Selective browsing behaviour of ungulates influences the growth of *Abies alba* differently depending on forest type

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Highlights

- Browsing only buds vs. a large part of the annual leader shoot was crucial.
- Within-tree browsing intensity on *Abies alba* saplings was lower in *Fagus*-dominated forests.
- Due to selective browsing, lightly browsed saplings grew better than unbrowsed ones.
- Strong browsing on leader shoots contributes to shifts in the species' growth ranking.
- Surveying within-tree browsing intensity is recommended to accurately estimate browsing impacts.

Abstract

Ungulate densities and browsing have increased over the past decades in many forests in Europe. Browsing on tree saplings is a selective process dependent on forest type. This study tested whether the impacts of browsing are altered by differences in tree vigour and within-tree browsing intensity (browsing only buds vs. browsing a large part of the annual leader shoot), and if these effects are modulated by forest type.

The growth rate and within-tree browsing intensity of leader shoots were investigated for different height classes and species compositions at 18 sites (each with 14–64 plots) in spring before budburst and at 6 sites in autumn. The sites were situated in northeast Switzerland and comprised four major forest types that had *Abies alba* regeneration. Linear mixed-effects models were fitted for the relative growth rate of *Abies* and for the ratio of the relative growth rate of *Abies* to the relative growth rate of *Picea abies*.

More *Abies* saplings were present in *Fagus*-dominated forests than in *Fagus-Abies* or *Picea-Abies* forests, and within-tree browsing intensity on their leader shoots was lower. Lightly browsed *Abies* saplings grew better than those that were not browsed, which in turn grew better than strongly browsed saplings. This pattern, which occurred irrespective of forest type, was caused by selective browsing on vigorously growing trees and led to a greater impact of strong browsing in comparison to light browsing on the growth of *Abies* saplings.

The ratio of the relative growth rate of *Abies* to *Picea* was altered by within-tree browsing intensity, forest type and soil depth. Generally, this ratio was highest in shallow soiled *Fagus*-dominated forests after light browsing and lowest in *Fagus-Abies* forests after strong leader shoot browsing, indicating a browsing-induced shift in the relative difference in growth rate between species towards *Picea* in *Fagus-Abies* and *Picea-Abies* forests but not in *Fagus*-dominated forests.

Because the main factor influencing the growth of *Abies* saplings was the amount of tissue loss on the leader shoots (bud vs. entire or large parts of leader shoots), browsing inventories neglecting to assess the within-tree browsing intensity are not recommended. The within-tree browsing intensity of leader shoots is a simple but objective measurement that should be used in forest regeneration inventories of *Abies* for improving estimates of the impact of ungulate browsing.

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Keywords

forest inventory, growth rate, herbivory, silver fir, tree regeneration, ungulate browsing

Introduction

Large mammalian herbivores depend on plant communities for their existence. Leaves, shoots and bark of tree saplings are part of the normal diet of ungulate species such as red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.) (Cornelis et al., 1999; Tixier et al., 1997). However, it is known that ungulates browse selectively on particular tree species (Boulanger et al., 2009; Côté et al., 2004). For example, European silver fir (*Abies alba* Mill.) has been identified as one of the most selected species, while Norway spruce (*Picea abies* L.) is usually one of the least selected species in Europe (e.g. Gill, 1992a; Kupferschmid et al., 2015a). In addition, tree species differ in their tolerance to browsing (Kupferschmid, 2017). Browsing may thus lead to shifts in the relative rates of growth of different tree species, which can in turn result in changes in the relative abundance of different tree species that successfully regenerate (e.g. Gill and Beardall, 2001; Krueger et al., 2009). Several empirical (Augustine and McNaughton, 1998) and modelling studies (Didion et al., 2009; Didion et al., 2011) have shown that selective browsing can affect the development of a forest stand and cause major changes in plant community composition and structure. For the example of fir and spruce, under continuously high browsing pressure, fir-spruce forests are expected to become spruce forests (Kupferschmid and Brang, 2010; Tremblay et al., 2007).

Feeding selectivity of herbivores is not limited to the degree to which different plant species suffer tissue loss, as it also includes selectivity among individual trees of the same species. At the local scale, a single ungulate selects food items by choosing among tree species, individual trees (e.g. according to tree height or vigour) and parts of trees (forage quality), and it additionally decides how much biomass to remove (forage quantity). Generally, there seems to be a connection between individual plant morphology and feeding behaviour (e.g. Hartley et al., 1997). Larger saplings with a large crown volume have been found to be more likely to be browsed by ungulates (Iason et al., 1996; Kupferschmid et al., 2015b). Moreover, a close relationship between shoot size and bite size has been reported (Danell et al., 1994; Shipley et al., 1999). Thus, herbivore species probably feed selectively on vigorously growing plants or plant parts, as suggested by the plant vigour hypothesis (Price, 1991). However, in a study in Swiss (fir-) beech forests, vigorously growing *Abies alba* saplings remained larger even after browsing (Kupferschmid et al., 2013). Therefore, the role of individual tree selection and forage quantity on the growth-rate ranking of different tree species remains unclear.

Site characteristics like soil pH and depth, as well as forest stand basal area, type and developmental stage, influence the availability of resources such as nutrients, water and light. This resource availability affects i) the forage availability (tree saplings and ground vegetation) and thus ungulate selection (Cornelis et al., 1999), ii) the growth rate of tree saplings (e.g. Vandenbergh et al., 2008) and iii) the ability of trees to react to browsing (i.e. ‘stress status hypothesis’, see Kupferschmid, 2017). In addition, by browsing different parts and numbers of tree saplings, herbivores can alter the resource that limits a plant’s fitness and thus its tolerance to herbivory (i.e. ‘limiting resource model’, see Wise and Abrahamson, 2005). Therefore, it is important to understand interactions between site characteristics and ungulate browsing.

Kupferschmid et al. (2015b) proposed, based on their experiment, that within-tree browsing intensity — i.e. the amount of tissue ungulates eat, such as leader buds only (decapitation), part(s) of the annual leader shoot, the entire annual leader shoot, or much more than just the annual leader shoot — should be integrated into assessments of browsing in order to better estimate the browsing

impact at different sites. In this study, I tested a simple and quick approach involving measurements of within-tree browsing intensity and tree vigour in forest inventories to address browsing impact more effectively than is possible when only the proportion of browsed trees is assessed. My specific questions were:

- Does within-tree browsing intensity influence the growth rate of *Abies alba* saplings?
- Does within-tree browsing intensity influence the ratio of the relative growth rate of *Abies alba* saplings to the relative growth rate of *Picea abies* saplings and thus lead to shifts in the species' growth ranking?
- Are there interactions between within-tree browsing intensity and site characteristics like forest type, soil pH, soil depth and forest stand basal area and/or developmental stage?

Materials and methods

Study sites

In order to investigate the influence of ungulate browsing on tree saplings on a regular basis, indicator areas (Rüegg and Nigg, 2003) or sites with surveys of juvenile growth and damage in forests (Amt für Wald Graubünden, 2005) have been established and repeatedly monitored in the cantons of St. Gallen and Grisons in Switzerland. Such sites typically comprise a continuous forest area with different forest developmental stages and forest types. Each site contains a rectangular grid with a fixed grid size of 100 m between the circular sampling plots, resulting in 14–64 plots per site. The plot centres are permanently marked.

For this study, 17 sites in St. Gallen and 7 in the adjacent north-western part of Grisons were selected on a purposive basis (Table 1). Sites were selected that i) had seed-producing *Abies alba* trees in the canopy (at least 5% of canopy trees) and ii) contained at least some sampling plots where *Abies alba* saplings were present. Once a site was selected, all plots of the site were visited. This resulted in a total of 535 plots with very different densities of saplings (0.01–8.98 *Abies alba* saplings per m²) and browsing intensities (0–92%; Table 1).

Table 1: Details of the 24 assessed sites in the two Swiss (CH) cantons St. Gallen (SG) and Grisons (GR), including coordinates; the prevailing forest types at each site (*Acer-Fraxinus-Tilia*, *Fagus*, *Fagus-Abies* and *Abies-Picea*); the number of chamois (Cham) and red deer (Red) present in relation to the number of roe deer (n = no, f = few < 5%, m = many > 5%); the density (Dens); and the proportion of leader browsing (PLB) found in the year 2014 by means of repeated assessments in the St. Gallen indicator areas or through measurements in circles of 2 m radius in 2016 and 2017; the year and period of the field assessment; soil pH and depth; hill slope; forest stand basal area; range in elevation above sea level (EL); number of plots assessed; and number of *Abies* saplings and of *Abies/Picea* pairs that were measured via the nearest tree method.

Site	CH	Coordinates		Forest type	Ungulates		Abies		Picea		Year	Soil		Slope [%]	BA	EL		Plots N	Abies N	Abies/Picea N
		x	y		Cham	Red	Dens	[m ⁻²]	PLB [%]	Dens		[m ⁻²]	PLB [%]			pH	depth [cm]			
Nieselberg (Zuzwil)	SG	722800	258900	Fa	n	n	0.43	16.9	0.06	0.0	2015	5.5	30.8	18.8	9.1	610-700	15	133	62	
Altenberg (Degersheim)	SG	729600	250000	Fa(AcFrTi)	f	n	0.26	59.5	0.33	7.6	2015	5.1	33.5	18.3	7.6	770-840	16	100	41	
Bernhardzellerwald (Waldkirch)	SG	742900	258000	Fa(AcFrTi)	n	n	1.57	31.3	0.30	0.0	2015	4.5	27.5	22.6	8.8	660-790	16	234	183	
Wildberg (Jonschwil)	SG	725700	252800	Fa(AcFrTi)	f	f	8.98	51.2	3.81	11.5	2015	4.5	38.2	18.9	9.4	740-810	15	115	60	
Hasenstrick (Goldach)	SG	755000	258000	Fa	n	n	0.35	48.5	0.19	10.0	2015	3.7	40.9	35.4	6.0	700-830	18	129	86	
Moos (Buchs)	SG	751600	223600	Fa-Ab(AcFrTi)	m	m	0.21	41.1	0.16	0.0	2015	4.4	31.8	42.6	4.1	1110-1250	15	56	25	
Spaltenstein (Gams)	SG	750300	231800	Fa-Ab(AcFrTi)	m	m	0.32	4.1	0.11	0.0	2015	5.7	35.5	26.5	7.5	800-920	15	73	51	
Laubwald (Amden)	SG	734900	225700	Ab-Pi(Fa-Ab)	m	m	0.30	21.4	0.18	2.7	2015	3.7	46.1	23.2	9.4	1180-1330	15	136	128	
Hofstetten (Hemberg)	SG	730600	241200	Fa(Fa-Ab)	n	f	0.74	15.3	0.79	5.5	2015	3.4	48.1	24.0	7.0	730-870	15	132	115	
Rumpf (Wattwil)	SG	721100	238900	Fa-Ab	f	n	0.24	34.1	0.27	0.0	2015	4.5	28.0	43.0	8.6	940-1140	16	66	51	
Neckerwald (Krummenau)	SG	734600	236200	Ab-Pi(Fa-Ab)	m	m	0.03	14.6	0.06	0.0	2015	3.3	29.3	38.0	9.0	1010-1330	15	41	20	
Salawald (Mastrils)	GR	758247	201895	Fa-Ab	m	m	0.12	51.11	0.10	25.64	2016	5.8	28.7	45.4	16.9	1140-1260	25	21	15	
Hinteralpwald (Tamins)	GR	749397	192839	Ab-Pi	m	m	0.12	15.97	0.27	2.38	2016	6.8	36.5	60.0	18.2	1360-1560	22	13	9	
Planderleina (Mastrils)	GR	759245	202703	Fa	m	m	0.03	40.00	0.00	NA	2016	5.3	26.7	38.5	10.8	870-970	15	6	3	
Müllers Los (Tamins)	GR	749799	191691	Ab-Pi	m	m	0.22	12.50	0.22	0.00	2016	6.4	28.6	38.8	12.7	1320-1370	14	7	5	
Bausch (Seewis)	GR	767270	208410	Fa-Ab	m	m	0.02	16.67	0.03	4.76	2017	6.0	62.1	45.8	23.7	1060-1340	25	7	4	
Pudenal (Seewis)	GR	768680	210660	Ab-Pi(Fa-Ab)	m	m	0.04	0.00	0.12	5.56	2017	5.7	38.6	59.8	46.7	1280-1480	24	7	6	
Geissegggen (Fanas)	GR	769650	207840	Fa-Ab(Ab-Pi)	m	m	0.09	18.71	0.25	0.33	2017	5.9	52.5	70.7	28.2	1180-1400	24	16	10	
all 18 sites with assessment in spring																		320	1292	874
Langegg (Oberuzwil)	SG	727200	252400	Fa	f	n	1.69	25.2	1.08	0.0	2015	4.2	23.1	27.5	35.7	720-830	32	40	40	
Plumperwald	SG	755400	239000	Fa-Ab	m	n	0.04	5.9	0.08	0.6	2015	4.8	25.8	54.8	22.2	1000-1460	29	24	24	
Zanuz (Valens)	SG	753850	204550	Ab-Pi(Fa-Ab)	m	m	0.01	69.3	0.22	47.8	2015	4.1	39.0	65.4	33.9	1310-1630	30	5	5	
Vättis (Vättis)	SG	751250	196900	Fa-Ab	m	m	0.03	42.6	0.16	18.6	2015	5.9	28.5	65.5	31.8	1030-1670	30	10	10	
Bläserberg (Pfäfers)	SG	756500	203000	Fa-Ab(Ab-Pi)	m	m	0.20	92.5	0.20	27.6	2015	5.7	30.3	66.6	35.6	1310-1620	64	37	37	
Rosswald (Wildhaus)	SG	745500	228600	Fa-Ab(Ab-Pi)	m	m	0.03	42.5	0.12	11.1	2015	5.1	52.8	33.4	21.3	1120-1230	30	39	39	
all 6 sites with assessment in autumn																		215	155	155
All 24 sites																		535	1447	1029

Data collection

In spring 2015 (11 sites), 2016 (4 sites) and 2017 (3 sites), before budburst, the five (2015 assessment) or two (2016 and 2017 assessments) trees nearest to the plot centre of every height class (hc1: 10–40 cm, hc2: 41–70 cm, hc3: 71–100 cm and hc4: 101–130 cm) and every species were assessed. The maximal search distance from the plot centre was 10 m and the measured distance to the saplings was noted in order to calculate sapling density (for details of nearest tree method see Kleinn et al., 2009). The current tree height and the length of the annual increment of the leader shoot formed in the previous year were measured. In cases where the leader shoot was browsed, the remaining part of the annual increment of the leader shoot was measured instead. The within-tree browsing intensity on the leader shoot formed in the previous year was classified into not browsed, lightly browsed (only removal of bud), strongly browsed (loss of a large part of the annual increment), or no leader shoot in that year (owing to older damage).

As summer browsing was sometimes hard to detect, in particular for deciduous trees, on six sites the assessment of the nearest two trees took place in autumn 2015. Therefore, the length of the annual leader shoot formed in 2015 was measured and within-tree browsing intensity was noted for winter 2014/2015 and for summer 2015. As very few saplings of *Abies alba* were browsed in summer (and were thus omitted from the analysis), this assessment serves as a measure of recovery after different within-tree browsing intensities.

In order to evaluate factors that may influence the frequency of browsing and tree regeneration, the monitoring was complemented with measurements of the stand basal area [m^2/ha] of living trees (quantified using angle count sampling with a counting factor of 4 (Bitterlich, 1984)); hill slope [%]; stand developmental stage [young growth and thicket (1), polewood (2), dominated by small timber trees (3), dominated by medium timber trees (4), dominated by large timber trees (5) or mixed stages (6)]; approximate soil depth [cm], measured in 5 places within the plot with a hand soil driller); pH of soil A-horizon (potentiometrically determined in the lab with 10 mM CaCl_2 , soil: solution ratio = 1:2, equilibration time 30 min); and forest type. The four forest types were defined by the dominant tree species in the canopy, i.e. the ‘*Acer-Fraxinus-Tilia*’ type was dominated by *Acer pseudoplatanus*, *A. platanooides*, *Fraxinus excelsior*, *Tilia cordata*, and/or *T. platyphyllos*, the ‘*Fagus*’ type by *Fagus sylvatica*, the ‘*Fagus-Abies*’ type by *Fagus sylvatica* and *Abies alba*, and the ‘*Abies-Picea*’ type by *Abies alba* and *Picea abies*).

Statistical analysis

The relative growth rate of each sapling was calculated by dividing the length of the intact part of the annual leader shoot (only the remaining part of the shoot in the case of winter browsing) by tree height. For each plot and tree height class, the ratio of the relative growth rate of *Abies alba* to the relative growth rate of unbrowsed *Picea abies* saplings was derived from the nearest trees to the plot centres and, if available, the second- up to the fifth-nearest neighbouring *Abies* and *Picea* saplings. *Picea abies* was chosen for this tree-by-tree comparison of species effects rather than *Fagus*, *Acer*, *Fraxinus* or other tree species because i) *Picea* saplings were available in all forests types and ii) determining the leader axis and measuring leader shoot length is comparable for *Picea* and *Abies* saplings.

Abies sapling density was calculated for each plot that contained *Abies* saplings by means of the plot radius based on the distance of the nearest *Abies* sapling (dist_1) plus half of the distance to the second nearest *Abies* sapling (dist_2 , i.e. $r = \text{dist}_1 + 0.5 * (\text{dist}_2 - \text{dist}_1)$, (Kleinn et al., 2009)). *Abies* saplings that did not form a leader shoot (within-tree browsing intensity = ‘no leader shoot in that year’) or with summer browsing in 2015 were excluded from the statistical analysis owing to low sample size. The analysis was carried out separately for the spring (18 sites) and autumn (6 sites) assessments.

Linear mixed-effects models were fitted for the relative growth rate of *Abies*, for the ratio of the relative growth rate of *Abies* to the relative growth rate of *Picea*, and for the *Abies* sapling density in plots containing *Abies* saplings. Fixed effects included in the model were forest type (either the four individual types, or coniferous vs. deciduous forest), stand developmental stage, hill slope, soil depth, soil pH, stand basal area and leader shoot browsing (either within-tree browsing intensity or presence/absence). Site was included as a random effect. Interactions between the fixed effects were also tested, in particular those involving within-tree browsing intensity. For the ratio of the relative growth rate of *Abies* to *Picea* saplings, the interaction between forest type and within-tree browsing intensity was integrated into the statistical model as one factor owning 10 levels, owing to an insufficient number of browsed saplings in the *Acer-Fraxinus-Tilia* forest type (4 forest types * 3 within-tree browsing intensity levels minus the two *Acer-Fraxinus-Tilia* levels).

All statistical analyses were completed with R version 3.3.2 (R Core Team, 2016), using the package *lme4* (Bates et al., 2015) with the function *lmer*. The target variables were transformed using the natural logarithm, except for the relative growth rate of *Abies*, which was square-root transformed. Variables and interactions with non-significant effects were removed from the model. The best candidate models were selected by using likelihood ratio tests (function *anova*) for differentiation of the models or, in case of unequal N, the lowest Akaike's information criterion (AIC approach, as in Stauffer, 2008). When a factor had a significant effect and was thus retained in the selected models, a pairwise comparison between the categories was performed (using a pairwise t-test).

Results

In the 24 sites, 535 plots were assessed, leading to a sample size of 1447 *Abies alba* saplings and 1029 pairs of *Abies* and *Picea* saplings (Table 1). Although 51% of all plots were situated in sites dominated by forests with *Fagus-Abies* associations, *Abies* saplings were found, on average, in only 10.4% (median; 25Q = 6.5%, 75Q = 19.2%) of the possible plot–height class strata, and *Abies-Picea* pairs were found in only 7.9% (4.9, 16.0%) of the cases. Similarly, in sites dominated by forests with *Abies-Picea* associations (21% of all plots), only 6.8% (3.3%, 21.6%) of the assessed plot–height class strata included *Abies* saplings and 4.8% (2.9%, 15.7%) had *Abies-Picea* pairs). In contrast, only 28% of the plots were situated in sites dominated by forests with *Fagus* associations, but 37.1% (19.5%, 44.3%) of the possible plot–height class strata included *Abies* saplings and 20.3% (13.5%, 34.7%) included *Abies-Picea* pairs. This finding was mainly due to i) plots without any *Abies* regeneration and ii) plots without *Abies* saplings in the taller height classes in sites dominated by *Fagus-Abies* and *Abies-Picea* forests (apart from site Laubwald; Table 1). As a consequence, a separate analysis was not undertaken for each of the four height classes.

Abies alba saplings were significantly more frequent in plots that contained *Abies* regeneration when situated in *Fagus* forests than when in the other three forest types (Fig. 1a, Tables 2 and 3). *Abies* density was also higher when the *Abies* saplings nearest to the plot centre were only lightly browsed compared with plots where the saplings were unbrowsed or strongly browsed (Fig. 1b). In addition to effects of forest type and within-tree browsing intensity, soil pH had a negative and hill slope a positive effect on *Abies alba* sapling density in plots that contained *Abies* regeneration (Table 3). Stand developmental stage also had an effect on the *Abies* density when *Abies* saplings were present (Table 3), in that stands with large timber trees contained more *Abies* saplings than types 2–4 and stands with mixed stages, and these more than young growth and thickets (Supplementary Material Fig. S1).

Table 2: Statistical results of main models for *Abies* sapling density, the relative growth rate of *Abies* saplings and the ratio of the relative growth rate of *Abies alba* saplings to the relative growth rate of unbrowsed *Picea abies* saplings of the same height class from the same plot. Akaike's information criterion (AIC) and *P* values (*P*) of the likelihood ratio tests ($. \leq 0.1$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$) for the full models (but excluding all interactions), the full models without the listed variable, and the selected models are given. In the last two lines, degrees of freedom (DF) and *P* values are relative to the selected models in order to indicate the importance of within-tree browsing intensity. Details of the selected models are given in Table 3.

	DF	<i>Abies</i> density spring assessment			Rel. growth <i>Abies</i> spring assessment			Rel. growth <i>Abies</i> / <i>Picea</i> spring assessment			Rel. growth <i>Abies</i> / <i>Picea</i> autumn assessment	
		AIC	P		AIC	P		AIC	P		AIC	P
full model ¹⁾	17 ²⁾	5091	full model		-2188	full model		2180	full model		407	full model
- hill slope	16	5101	0.001 ***		-2188	0.174		2178	0.883		405	0.992
- soil depth	16	5092	0.073 .		-2188	0.127		2186	0.006 **		405	0.932
- soil pH	16	5111	0.000 ***		-2185	0.023 *		2178	0.860		407	0.229
- developmental stage	12	5141	0.000 ***		-2168	0.000 ***		2181	0.051 .		403	0.408
- stand basal area	16	5091	0.223		-2184	0.011 *		2179	0.743		405	0.983
- forest type	14	5095	0.022 *		-2190	0.256		2187	0.005 **		402	0.743
- within-tree browsing intensity	15	5093	0.046 *		-2101	0.000 ***		2224	0.000 ***		409	0.046 *
selected model		5091	0.1164		-2184	0.012 *		2176	0.175		392	0.818
- within-tree browsing intensity	-2	5094	0.038 *		-2101	0.000 ***		2221	0.000 ***		395	0.031 *
+ browsing presence/absence	-1	5096	0.01 **		-2121	0.000 ***		2210	0.000 ***		397	0.010 *

¹ full model: within-tree browsing intensity + forest type + basal area + developmental stage + soil pH + soil depth + hill slope + (1 | site)

² Developmental stage 3 (i.e. small timber) did not occur in the sites with autumn assessment, resulting in DF = 16

Table 3: Statistical results of the selected models. For the fixed variables included in the selected models, the estimated coefficients $\pm$ 1 standard error and t values are indicated. *Abies* sapling density data and the ratio of the relative growth rate of *Abies alba* saplings to the relative growth rate of unbrowsed *Picea abies* saplings of the same height class from the same plot were transformed by natural logarithm, whereas the relative growth rate of *Abies* saplings was square-root transformed. Site was included as a random effect. The corresponding Akaike's information criterion (AIC) for each model is given in Table 2).

Selected models		<i>Abies</i> density			Rel. growth <i>Abies</i>			Rel. growth <i>Abies</i> / <i>Picea</i>					
		spring assessment			spring assessment			spring assessment			autumn assessment		
random effects:		Variance	Std.Dev.		Variance	Std.Dev.		Variance	Std.Dev.		Variance	Std.Dev.	
site		1.349	1.162		0.002	0.042		0.031	0.175		3.20E-16	1.79E-08	
residuals		2.821	1.679		0.010	0.099		0.678	0.824		0.6883	0.8296	
fixed effects:		Coef.	Std. error	t value	Coef.	Std. error	t value	Coef.	Std. error	t value	Coef.	Std. error	t value
intercept		-1.762	0.488	-3.61	0.320	0.014	23.59	0.981	0.177	5.55	0.051	0.075	0.69
within-tree browsing intensity	light	0.328	0.176	1.87	0.015	0.010	1.45	0.164	0.110	1.49	0.302	0.227	1.33
	strong	-0.260	0.165	-1.58	-0.105	0.011	-9.25	-0.747	0.110	-6.80	-0.458	0.215	-2.14
forest type	<i>Fagus</i>	0.782	0.245	3.19				-0.352	0.142	-2.47			
	<i>Fagus-Abies</i>	0.001	0.311	0.01				-0.556	0.158	-3.53			
	<i>Abies-Picea</i>	0.073	0.386	0.19				-0.384	0.178	-2.16			
stand basal area													
stand developmental stage	polewood	-0.139	0.182	-0.76	0.010	0.011	0.90						
	small timber	-0.442	0.242	-1.83	0.001	0.014	0.05						
	medium timber	0.103	0.173	0.60	-0.019	0.010	-1.87						
	large timber	0.966	0.187	5.17	0.011	0.011	0.99						
	mixed stages	0.057	0.256	0.22	0.037	0.015	2.48						
soil pH		-0.257	0.053	-4.83									
soil depth								-0.010	0.003	-3.73			
hill slope		0.017	0.005	3.54									
number of observations		1292			1251			874			155		
number of sites		18			18			18			6		
degrees of freedom		15			10			9			5

Fig. 1. *Abies alba* sapling density per square meter in plots that contained *Abies* regeneration in relation to forest type (1a) or within-tree browsing intensity of leader shoots (1b). Only the 18 sites with data collected in spring were used. Letters refer to significant differences at $P = 0.01$ between the forest types or the within-tree browsing intensity in the pairwise t-tests. Median (bold line), first and third quartile (bottom and top of the box) with whiskers at quartile $\pm 1.5 \times$ interquartile range and individual points more extreme in value (circles) have been drawn using *boxplot* in default R code. Extreme outliers were omitted for appropriate scaling. The width of the boxes represents the number of trees within the various categories.

Within-tree browsing intensity and growth rate of *Abies alba* saplings

Overall, the relative growth rate of *Abies* saplings was greatest for saplings that were lightly browsed on their leader shoot in that year, followed by saplings not browsed on their leader shoot in that year. The lowest relative growth rate was observed for saplings that were strongly browsed on their leader shoot (Fig. 2a, Table 3). The fit of the statistical model was significantly lower with presence/absence of browsing used in place of within-tree browsing intensity, but it was still better than the fit of a model without a browsing-related factor (Table 2). This pattern in relative growth was independent of forest type (no significant effect of forest type (Table 2) or of the interaction term with within-tree browsing intensity (AIC = -2175)), although this pattern tended to be less pronounced for *Fagus-Abies* and *Picea-Abies* forests, where saplings that were not browsed or lightly browsed grew equally well but unbrowsed saplings clearly grew better than strongly browsed trees (Fig. 2c).

The within-tree browsing intensity but not the growth of *Abies* saplings itself was influenced by forest type. This was shown by the fact that in *Fagus* and *Acer-Fraxinus-Tilia* forests more than half of the browsed *Abies* saplings were only lightly browsed, while in *Fagus-Abies* forests 2.5 times more and in *Abies-Picea* forests 2 times more *Abies* saplings were browsed strongly than lightly (% values shown in Fig. 2c). In addition, the percentage of browsed *Abies* saplings was higher in *Fagus* (16.6%) and *Fagus-Abies* forests (17.5%) compared with in *Picea-Abies* (10.6%) and *Acer-Fraxinus-Tilia* forests (7.1%; Fig. 2c).

Abies saplings in stands with ‘mixed stages’ had a higher relative growth rate of *Abies* saplings than all other stand developmental stages (Fig. 2b, Table 3). No significant effect on the relative growth rate of *Abies* saplings was found for soil pH, soil depth or stand basal area (Table 2). In addition, no significant interactions between within-tree browsing intensity and these variables were found. Thus, these three variables were removed from the statistical model for growth of *Abies* saplings (Table 3).

Fig. 2. Relative growth rate of *Abies alba* saplings in relation to within-tree browsing intensity of leader shoots (2a), stand developmental stage (2b), and *Abies alba* within-tree browsing intensity (no, light or strong browsing on leader shoots) in the four different forest types (2c). Only the 18 sites with data collected in spring were used. Letters refer to significant differences at $P = 0.01$ between the within-tree browsing intensities (2a) or the developmental stages (2b) and at $P = 0.05$ between the within-tree browsing intensities within each forest type (2c) in the pairwise t-tests. The number of *Abies* saplings per forest type (N) and the percentage of each within-tree browsing intensity within each forest type (%) are given.

Within-tree browsing intensity and ratio of the relative growth rate of *Abies* to *Picea*

In cases where the ratio of the relative growth rate of *Abies* saplings to the relative growth rate of *Picea* saplings was higher than one, the *Abies* sapling of the respective height class and plot was growing better than the unbrowsed *Picea* sapling, and in cases where the value was lower than one, the unbrowsed *Picea* sapling was growing better. This ratio was higher if all *Abies-Picea* pairs with lightly browsed *Abies* saplings were considered than if the unbrowsed *Abies* saplings were considered, which in turn was higher than if strongly browsed *Abies* saplings were considered (Table 3 and all sites in Fig. S2). However, there were significant differences between forest types (Table 3). For all *Abies-Picea* pairs, and in particular for those calculated with lightly browsed or unbrowsed *Abies* saplings (Fig. 3), the ratio was higher in *Fagus* forests than in *Fagus-Abies* forests, and a ratio intermediate to the values of these two forest types was found in *Picea-Abies* forests. When viewed in greater detail, it is apparent that lightly browsed *Abies* saplings in *Fagus* forests grew, on average, twice as well as *Picea* saplings and thus significantly better than unbrowsed *Abies* saplings in *Fagus* forests, while there was no statistically significant difference between the rate of relative growth of *Abies* to *Picea* saplings for lightly and unbrowsed *Abies* saplings in *Fagus-Abies* and *Picea-Abies* forests (Fig. 3). The ratio of the relative growth rate of unbrowsed *Abies* saplings to unbrowsed *Picea* saplings was around (*Fagus-Abies* forests) or higher than one (other forest types), and it always tended to be higher than rates for strongly browsed *Abies* saplings, though only significantly higher in *Fagus* forests (Fig. 3). Browsing led to a shift in the growth rate rank of *Abies* compared with *Picea* saplings, but only in cases where the within-tree browsing intensity was strong (Fig. 3).

At the single site level the overall pattern remained the same, although there were some differences. In particular, two sites dominated by *Fagus* forests showed similar or a tendency of less growth of pairs with lightly browsed *Abies* saplings compared with unbrowsed ones (i.e. Altenberg, Hofstetten) but still more growth compared with strongly browsed trees (Fig. S2).

No significant effects of or interactions between soil pH, stand basal area and stand developmental stage in relation to the ratio of the relative growth rate of *Abies* to *Picea* saplings were found (Table 2). However, soil depth significantly increased the model goodness of fit (Table 2). On the one hand, soil depth may represent differences between *Fagus-Abies* and *Abies-Picea* forest types. Soil was shallower in *Fagus-Abies* forests than in *Abies-Picea* forests, in particular in plots with pairs containing browsed *Abies* saplings (Fig. 4). On the other hand, when the soil within every individual forest type were compared, shallower soil tended to be associated with light browsing but no clear pattern could be detected (Fig. 4).

Regarding the growth ratio of *Abies* saplings one year after browsing (measurements completed in autumn 2015), *Abies* saplings in pairs with previously lightly browsed *Abies* saplings grew better than those in pairs with unbrowsed *Abies* saplings and often also grew better than those in pairs with strongly browsed *Abies* saplings (Fig. 5, Table 3). This finding indicates that lightly browsed *Abies* saplings have higher growth rates, not only in the year they are browsed (Fig. 3 and all sites in Fig. S2), but also in the successive year (Fig. 5).

Fig. 3. Ratio of the relative growth rate of *Abies alba* saplings to the relative growth rate of unbrowsed *Picea abies* saplings of the same height class from the same plot in relation to *Abies alba* within-tree browsing intensity (no, light or strong browsing on leader shoots) for each forest type. The grey line indicates equal growth of *Abies* and *Picea* saplings in the plot. Only the 18 sites with data collected in spring were used. The number of pairs per forest type (N) and the percentage of each within-tree browsing intensity within each forest type (%) are given. Letters refer to significant differences at $P = 0.05$ in the pairwise t-tests.

Fig. 4. Ratio of the relative growth rate of *Abies alba* saplings to the relative growth rate of un browsed *Picea abies* saplings of the same height class from the same plot in relation to *Abies alba* within-tree browsing intensity (no, light or strong browsing on leader shoot) along the soil depth gradient for each of the four forest types. For a better overview, a slight irregular movement of max 3 cm was added to soil depth values (function jitter() in R).

Fig. 5. Ratio of the relative growth rate of *Abies alba* saplings to the relative growth rate of *Picea abies* saplings of the same height class from the same plot in relation to *Abies alba* within-tree browsing intensity in the preceding winter (no, light or strong browsing on leader shoots). Grey lines indicate equal growth of *Abies* and *Picea* saplings in the plot. Only the six sites with data collected in autumn 2015 were used, and in the last panel only sites with N > 20 trees were considered. N = the number of pairs within each site. Letters refer to significant differences at $P = 0.05$ in the pairwise t-tests.

Discussion

The growth of *Abies alba* saplings with different degrees of leader shoot browsing (within-tree browsing intensity) were compared among four major forest types in Switzerland. In the absence of browsing, the relative growth rate of *Abies* saplings did not differ among forest types. However, lightly browsed *Abies* saplings were more frequent in *Fagus*-dominated forests than in *Fagus-Abies* or *Abies-Picea* forests. This finding is particularly important because lightly browsed *Abies* saplings had no growth losses compared with unbrowsed trees. In contrast, strongly browsed *Abies* saplings clearly grew less than unbrowsed trees. For example, in *Fagus* forests an average of 16.6% of the *Abies* saplings were browsed (defined as ‘browsing intensity’, Berwert-Lopes, 1996), but only 5.3% of the *Abies* saplings were strongly browsed and these effectively suffered from a browsing impact. In addition, sapling density was higher in such *Fagus* forests, as also found in other studies (Kramer et al., 2014), and the overall impact of a similar proportion of browsed trees was much lower in *Fagus* compared with in *Fagus-Abies* or *Abies-Picea* forests. This finding would not have been revealed if only the presence or absence of browsing was taken into account.

The importance of within-tree browsing intensity for *Abies* sapling growth was even more pronounced than that of forest type, as lightly browsed *Abies* saplings grew better than unbrowsed saplings in the year of browsing and also in the season after browsing. Generally, conspicuous tree saplings that stand out from the other vegetation are more likely to be browsed than partially obscured plants (Kupferschmid et al., 2015b; Miller et al., 1982). For example, dominant *Picea abies* saplings in a regeneration cluster were browsed more often than other trees in the cluster (Näscher, 1979). If the morphologically dominant trees, i.e. the most vigorously growing trees, are more often browsed (Häsler and Senn, 2012; Iason et al., 1996) but, perhaps owing to the presence of more saplings, only lightly (i.e. only leader bud removal), then even repeatedly browsed *Abies* saplings can continue to grow faster than unbrowsed and otherwise suppressed ones (Kupferschmid et al., 2013). In this case, I would expect to find i) a higher frequency of lightly than strongly browsed saplings, ii) a higher relative growth rate of lightly browsed than unbrowsed or strongly browsed saplings, and iii) no shift in the relative difference in growth rates between species. This coincides with what I found in most of the assessed *Fagus* forests, where there was no detectable shift in the growth rate rank between *Abies* and *Picea* saplings (Fig. 3). As it is typically desirable to maintain the most vigorous trees in forests that are managed for timber, such selection by ungulates may have the important impact of reducing the potential timber value of a stand (Edenius et al., 2002; Wallgren et al., 2014).

If, however, the most vigorously growing trees are browsed at a higher frequency and with a greater quantity of material removed (Hartley et al., 1997), it is likely that their status will change over time and that ungulates will subsequently select previously unbrowsed trees (Duncan et al., 1998). This tendency may lead to only the least vigorous trees remaining, resulting in an underestimation of the real height growth rate of tree saplings (Bergquist et al., 2003). In contrast to the effects of light browsing by ungulates, strong browsing on vigorously growing saplings may therefore lead to shifts in the relative rates of growth of different tree species, as was the case in the assessed *Fagus-Abies* and *Abies-Picea* forests (Fig. 3). Such an ungulate-induced species shift has also been found in many other forest types (e.g. Tripler et al., 2005). For example, birch saplings grew better than beech without browsing, but vice versa with browsing, as beech sapling growth was not reduced by herbivory (Krueger et al., 2009). Species that are resistant to browsing can have a competitive advantage and this can shift forest composition, e.g. from *Abies balsamea* to *Picea* spp. (Tremblay et al., 2007) or from *Nothofagus* spp. to *Pseudowintera colorata* (Husheer et al., 2003).

In the majority of cases, the degree of growth loss and stem deformation, as well as the likelihood of death, caused by browsing increases with the severity of browsing (Gill, 1992b; Wallgren et al., 2014). As solitary (and in particular planted) tree saplings are more likely to be browsed than densely regenerated recruitments (Čermák et al., 2009; Reimoser and Gossow, 1996; van Beeck Calkoen et al., 2018) and are probably also more severely browsed, the mortality induced by ungulate browsing

may prevent the upgrowth of such saplings (Kupferschmid et al., 2014). The apparently relatively low number of *Abies* saplings, and in particular of browsed *Abies* saplings, in the assessed *Fagus-Abies* and *Abies-Picea* forests may thus be the result of a combination of overall poor regeneration conditions and high browsing-induced mortality. Within-tree browsing intensity could serve to distinguish between light and strong browsing of vigorously growing trees; further, in the case of strong browsing, this variable suggests that a higher browsing-induced mortality rate could mask an underlying higher browsing percentage. Thus, within-tree browsing intensity would therefore be a much better estimator of the current ungulate impact than the commonly used proportion of browsed trees.

Site characteristics define the availability of resources such as nutrients, water and light, and thus have a large impact on the establishment, growth and mortality of tree saplings and other vegetation. Apart from forest type, stand developmental stage, pH of the soil A-horizon and hill slope affected the observed *Abies* sapling density (Table 3), i.e. the establishment rate of *Abies alba*. In contrast to findings from an analysis of windthrow sites in Switzerland (Kramer et al., 2014), higher pH values were associated with lower sapling density overall (cf. Table 3) and in each individual forest type (no significant interaction term). A confounding effect of forest type can therefore be excluded in my study. As the availability of nutrients and the concentration of nutrients in the *Abies* saplings are related to soil pH, pH generally has an influence on *Abies* sapling growth (Entry et al., 1987). However, in my study soil pH had no influence on the growth of *Abies* saplings and also no effect on the within-tree browsing intensity. Jensen et al. (2011) found no difference in soil pH between *Tsuga canadensis* stands with high deer-use and low deer-use. Perhaps in field surveys an influence of pH is masked by other site characteristics such as soil depth. Indeed, in my study, deeper soil was associated with less growth of *Abies* saplings in relation to the growth of *Picea* saplings (Table 3). As ungulates select the most vigorously growing trees (Price, 1991), the attractiveness of *Abies* for browsing should thus tend to be lower in deeper soils. Browsing incidence did not vary along the gradient of soil depth, although somewhat shallower soils tended to be associated with light browsing (Fig. 4). The exact relationship between soil depth or pH and the within-tree browsing intensity needs to be investigated more closely.

More *Abies* saplings were observed in stands with large timber trees, but a higher relative growth rate of *Abies* saplings was measured in mixed-stage stands. Stand basal area, which can be interpreted as a further proxy for light, had a significant influence on neither *Abies* sapling density nor *Abies* growth. These results indicate the high shade tolerance of *Abies alba* saplings (i.e. Landolt indicator value of 1, see Lauber and Wagner, 1996). In addition, no interaction of stand developmental stage or stand basal area with within-tree browsing intensity was found, which suggests no general effect of light on within-tree browsing intensity.

Growth and mortality are not the only variables that are affected by browsing. In tree species with strong apical dominance, anomalies in stem structure can result from browsing (Gill, 1992b). Such changes in stem structure can appear even after leader bud removal, i.e. light browsing, owing to the loss of apical dominance. Formerly dormant meristems resume growth following the damage to the shoot apex (Aarssen, 1995), resulting in bushy and/or multi-stemmed trees (Kupferschmid and Bugmann, 2013; Strauss and Agrawal, 1999). However, the influence on tree quality has generally been found to be larger after strong, and in particular after repeated, browsing (Eiberle, 1978; Wallgren et al., 2014).

To conclude, within-tree browsing intensity influences i) the growth of *Abies alba* saplings, ii) the ratio of the relative growth rate of saplings of *Abies alba* to saplings of *Picea abies*, leading to shifts in the growth ranking of different tree species, and iii) depends on forest type and probably also soil depth. Thus, within-tree browsing intensity is an informative indicator with regard to browsing impact that should be incorporated into future browsing inventories.

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Supplementary material

Fig. S1: *Abies alba* sapling density in relation to stand developmental stage.

Fig. S2: Relative growth rate of *Abies alba* saplings in relation to within-tree browsing intensity of leader shoots for individual sites.

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Supplementary material

Selective browsing behaviour of ungulates influences the growth of *Abies alba* differently depending on forest type

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Fig. S1 *Abies alba* sapling density per square meter in plots that contained *Abies* regeneration in relation to stand developmental stage. Only the 18 sites with data collected in spring were used. Letters refer to significant differences at $P = 0.01$ between the developmental stages in the pairwise t tests. Median (bold line), first and third quartile (bottom and top of the box) with whiskers at quartile $\pm 1.5 \times$ interquartile range and individual points more extreme in value (circles) have been drawn using *boxplot* in default R code. Extreme outliers were omitted for appropriate scaling. The width of the boxes represents the number of trees within the factor categories.

Fig. S2 Ratio of relative growth rate of *Abies alba* saplings to relative growth rate of *Picea abies* saplings of the same height class from the same plot in relation to *Abies alba* within-tree browsing intensity (no, light or strong browsing on leader shoot) for each site with more than 20 pairs of *Abies-Picea*. N = the number of pairs within each site. Grey lines indicate equal growth of *Abies* and *Picea* saplings in the plot.