Forest Ecology and Management 429 (2018) 317–326

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Andrea Doris Kupferschmid*

Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

ARTICLE INFO

Keywords:
Forest inventory
Growth rate
Herbivory
Silver fir
Tree regeneration
Ungulate browsing

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.

1. 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; Coté 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).

* Address: Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.
E-mail address: andrea.kupferschmid@wsl.ch.

https://doi.org/10.1016/j.foreco.2018.06.046
Received 23 February 2018; Received in revised form 28 June 2018; Accepted 29 June 2018

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 (BA); 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	Ungulates		*Abies*		*Picea*		Year	Soil		Slope	BA	EL	Plots	*Abies*	*Abies/Picea*
		x	y	type	Cham	Red	Dens [m^{-2}]	PLB [%]	Dens [m^{-2}]	PLB [%]		pH	depth [cm]	[%]		max–min	N	N	N
Nieselberg (Zuzwil)	SG	722,800	258,900	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	729,600	250,000	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	742,900	258,000	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	725,700	252,800	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	755,000	258,000	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	751,600	223,600	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	750,300	231,800	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	734,900	225,700	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	730,600	241,200	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	721,100	238,900	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	734,600	236,200	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	758,247	201,895	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	749,397	192,839	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	759,245	202,703	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	749,799	191,691	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	767,270	208,410	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	768,680	210,660	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
Geisseggen (Fanas)	GR	769,650	207,840	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	727,200	252,400	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	755,400	239,000	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	753,850	204,550	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	751,250	196,900	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	756,500	203,000	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	745,500	228,600	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