 n
Tree ring width 2006 ^b	68 (79)	3880.3**	26.0***	4.0**	76.5***	3.5°
Number of new leader shoots	68 (79)	330.2**	3.2°	13.8***	1.0 n	3.0°

In the upper part, *F* values are given with clipping treatment and in the lower part with reaction type as explanatory variable. The number of trees (*N*) is 79 (due to a missing value in the tree ring width measurements), except for fresh and dry weight of shoots 2006 with only 71 observations, because reaction type 'no shoot' had no 2006 shoots that could be weighted. There was no interaction between light and clipping treatment or reaction type; therefore, the interaction term was omitted from the analysis. Significance levels: n, not sign.; °tendency with $p \leq 0.1$, *sign. at $p \leq 0.05$, **sign. at $p \leq 0.01$, ***sign. at $p \leq 0.001$

^a Data were log transformed

^b Data were square root transformed

before clipping had a positive effect on tree size after clipping.

Shoot weight after clipping

Considering the different lengths of leader shoots in 2006, shoots of trees with the response type 'flagging' were heavier compared to shoots out of 'pseudoend' or 'terminal buds', and these in turn were heavier than shoots out of 'visible buds' or 'basal buds' (Table 2; Fig. 5g). This was the case for relative fresh and dry weights. In contrast, the dry-to-fresh weight ratio was similar for all reaction types and clipping treatments (Table 2).

Light availability had no influence on the fresh and dry relative shoot weights (Table 2; Fig. 5c). The dry-to-fresh weight ratio was significantly higher in full sun than under artificial shade, suggesting lower water content in shoots growing in full sun (Table 2).

Multi-trunking due to clipping

Simulated browsing was found to cause multi-trunking. The number of terminal shoots was highest for saplings clipped 'before budburst' (mean \pm SD = 3.4 ± 1.3), regardless of the response. Saplings clipped in 'autumn' (2.3 ± 1.7) and 'after budburst' (1.7 ± 0.8 , with mainly the response type

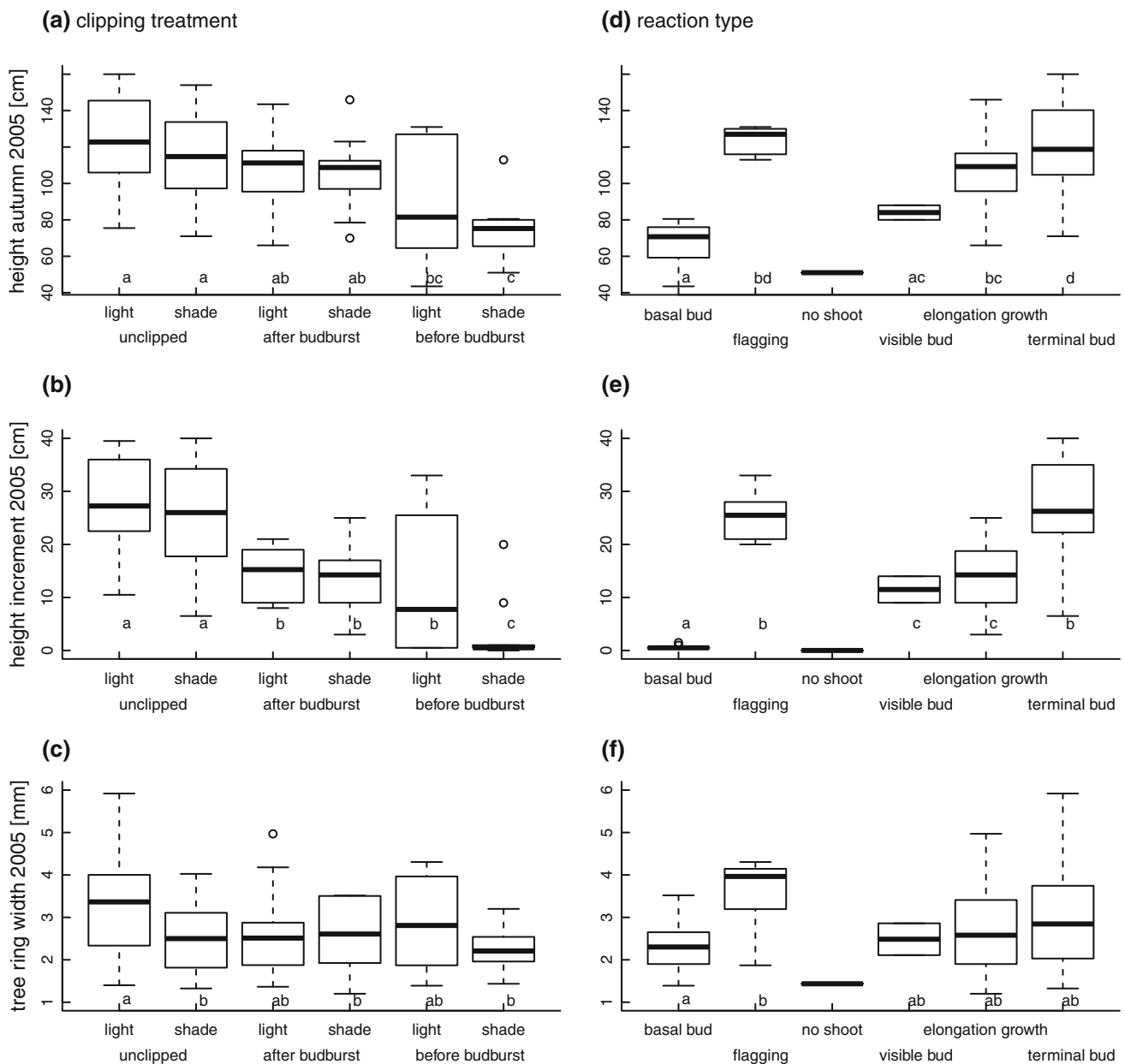


Fig. 4 Height, shoot increment and tree ring width in autumn 2005 (before autumn clipping) for *Abies alba* saplings classified according to the clipping treatment (note that ‘autumn’ clipping is included as ‘unclipped’) or their response type in the first growing season after

‘pseudoend’) were mostly forked, while all ‘unclipped’ trees had a single terminal shoot (1 ± 0). Light availability had no significant influence on the number of new terminal shoots (Table 2).

Discussion

The response of 9-year-old, 60–120 cm tall *A. alba* saplings growing in full light or under artificial shade was

clipping (cf. Fig. 1c). Different letters are used for significant differences at $p < 0.05$. Only one tree reacted with ‘no shoot’ after the first growing season and was excluded from statistical analysis

tested with regard to simulated leader shoot browsing applied before budburst, shortly after budburst, or in autumn. Given that no sapling died in our experiment, survival was unaffected by clipping. This coincides with other experiments on fir that dealt with single (Häsler et al. 2008; Vandenberghe et al. 2008) or repeated clipping (Eiberle 1975, 1978). As hypothesised, the timing of clipping, light availability and the constitution of the saplings prior to clipping played an important role in response to clipping.

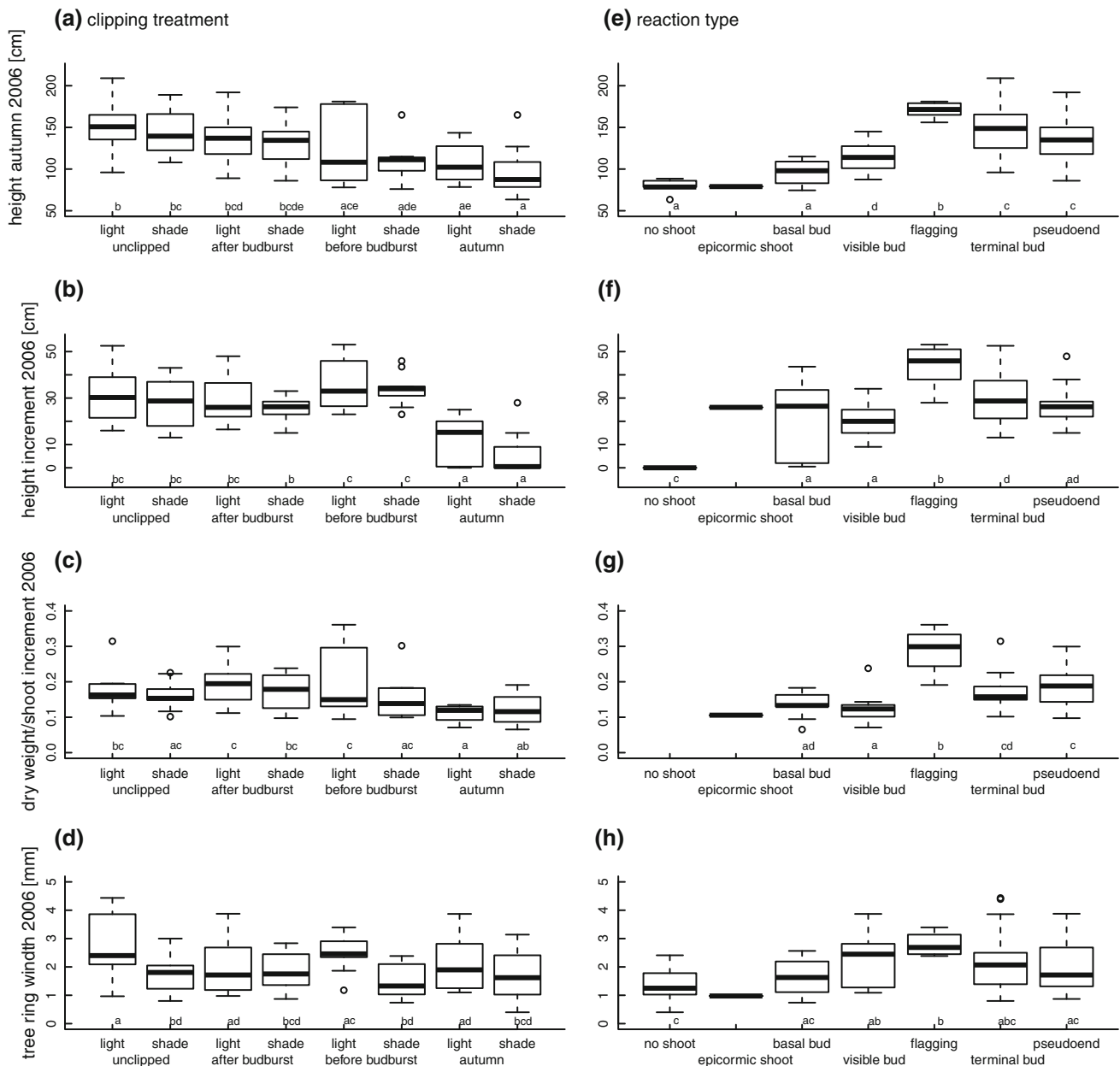


Fig. 5 Height, shoot increment, relative dry weight of shoots (g/cm) and tree ring width in autumn 2006 for *Abies alba* saplings classified according to the clipping treatment or their response type in the second growing season after clipping (except first season for autumn clipping, reaction types cf. Fig. 1c). Different letters are used for

significant differences at $p < 0.05$. Only one tree reacted with ‘epicormic shoots’ after the second growing season and was excluded from statistical analysis and no dry weight could be measured when no new shoot had been built

Timing of clipping

Those *A. alba* saplings where mature woody tissue was clipped (i.e. saplings with treatments ‘before budburst’ and ‘autumn’) reacted differently than saplings where fresh annual shoots were clipped (treatment ‘after budburst’). It is noteworthy that these differences did not occur primarily because of clipping in the dormant versus the growing period (as has often been reported, cf. Canham et al. 1994;

Senn and Haukioja 1994; Hester et al. 2004), but rather because of clipping fresh versus woody tissue: we clipped a few additional *A. alba* saplings in the growing period down to the woody tissue of the previous year, and they all reacted exactly like those saplings that were clipped in the dormant period before budburst (results not shown).

Probably due to our clipping treatment (fresh vs. woody tissue), saplings were not generally more impaired by leader shoot browsing after budburst than in the dormant

season (as hypothesised in the Introduction). The same has been found for *Pinus sylvestris* (Millard et al. 2001; Hester et al. 2004) and *P. abies* (Kristöfel and Pollanschütz 1995). We almost found the contrary: although trees clipped ‘after budburst’ (i.e. with ‘pseudoend’ shoots) were smaller than trees clipped ‘before budburst’ that reacted by ‘flagging’, they were larger than those reacting with shoots out of either ‘visible buds’, ‘basal buds’ or ‘epicormic shoots’ (cf. Fig. 5e). Yet, *Pinus sylvestris* had more ‘inter-whorl’ shoots (probably equal to shoots out of regular distal buds) following clipping after budburst than after winter clipping or than unclipped saplings (Hester et al. 2004).

In our experiment, shoot loss in autumn was not less detrimental than shoot loss before budburst (cf. Fig. 5a). Many fir saplings clipped in ‘autumn’ did not react in the following growing season (cf. reaction type ‘no shoot’ in the first year), while most saplings clipped ‘before budburst’ reacted with shoots out of ‘basal buds’ (Fig. 2). Also, Eiberle (1975) found that clipping for two years in autumn resulted in 20 % smaller *A. alba* saplings than two clippings in the same year, that is, before budburst and in autumn. We are not aware of a good explanation for this fact and suggest further experiments.

Light dependency

Trees under artificial shade were probably somewhat more stressed than the unshaded saplings, as they had smaller tree ring widths and fewer lateral buds per unit shoot length before clipping (cf. Table 1). The response type ‘flagging’ was more frequent in unshaded compared with shaded trees clipped ‘before budburst’. For ‘autumn’ clipping, shoots out of ‘visible buds’ were more frequent in full sun than shoots out of ‘basal buds’ and ‘no shoots’, and vice versa in the shade (Fig. 2). Häsler et al. (2008) have already found twice as much flagging after clipping before budburst in *A. alba* saplings growing in full light compared with those under artificial shade; almost half of the shaded saplings did not form a new leader shoot in the year of clipping, and ca. 2.5 % still had no new leader shoot in the second year. As hypothesised, fir saplings have a higher tolerance to simulated leader shoot browsing in full sun than under shaded conditions. This has also been found for other tree species (McLaren 1996; Harmer 1999; Baraza et al. 2004; Hódar et al. 2008).

In the second year after clipping, light did not have a significant effect on leader shoot growth in our experiment (Table 2). The same was found for fir biomass change in a grazing experiment (Vandenberghe et al. 2008). Although silver fir saplings have a high plasticity of morphological traits in response to different levels of irradiance, maximum leader shoot length was found under 18 % irradiance (neutral shade net) compared to 100, 48 and 8 % irradiance

(Robakowski et al. 2003). Our artificial shade resulted in a reduction of about 70 % PAR and thus probably did not constitute a large stress factor for the shade tolerant *A. alba*. In closed forest stands with lower PAR values, shading may be a considerable stress factor leading to smaller diameter and height increments of fir saplings (cf. Dobrowolska 2008), fewer internodal shoots (Stancioiu and O’Hara 2006) and, in extreme cases, even mortality (Chmelař 1959). Under such shaded conditions, browsed fir saplings may more often react with ‘no shoots’ in the first year (Osterloher and Wiechmann 1993) and, therefore, be much smaller than unbrowsed trees (e.g. Ammer 1996). It is noteworthy that shaded balsam fir saplings were already suppressed to the same extent as those in a severe clipping treatment (McLaren 1996). Thus, the reduction effect of light and browsing on silver fir is clearly not additive. Experiments with stronger artificial shading or with *A. alba* saplings that grow in closed forest stands would be desirable.

Tree ring width and the number of lateral buds per unit shoot length were more sensitive to light availability than height growth (Table 1). This fact has already been demonstrated by assessing the influence of competition by ground vegetation on conifer seedlings and saplings (e.g. Lautenschlager 1999; Küssner et al. 2000) and by analysing the ratio of height to diameter at breast height of trees in forest stands (Mitscherlich 1978; Kramer 1988). In our experiment, height prior to clipping was a better predictor of the effect of browsing than tree ring width (Table 2). This confirms the findings by Mitscherlich and Weise (1982) who concluded that similar diameters may be due to multi-trunked, very bushy *P. abies* saplings that have a similar leaf area regardless of the occurrence of browsing.

Irrespective of light availability and the response type, all clipped saplings formed several new leader shoots. Multi-trunking due to the loss of apical dominance has often been reported (Mitscherlich and Weise 1982; Långström and Hellqvist 1992; Bergquist et al. 2003). For forest management, the development of multi-trunking is probably a much more serious consequence of a single browsing event than reduced height growth (Welch et al. 1992). Yet, recovery in the sense that the strongest leader becomes dominant and the other leaders turn into branches has frequently been observed at least for *Picea* saplings (Welch et al. 1992; Bergquist et al. 2003).

The facts that in our experiment, (1) the focal resource light did at least to some extent limit plant growth prior to clipping and (2) the tolerance to clipping ‘before budburst’ or in ‘autumn’ was generally larger in full sun, supporting the limiting resource model (cf. Wise and Abrahamson 2005) as well as the compensatory continuum hypothesis (Maschinski and Whitham 1989; Whitham et al. 1991). However, there was no light-induced difference for trees clipped ‘after budburst’ (Fig. 2), and many response types

were found after clipping in the dormant period, which had a large influence on height after clipping (cf. Fig. 5e). We are convinced that the timing of clipping and tree vigour were much more important in our experiment for explaining height differences after clipping than the direct effect of light (at least for the level of shading considered in our experiment).

Tree vigour

As hypothesised in the Introduction, fir saplings respond more efficiently to leader shoot browsing when they have a higher ‘vigour’—expressed as larger height and larger ring width relative to neighbouring fir saplings of the same age. Fast-growing *A. alba* saplings—that is, the tallest saplings (cf. Fig. 3a, b) with the largest tree ring widths—typically bent up twigs to form new leader shoots (i.e. response type ‘flagging’). Saplings characterised by intermediate growth tended to develop new shoots out of ‘visible buds’. Again, somewhat smaller saplings usually reacted with shoots out of ‘basal buds’, while slow-growing saplings (i.e. the smallest individuals; Fig. 3a, b) did not normally react in the first growing season after clipping at all (i.e. reaction type ‘no shoots’ and ‘epicormic shoot’ in the second year; Fig. 3a, b). Häslér et al. (2008) have already suggested that flagging is a reaction type of dominant saplings, while the exclusive formation of real epicormic shoots is more characteristic of suppressed *A. alba* saplings. Thereby the constitution and the reaction types seem to be light-dependent (see above).

In our experiment, trees that had high ‘vigour’ were even able to overcompensate a single loss of their leader shoot (Figs. 3, 5e). Overcompensation in the case of flagging has already been reported for tall *Picea sitchensis* saplings (Welch et al. 1992). *P. sylvestris* that reacted with flagging had larger height increments and higher branch basal area than trees reacting with distal epicormic shoots (i.e. leaders originating from interfascicular buds, Långström and Hellqvist 1992). Generally, overcompensation has often been found in clipping experiments conducted with saplings in pots or cultivated in gardens and applying a single or light treatment (e.g. Hjäältén et al. 1993; Kristöfel and Pollanschütz 1995; Hester et al. 2004). Trees are likely to overcompensate height loss if they are somewhat stressed, as plants that grow close to their maximum capacity are unlikely to be able to further increase relative growth rates (Hilbert et al. 1981; Osterheld and McNaughton 1991).

Strongly stressed trees, in turn, are unlikely to be able to compensate because herbivory removes buds, photosynthetically active tissue (needles) and nutrients from the plant that are not easily replaced (Bryant et al. 1983; Osterheld and McNaughton 1991). For example, the slow-growing saplings in our experiment showed a very slow

reaction, and therefore, the height difference induced by simulated browsing even increased in the first year of the response (Figs. 3, 5e). No compensation has also been found in repeated browsing experiments conducted with *A. alba* (Eiberle 1978). Repeated browsing is a very common phenomenon in forest stands, which further reduces tree ‘vigour’ and clearly slows down the growth rate of regeneration (e.g. Kupferschmid and Bugmann 2008; Mitscherlich and Weise 1982) and thus may lead to indirect mortality due to changes in species-specific growth ranks (cf. Krueger et al. 2009; Vandenberghe et al. 2008; Kupferschmid and Brang 2010). In forest stands, conditions that would allow for overcompensation are found very rarely, and trees whose leader shoot has been (repeatedly) browsed will typically remain smaller than unbrowsed trees (Ammer 1996; Kupferschmid and Bugmann 2008).

Leader shoots from trees with the response type ‘flagging’ were heavier than those of ‘unclipped’ trees (cf. Figs. 5g). This can be explained by a massive formation of compression wood in the latewood (i.e. high density of lignin, cf. Wagenführ 1999) that is present not only in the shoot piece that bends up, but in the subsequent shoots, leading to thicker and heavier shoots. It is likely that these structural changes have negative consequences for the palatability of the shoots (e.g. red deer preferred *Picea sitchensis* saplings with longer and thicker shoots in an enclosure experiment (Iason et al. 1996), and shoots with longer needles (Häslér and Senn 2012)).

Our experimental data show that there is definitely a continuum of responses, where not only some tree species are less flexible than others (cf. Whitham et al. 1991), but individual trees react differently (cf. Hjäältén et al. 1993; Hódar et al. 2008), depending mostly on the stress status of the trees and the time of browsing.

Conclusion

Overall, the present experiment shows that there is no single response to browsing but a continuum of responses where some saplings overcompensate leader shoot loss and some compensate it while for many trees the height difference induced by simulated browsing even increases in the first year(s) after browsing.

The three factors hypothesised to be important are indeed crucial for explaining the observed responses:

(1) The timing of clipping (browsing) explains differences that are induced by different response types of saplings with not yet fully expanded shoots in spring versus those where woody tissue is clipped.

(2) The light conditions and (3) the vigour of a tree at the time of browsing determine (1) the type and (2) the rate

of its response, as fast-growing *A. alba* saplings were found to bend up twigs ('flagging') and overcompensate height loss, whereas slow-growing, mostly shaded saplings had no new leader shoot after the first growing season but formed new epicormic leader shoots in the subsequent year only.

It is noteworthy that sapling vigour can, to some extent, be manipulated by forest management, and thus, the response to browsing can be influenced indirectly. If conditions for *A. alba* regeneration are optimised to enhance tree vigour, for example, by providing more light at the forest floor, saplings will more often respond with 'flagging' or at least with shoots out of 'visible buds' in the first vegetation period after browsing. Attention must be paid (1) not to promote only completely unshaded, dominant saplings, as these tend to be browsed more often than suppressed specimen (cf. Näscher 1979; Reimoser and Gossow 1996), and (2) to avoid the growth of fast-expanding ground vegetation, which often hinders the establishment of fir seedlings in open areas (cf. Paluch 2005). Hence, there is a subtle relationship between sapling reaction, light conditions and forest management in *A. alba* regeneration that needs further attention.

Acknowledgments We express our gratitude to Sepp Senn and Helene Häslér (Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf) for allowing us to use their planting experiment, that is, the *Abies alba* saplings and the artificial shading system. We are indebted to Anton Burkart (WSL) and his nursery team for their help with the artificial shading system. We thank Martina Hobi (former M.Sc. student at ETH Zurich) for the tree ring measurements. We are grateful to Jan Wunder (ETH Zurich) for inspiring discussions about the statistical analysis. The work of the first author was funded by the Swiss Federal Office for the Environment via the project 'Langfristige Walddynamik unter Ungulaten-Einfluss', contract No. 00.01138.PZ/H362-1153.

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