CrossMark

ORIGINAL ARTICLE

Ursula Nopp-Mayr · Iris Kempter · Gerald Muralt
Georg Gratzer

Herbivory on young tree seedlings in old-growth and managed mountain forests

Abstract Herbivory of invertebrates and rodents on tree seedlings in Northern temperate forests has been largely underestimated in the past and rarely addressed in studies. There is evidence that masting-cycles of forest trees and subsequent rodents outbreaks become more frequent, leading to enhanced browsing pressure on forest regeneration. Consequently, studies exploring tree seedling mortality caused by different herbivores are required. We conducted a study on tree seedling losses in the Wilderness Area Dürrenstein, Austria on two old-growth and one managed forest site. We conducted an exclosure experiment in two subsequent study years, using transplanted two-month-old tree seedlings of *Picea abies*, *Abies alba*, and *Fagus sylvatica*. Exclosures allowed access for invertebrates, invertebrates/rodents, and all potential herbivores. We also installed total exclosures, recording seedling losses due to climatic factors or pathogens. We calculated ZINB regressions assuming that seedling losses and seedling survival are distinct processes. Our results did not reveal fully consistent trends for both study years. The factor "treatment", however, was significant in the ZINBs in both study years. Herbivory was a driving factor for tree regeneration in the studied forests depending on specific conditions in different years or tree species. In 2005, losses in the total exclosures and herbivory of rodents and invertebrates in the other treatments reached comparable extent. Loss rates differed not only in terms of forest management, but also between the two old-growth forests. This, in connection with different herbivory of different tree species (higher losses of *A. alba*), strongly suggests the necessity of considering different herbivore guilds as drivers of tree species composition in late successional mountain forests.

Keywords Herbivory · Current year tree seedlings · Mammals · Ungulates · Rodents · Invertebrates · Zero-inflated negative binomial regression

U. Nopp-Mayr · I. Kempter (✉) · G. Muralt
Department of Integrative Biology and Biodiversity Research,
Institute of Wildlife Biology and Game Management, BOKU,
University of Natural Resources and Life Sciences,
Gregor Mendel-Strasse 33, 1180 Vienna, Austria
E-mail: iris.kempter@boku.ac.at
Tel.: +43 1 47654-4466
Fax: +43 1 47654-4459

U. Nopp-Mayr
E-mail: ursula.nopp-mayr@boku.ac.at

G. Gratzer
Department of Forest- and Soil Sciences, Institute of Forest Ecology, BOKU, University of Natural Resources and Life Sciences, Peter Jordan-Strasse 82, 1190 Vienna, Austria
E-mail: georg.gratzer@boku.ac.at

Present address:
G. Muralt
Hunting Organisation of Carinthia, Mageregger Strasse 175,
9020 Klagenfurt am Wörthersee, Austria
E-mail: gerald.muralt@boku.ac.at;
gerald.muralt@kaerntner-jaegerschaft.at

Introduction

The early life stages of plants are critical for plant survival and are major drivers of vegetation dynamics (Grubb 1977). In the establishing and early growth phases, plants are subjected to a number of pressures and mortality risks unique to those life stages causing low survival rates. In general, herbivory is a major driver of vegetation dynamics at short time scales. At longer time scales, it strongly shaped plant evolution (e.g. Crawley and Harral 2001). This is reflected in a multitude of plant defence mechanisms and strategies. Herbivory not only affects species-specific mortality patterns and subsequent competition of tree species (Hanley 1998; Munier et al. 2010) but also influences defence reactions, chemical status, and morphology of feeder plants (Massei et al. 2000). Owing to their carbon rich but nutrient poor support structures, particularly trees show, compared to herbs, grasses or aquatic plants, relatively low consumption rates (Coley and Barone 1996; Crawley 1997). This, however, is not true for early life stages, which hold

a higher risk of herbivory-caused mortality (Fenner et al. 1999). This is due to higher impacts of herbivory on low biomass individuals, a higher ratio of nutrient rich versus nutrient poor (woody) plant materials and a greater variety of potential herbivores being able to feed on the individual plant. Studies on ontogeny of direct defence presented both increased and decreased defence with plant age (Boege and Marquis 2005). However, particularly in the developmental stage after the plant's stored carbohydrate reserves in seeds and cotyledons are used, plants are assumed to go through a stage of low availability of non-structural carbohydrates for allocation into chemical and structural defences thus increasing the vulnerability of seedling stages to herbivory (Kabeya and Sakai 2003; Boege and Marquis 2005; Hanley et al. 2007).

In ecosystems with anthropogenically altered trophic structures and strong reduction or total loss of larger predators, seedling herbivory by ungulates is seen as a major threat to successful tree regeneration (Hanley 1998). In mountain areas, delayed tree regeneration may affect ecosystem functions and increase risks for erosion and disturbances like avalanches and floods (Dorren et al. 2004).

Particularly in Central Europe, ungulates are solely held responsible for seedling losses and the reduction of ungulate densities is seen as prior measure for assuring successful forest regeneration. Herbivore guilds are more diverse, however: particularly the impact of invertebrates and rodents on tree seedlings has been largely underestimated in the past and has rarely been included in studies of herbivore effects on tree regeneration (Hanley 1998). Their impact on tree seedlings can be severe and frequently shows temporal fluctuations. These fluctuations might be driven by climatic conditions and by food supply (Pucek et al. 1993). In case of small mammals, both factors seem to be important. There is some evidence that masting cycles of forest trees and subsequent small mammal outbreaks are becoming more frequent (e.g., Kantorowicz 2000; Övergaard et al. 2007) with possible consequences for forest regeneration (Nopp-Mayr et al. 2012). As shown by previous studies, masting of forest trees does not necessarily lead to high inputs into tree regeneration (Kutter 2007; Nopp-Mayr et al. 2012) as seed predation by small mammals may contribute to an almost complete failure. Large mammalian herbivores show lower energy requirements per mass unit of forage than small herbivores but need higher food biomass. Consequently, small herbivores might successfully compete with large herbivores when food supply decreases (Illius and Gordon 1987). Thus, herbivore pressure on few remaining seedlings might be high in years after masting even if small mammal abundances crash.

Different herbivore species also interact: Small rodents or invertebrate herbivores may be impaired by preceding ungulate herbivory (McShea and Rappole 2000; Martinez and Wool 2003). Mammalian herbivory can modify habitat quality for arthropods significantly, expressed in terms of arthropod abundance, biomass, diversity, and species composition (Feber et al. 2001; Suominen et al. 2008).

Different approaches are used to study effects of herbivores on forest regeneration: Methods range from exclosure experiments in natural environments (Reimoser 1991; Heikkilä and Härkönen 1996; Kuijper et al. 2010b; Kupferschmid et al. 2014) to feeding experiments (O'Reilly-Wapstra et al. 2007), simulated herbivory (clipping; e.g. Riipi et al. 2005) or enclosures/grazing trials (Pietrzykowski et al. 2003). As for natural regeneration, standardization of study conditions is a challenge as sites of tree regeneration may vary distinctly at micro-site scale and plant density, distribution and species composition may influence the degree of herbivory (Hanley 1998). In forest inventories, browsing intensity on terminal shoots is usually recorded along transects (Homolka and Heroldova 2003; Cavieres and Fajardo 2005). In many cases, not first season seedlings but older plants were studied (Pietrzykowski et al. 2003). Few studies focussed on planted seedlings (e.g., Hewitt and Kellman 2004; Munier et al. 2010) and effects of different biotic mortality factors on tree seedlings (i.e., fungal diseases, arthropods, small mammals etc.) were studied by applying biocides (fungicides, insecticides) or mammal repellents, respectively (Siemann and Rogers 2003; Hewitt and Kellman 2004). Given the strong potential impact of a combination of herbivore guilds on tree seedlings, we only found a few studies synchronously exploring the impact of deer and rodents on tree regeneration using exclosures (Ito and Hino 2005; Lyly et al. 2014; Ravolainen et al. 2014). We found no study synchronously characterising effects of ungulates, small mammals, and invertebrates on transplanted tree seedlings with accompanying monitoring of background seedling losses due to fungal infections and microsite conditions.

Installing the exclosure experiment with planted current-year seedlings, we thus addressed the following questions:

(1) Which factors cause seedling losses or, vice versa, seedling survival?
(2) Are there differences in loss rates between old-growth and managed forests?
(3) To which extent do current-year seedlings of different tree species differ in mortality patterns?

Materials and methods

Study areas

We conducted the study in 2005–2006 in the Wilderness Area Dürrenstein (47°48′ to 47°45′N, 15°01′ to 15°07′E), a part of the northern Limestone Alps in Lower Austria. The climate of the region is sub-maritime with long winter periods and short, cool summers. Mean annual

temperature in the area is 3.7 °C. January is the coldest month with an average temperature of −4.7 °C and in July the mean temperature is 12.8 °C. Annual precipitation can reach a maximum of 2,300 mm and shows a bimodal pattern with one maximum during the vegetation period in June/July and another one at wintertime. Snowfall occurs between October and May, yielding a continuous snow cover of about 200 days per year. The parent material of the area is Dolomite and banked limestone, the soils show a mosaic of Rendzinas and relictic loams (Zukrigl et al. 1963). Forests are classified as *Asperulo–Abieti–Fagetum*, a higher altitude subtype of a *Galio–odorati–Fagetum* and *Adenostylo–glabrae–Fagetum* (Willner and Grabherr 2007). European beech (*Fagus sylvatica*) dominates on all sites, particularly on slopes. The co-dominant Norway spruce (*Picea abies*) and Silver fir (*Abies alba*) grow 10–15 m taller (up to 58 m) than *F. sylvatica*, forming a two-layered canopy (Zukrigl et al. 1963).

Within the Wilderness Area, three experimental sites were selected: two old-growth forest sites at altitudes of 1,000 m and 1,100 m a.s.l., and one managed forest site at 1,050 m a.s.l. The managed forest (MF) is a mature timber stand (20 ha) with dominance of *P. abies* and admixed *F. sylvatica* and *A. alba*. It lies adjacent to one old-growth forest and only differs in stand features (i.e. tree species composition, canopy cover, and cover of ground vegetation), but not in site conditions. The small old-growth forest (SOF) and large old-growth forest (LOF) do not only differ in size (56 ha vs. 240 ha) but also in topography: While LOF is located on steep slopes, SOF is located more or less even in a basin. Furthermore, the two old-growth sites differ in stem density and in density of tree regeneration (Table 1).

Within the study area, three species of ungulates occur: Red deer (*Cervus elaphus*) with densities of approximately 4 individuals 1 km^{-2} in the wider area and chamois (*Rupicapra rupicapra*) with about 5 individuals 1 km^{-2}. Roe deer (*Capreolus capreolus*) inhabits the study area only at low densities. While red deer and roe deer visit the study area primarily in summer and move to lower altitudes in winter, chamois moves from areas above the treeline into higher parts of LOF in winter (Splechtna 2001). Mountain hare (*Lepus timidus*) occurs

frequently in the Wilderness Area Dürrenstein but prefers open areas and alpine pastures and moves to lower altitudes in the forest only in strong winters with high depths of snow. In contrast, European hare (*Lepus europaeus*) occurs only occasionally during summer in the study area (Leditznig & Pekny 2009). A long-term monitoring of small mammals provided evidence of several herbivore rodent species (Kempter and Nopp-Mayr 2013): the yellow-necked mouse (*Apodemus flavicollis*), the bank vole (*Myodes glareolus*), the field vole (*Microtus agrestis*), the European pine vole (*Microtus subterraneus*), the fat dormouse (*Glis glis*), and the hazel dormouse (*Muscardinus avellanarius*). In both study years (2005 and 2006), no outbreaks of herbivore insects were observed within the study period.

Experimental design

We conducted an exclosure experiment with transplanted two-month-old tree seedlings in two growing seasons. We transferred seedlings of the dominating tree species, i.e. Norway spruce (*P. abies*), Silver fir (*Abies alba*), and European beech (*F. sylvatica*) to the study sites, using site-specific proveniences. The seedlings were grown out-door in a commercial plant nursery without application of fertilizers considering the carbon-nutrient balance hypothesis (Bryant et al. 1983; Tripler et al. 2002; McArthur et al. 2003). Seedlings of European beech still had their cotyledon. Seedlings of all three tree species were planted within a 1 × 1 m area per treatment to minimize the spatial impact of the experiment on the old-growth forest (IUCN category Ia) and to ensure a complete removal of seedlings and adjacent soil material after ceasing the field trials. We installed four types of treatments, i.e. three different exclosures and one open access trial. The exclosures were cage-cubes (1 × 1 × 0.25 m) with different mesh widths: (1) a 1.3 × 1.3 cm wire mesh, covered with a light green synthetic gaze, excluding all potential herbivores (i.e., control treatment for monitoring plant losses due to climatic conditions, fungal diseases or microsite conditions); (2) a 1.3 × 1.3 cm wire mesh without synthetic gaze allowing for access of invertebrates (mainly arthropods such as

Table 1 Characteristics of the three different study areas

	SOF	LOF	MF
Slope inclination (at study plots)	±0°	15–25°	±0°
Tree species composition	Spruce 15 %	Spruce 15 %	
	Fir 15 %	Fir 15 %	
	Beech 70 %	Beech 70 %	Spruce 100 %
Stem density (no. of individuals with dbh > 10 cm per ha ± SD)	342 (±42)	259 (±38)	–
Density of forest regeneration (no. of individuals with dbh ≤ 10 cm per ha ± SD)	55,351 (±4,071)	30,752 (±3,315)	–
Cover of forest regeneration	25–50 %	–	< 5 %
Canopy cover of ground surface	5/10	–	5/10
Cover of deadwood	15 %	–	< 5 %

SOF small old-growth forest, *LOF* large old-growth forest, *MF* managed forest, *dbh* diameter at breast height (1.30 m), *SD* standard deviation

Lepidoptera larvae or weevils but also slugs); (3) a 3.0×3.0 cm wire mesh, offering access for invertebrates and small rodents, but not for ungulates and/or hares and (4) open access plots, where all potential herbivores could feed on the seedlings.

Each treatment was replicated six times on old-growth forest sites and three times in the managed forest, yielding in total 24 treatment plots per old growth forest site and 12 treatment plots in the managed forest per year (in sum 60 treatment plots per year). Treatment plots were placed at distances of 10–15 m on all three study sites, both ensuring comparable micro-site conditions for seedlings and appropriate micro-relief for the fixing of exclosures on the ground. As seedling densities were very high in the plant nursery in 2005, we transplanted clusters of seedlings to the experimental sites to avoid root injuries caused by a separation of seedlings. Thus, we planted at least seven seedlings of each tree species per treatment, in total 524 seedlings of Norway spruce, 529 seedlings of Silver fir and 511 seedlings of European beech. The experiment started on 15-Jun-2005 and 16-Jun-2005. In 2006, no beechnuts were available throughout Austria, neither in nature nor commercially. Consequently, only spruce and fir seedlings were transplanted. In that year, *Phytophthora* sp. infections destroyed the majority of fir seedlings in many plant nurseries. Thus, we used wild seedlings from forests adjacent to the Wilderness area for the exclosure trials. In 2006, we planted 5 seedlings per tree species and treatment, in total 300 seedlings per tree species. Due to a long winter with high snow depths and snowfall in June, both the development of seedlings and the accessibility of the study area were delayed. Consequently, we started the field trial about 3 weeks later than in 2005, i.e. on 3-Jul-2006 and 4-Jul-2006. In both years, we transferred seedlings promptly from the germination sites to the experimental sites. We revisited the seedlings once a week up to a three-week interval, counting surviving seedlings and recording visible signs of mortality as far as possible. Seedlings were classified as "dead", if the hypocotyl or apical meristem was destroyed (see Nystrand and Granström 2000). Clusters of tree seedlings without any loss of individuals were termed as "full survival plots" per tree species. We ceased the experiment on 3-Oct-2005 and 13-Oct-2005, and on 4-Oct-2006 and 5-Oct-2006. Planted seedlings, cages, and soil were completely removed from the area. Finally, we tested the reduction of solar radiation in the total exclosures by the synthetic gaze in the laboratory using the PAR sensor of a LICOR 6400. Thirteen pairs of measurements were made below and above the exclosures in an open area, thus avoiding heterogeneous light conditions between the below and above reading. The synthetic gaze in the total exclosures caused a mean reduction of photosynthetic photon flux density of 18.2 ± 2.71 %.

We monitored the population status of small mammals using live traps. We installed two traps at each grid point of a 15×15 m grid, placing in total 50 traps per sample area. In 2005, we used wooden box traps ($17.0 \times 7.0 \times 5.0$ cm, Fa. Ehlert & Partner, Germany) and in 2006, we used both a wooden box trap and a plastic trap ($38.7 \times 6.0 \times 8.0$ cm, Field Trip Trap, Alana Ecology, Shropshire, UK) per grid point conducting an accompanying trapability study. The traps were baited with butter cookies, peanut butter, and a piece of apple. Trapping occurred for two or three consecutive nights in 2005 and in 2006; we controlled the traps in the morning and in the evening, respectively. We identified catches following Niethammer and Krapp (1978, 1982), marked the animals by fur cutting and released them into the field at the point of capture.

Statistical analyses

We calculated seedling loss rates per treatment plot, referring the numbers of remaining plants at the last day of control to the number of initially planted seedlings. Considering both the distribution of seedling losses and overdispersion of data (i.e., variances greater than the mean), we first used a GLM procedure (negative binomial regression NB; Hilbe 2011; see also Gómez et al. 2003) for analysing loss rates. The negative binomial regression fits to Poisson-like-distributed data, being a Poisson-gamma mixture model (Hilbe 2011).

We used loss rates of seedlings per treatment plot as response variable and the factors "tree species", "area" and "treatment" as independent variables. We also considered all computable two-way interactions in the models. In a second step, we calculated corresponding zero-inflated negative binomial regressions models (ZINB) assuming that seedling losses and seedling survival (i.e. frequently occurring zero loss rates within a planted cluster of seedlings) are two distinct processes, potentially driven by different factors and mechanisms. Zero-inflated models comprise two distinct model components, i.e. a count submodel and a zero-inflated submodel. Thereby, data sets are split into two datasets, one of them representing only positive counts (seedling loss rates, i.e. count submodel) and the other one giving the presence/absence of complete seedling cluster survival (i.e. zero-inflated submodel). The probability density function for negative binomial distribution is given by (McNeil et al. 2009):

$$f(y|\mu, \theta) = \frac{\Gamma(\theta + y)}{\Gamma(\theta)y!} \left(\frac{\theta}{\theta + \mu} \right)^{\theta} \left(\frac{\mu}{\theta + \mu} \right)^{y} \qquad (1)$$

where μ is the mean, θ the size parameter and y the seedling loss rate observed in n sets. The value of μ_i can be estimated for any given set, i, with a linear model structure:

$$\log(\mu) = \beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n \qquad (2)$$

where β_0 is the intercept, β_i are the model coefficients and x_i the factors (i.e. species, area, treatment).

The absence/presence of full cluster survival is described per set by a Bernoulli probability density function:

$$y = \begin{cases} 0, & \text{with probability } p \\ 1, & \text{with probability } 1 - p \end{cases} \qquad (3)$$

where p is modelled with covariates and a logit link function:

$$\text{logit}(p_i) = \gamma_0 + \gamma_1 x_1 + \cdots + \gamma_n x_n \qquad (4)$$

where γ_0 is the intercept, γ_i are the model coefficients and x_i the factors (i.e. species, area, treatment).

For model computation, we used "glm.nb" function in the "MASS" package for negative binomial GLM and the "zeroinfl" function in the "pscl" package for ZINB in R version 3.1.0 (The R Foundation for Statistical Computing).

For both models' (NB and ZINB) testing, we first compared the saturated models with the respective null (intercept-only) models and then stepwise removed non-significant independent variables. For model comparisons, we used Chi–square tests ("pchisq" function from package "stats" in R) on the difference of log likelihoods, respectively and the Vuong test (Vuong 1989, "vuong" function from package "pscl" in R), a likelihood-ratio based statistics, which uses the Kullback–Leibler Information Criterion.

Although previous capture-mark-recapture studies on small mammals in the study area did not provide any indication of considerable adult survival for more than one year (one single recapture in the consecutive year during a 10-year period of small mammal monitoring, Kempter et al., unpubl. data), we were aware of the fact, that nearly all potential herbivore guilds in the study area (particularly ungulates, hares, small rodents and molluscs) have been proved to live more than one year (Niethammer and Krapp 1978, 1982, 1986; Bogon 1990; Krapp 2003) and that sample years should thus not be regarded as statistically independent events. Consequently, we calculated separate models for the two study years to avoid autocorrelations. For both years, zero-inflated negative binomial models performed better in terms of Vuong test statistics than the referring negative binomial model without zero-inflated part (2005: Vuong test statistic = 2.54, ZINB2005 > NB2005, $p = 0.006$; 2006: Vuong test statistic = 3.05, ZINB2006 > NB2006, $p = 0.001$).

To interpret the interaction terms in the ZINB model "2006", we calculated incidence rate ratios (IRR), using formula 5 (Hilbe 2011):

$$\text{IRR}_{\text{treespecXtreatment}} = \exp(\beta_1 + \beta_4 x) \qquad (5)$$

where β_1 is the model coefficient of the factor "tree species", β_4 the coefficient of the interaction and x the level of the factor "treatment".

Results

In both study years, mortality of seedlings within the total exclosures (i.e. control treatment) highly varied between the tree species and experimental sites (Fig. 1). In 2005, mean loss rates of spruce within the control treatment ranged from 3.0 up to 10.0 %. For fir, mean loss rates spanned between 50.1 and 68.0 % and for beech between 24.3 and 75.9 %. In the following year (2006), with only spruce and fir seedlings available, 0.0–23.3 % of spruce seedlings died on average in the control, whereas 10.0–26.7 % of fir seedlings got lost. In the treatments accessible only for invertebrates, we observed mean loss rates of spruce seedlings between 6.1 and 10.7 % in 2005, compared to 10-20 % in 2006. Loss rates of fir seedlings in the same treatment were between 30.0 and 57.7 % in 2005 and between 6.7 and 40.0 % in 2006. Referring values for beech seedlings were 6.0–55.7 % in 2005. Mean loss rates of seedlings in the ungulate/hare exclosures also showed a high variation: The values for spruce ranged from 0.0 up to 28.0 % in 2005 and from 0.0 to 40.0 % in 2006, for fir from 47.2 to 60.7 % in 2005 and from 0.0 to 46.7 % in 2006, and for beech from 14.7 to 47.2 % in 2005. The treatments accessible to all guilds of herbivores showed loss rates of spruce seedlings between 10.0 and 17.9 % in 2005 compared to 0.0–20.7 % in 2006, loss rates fir seedlings between 25.3 and 61.9 % in 2005 and 6.7–40.0 % in 2006, and beech seedlings between 9.0 and 41.1 % (2005). Summing up, loss rates showed high variation in terms of experimental sites, study years and trees species (Fig. 1).

In the ZINB models, the count submodels' regression coefficients of the factor "experimental site" indicated significantly higher mortality rates in the large old-growth forest (LOF) in both study years compared to the small old-growth forest (SOF; Table 2). In 2005, we additionally observed significantly lower mortality rates in the managed forest (MF) compared to both old-growth forest sites. As for the tree species, model "2005" yielded a higher, positive regression coefficient (i.e. higher loss rates) for fir, followed by beech and spruce. Moreover, significantly higher loss rates occurred within the total exclosures than in the mammal exclosures and on open access plots, whereas total exclosures and ungulate/hare exclosures did not significantly differ in seedling loss rates. For the second study year (model "2006"), spruce again showed lower loss rates than fir interacting with the treatment. Contrary to the model "2005", ungulate/hare exclosures were characterized by higher seedling loss rates compared to mortality rates in the total exclosures, whereas open access plots and mammal exclosures did not differ from total exclosures. Calculating the referring IRR, the interaction of tree species and treatment indicated higher losses of fir on open access (22 %) and in ungulate/hare exclosure plots (16 %) than in total exclosures and lower losses in mammal exclosures (19 %) than in total exclosures. Within the total exclosures, a higher portion (57 %) of fir seedlings died compared to spruce, which was also the case within total exclosures, where 35 % more fir than spruce seedlings died. As mentioned, both years' zero-inflated negative binomial models performed sig-
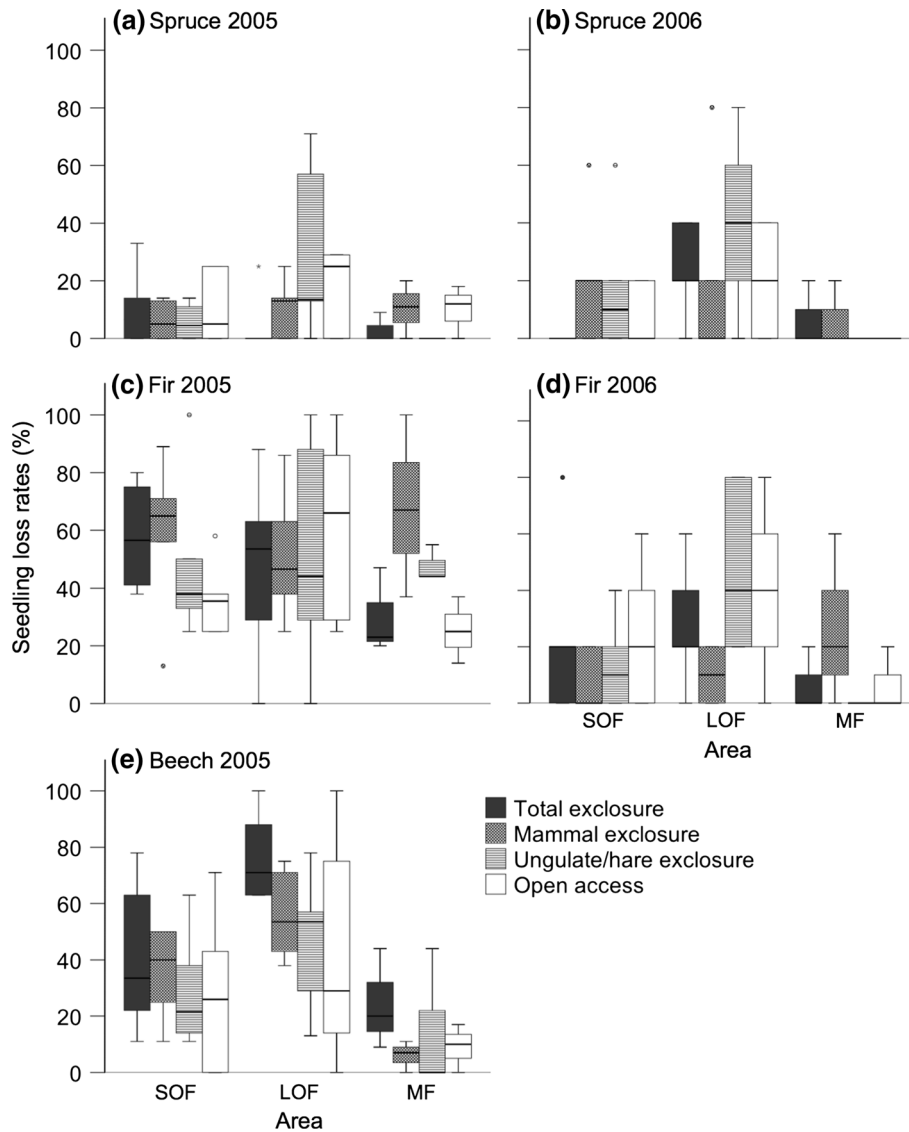
Fig. 1 *Box plots* of observed seedling loss rates (%) for spruce (*Picea abies;* **a**, **b**), fir (*Abies alba;* **c**, **d**), and beech (*Fagus sylvatica;* e) within the different study sites in 2005 and 2006, respectively (*SOF* small old-growth forest, *LOF* large old-growth forest, *MF* managed forest)

nificantly better than the pure negative binomial models, indicating that full survival of clusters of seedlings (each containing one tree species, respectively) and loss of seedlings were two distinct processes. For 2005, complete cluster survival was lower for fir than for beech and for spruce. In 2006, survival was a function of the experimental site with significantly lower complete cluster survival on LOF compared to SOF (Table 2).

We calculated relative trapping success in numbers of captured individuals per 100 trapping nights. We included recaptured individuals to represent feeding pressure on tree seedlings in a more realistic way than with pure numbers of newly caught specimen. In the study years 2005 and 2006, trapping success was low following a peak year of small mammal abundance in 2004 (Table 3). Two species of potential seedling predators (rodents) were caught in the study area during the study

period 2005–2006, i.e. the yellow-necked mouse and the bank vole.

Discussion

Factors causing seedling losses or seedling survival—total exclosures vs. other treatments

It is known from pot experiments that trees obtained from nurseries have to adapt to the new environment after transplantation (Kawaletz et al. 2014). During an adjustment period of a few weeks, increased mortality of seedlings frequently occurs, reaching about 23 % in a pot experiment of Kawaletz et al. (2013). In particular, bare-rooted, young seedlings seem to be highly vulnerable to desiccation and mechanic root injuries

Table 2 Model coefficients (Coeff.) of the final count submodels (negative binomial with log link function) and the zero-inflated submodels (binomial with logit link function) with corresponding standard errors (SE), 95 % confidence interval (CI) and p values for both study years, respectively

Study year/submodel	Independent variables	Coeff.	SE	CI		p value
Model 2005						
Count submodel	(Intercept)	3.04	0.14	2.77	3.31	< 0.001
	Fir	0.98	0.12	0.75	1.21	< 0.001
	Beech	0.71	0.12	0.48	0.94	< 0.001
	LOF	0.35	0.09	0.17	0.54	< 0.001
	MF	−0.28	0.12	−0.52	−0.04	0.023
	Mammal excl.	−0.24	0.12	−0.47	−0.004	0.046
	Ungulate/hare excl.	−0.17	0.12	−0.40	0.07	0.168
	Open access	−0.24	0.12	−0.48	−0.003	0.047
Zero-inflated submodel	(Intercept)	−0.07	0.26	−0.58	0.44	0.791
	Fir	−3.30	0.76	−4.80	−1.80	< 0.001
	Beech	−1.96	0.48	−2.89	−1.02	< 0.001
Model 2006						
Count submodel	(Intercept)	3.03	0.24	2.56	3.50	< 0.001
	Fir	0.30	0.26	−0.21	0.81	0.254
	LOF	0.29	0.14	0.02	0.56	0.039
	MF	0.06	0.25	−0.43	0.55	0.803
	Mammal excl.	0.39	0.28	−0.16	0.94	0.162
	Ungulate/hare excl.	0.53	0.27	0.005	1.05	0.048
	Open access	0.05	0.29	−0.51	0.61	0.864
	Fir x mammal excl.	−0.59	0.38	−1.35	0.16	0.124
	Fir x ungulate/hare excl.	−0.38	0.35	−1.06	0.31	0.280
	Fir x open access	0.15	0.36	−0.56	0.85	0.678
Zero-inflated submodel	(Intercept)	0.17	0.29	−0.40	0.73	0.565
	LOF	−1.16	0.43	−2.01	−0.30	0.008
	MF	0.93	0.55	−0.15	2.02	0.092

Spruce and small old-growth forest serve as references
LOF large old-growth forest, *MF* managed forest

Table 3 Trapping rates of the species *Apodemus flavicollis* and *Myodes glareolus* on the three study sites in the years 2004–2006 (expressed in newly and re-captured specimen per 100 trapping nights)

Study site/year	2004	2005	2006
Small old-growth forest	71.6	0.0	4.6
Large old-growth forest	64.4	1.1	12.3
Managed forest	41.2	1.1	5.1

(Burschel and Huss 1997). Thus, the successful transplantation of juvenile seedlings, reacting sensitively to root injuries, was a crucial point of our study design. In order to quantify seedling losses due to rooting failures or other impacts (e.g. fungal diseases), we installed total exclosures, an approach, which, to our knowledge, was used for the first time for current year seedlings in natural environments. In our study, transferred tree seedlings were covered with soil and transplanted during days with slight rain or at least high humidity and permanent cloud cover in order to reduce drought stress and root injuries as far as possible. Nevertheless, some injuries and a transplantation shock may have occurred resulting in a baseline mortality within all treatments. However, in our experiment, seedling mortality did not occur within the first two or three weeks after seedling transplantation, but was more or less evenly distributed over the whole study period, indicating that poor acclimatization was not the major driver of total seedling mortality. Diaci (2002) found the highest mortality of in situ germinated spruce seedlings within the period from germination till late summer and a decrease of seedling densities to 26 % of the initial density within the first year of life. In our total exclosures, the highest average loss rates of spruce seedlings reached 23 % in both study years, about 30 % for fir seedlings and about 45 % for beech seedlings, thus indicating a successful implementation of the transplantation trials.

In total, loss rates of transplanted seedlings in our study corresponded to observations in other studies, where also highly variable mortality rates were observed and seedling losses up to 80 % occurred within the first three months after transplantation without substantial impact of herbivores (Diaci 2002; Hewitt and Kellman 2004).

In our study, the ZINB model "2005" yielded higher loss rates of seedlings in the total exclosures compared to the mammal exclosures and open access plots, but no significant differences between total exclosures and ungulate/hare exclosures. The higher loss rates in the total exclosures might have occurred either due to reduced solar irradiation caused by the gauze or due to higher fungal infestation rates. If the first explanation had been correct, tree species should have reacted in a dif-

ferent way, reflecting their specific light requirements (i.e. highest shade tolerance and lowest response to differing light conditions in fir, and highest response in spruce; Ellenberg 1992; Stancioiu and ÓHara, KL, 2006; see also Ameztegui and Coll 2013). In particular, higher loss rates of spruce seedlings in the total exclosures compared to fir and beech seedlings would have been expected. However, the interaction between the treatment "total exclosure" and tree species did not enter the final model "2005", indicating that reduced solar irradiation probably did not play a major role in mortality, thus not being reflected in differing loss rates of tree species according to specific light requirements in the seedling stage. The second possible explanation—a higher fungal inoculation potential in the total exclosures due to reduced irradiation and higher humidity within the gauze—could not be proved directly in the study. Although monthly sums of precipitation greatly varied between 2005 and 2006 (Fig. 2a) with higher precipitation in July and September 2005 and lower values in June, August and September 2005 compared to 2006, monthly averages of daily temperature maxima as well as monthly sums of hours with sunshine were distinctly lower in 2005 than in 2006 (Fig. 2b, c). Thus, critical humidity in the total exclosures might have been reached in 2005, leading to higher infestation rates and losses of seedlings. As seedling losses on the ungulate/hare exclosure plots did not significantly differ from the losses in the total exclosures in model "2005", fungal infestations in the total exclosures and herbivory of small mammals and invertebrates in the other treatments may have caused mortality rates of comparable extent.

Losses on the open access plots were lower than in ungulate/hare exclosures (2005, 2006) and comparable to mammal exclosures (2005). Observations from large fences used for reducing ungulate impacts on forest regeneration indicate that hares may prefer such fences, as they provide partial protection against predators like foxes (Reimoser, pers. comm.). In our study, it might be assumed, that higher loss rates within the ungulate/hare exclosures compared to the open access plots originated from a similar phenomenon, i.e. small mammals preferentially feeding within cages not allowing for access of predators.

Results from the year 2006 did not corroborate the evidence of enhanced seedling losses in the total exclosures due to fungal diseases. Rather, the fact that loss rates of fir seedlings were highest in open access plots and in ungulate/hare exclosures point to small mammal browsing as causal factor for mortality.

Temporal variation in tree regeneration processes are caused by variation in tree seed production (Herrera et al. 1998; Kelly and Sork 2002) and concomitant fluctuations in seed predator populations (Nopp-Mayr et al. 2012) but also by interannual variations in precipitation and temperature (Fisichelli et al. 2013). The variation in the magnitude of drivers of mortality between years in our study is reflecting the prominent role of variation of biotic and abiotic factors for sensitive tree regeneration processes (Grubb 1977). It is also highlighting the role of stochasticity in tree regeneration. The factor "treatment", however, was significant in the ZINBs in both study years. Herbivory thus is a driving factor for tree regeneration in the studied forests but the magnitude of impact of different herbivore guilds strongly depends on specific conditions in different years (e.g. herbivore guild densities as a result of different carrying capacities) and tree species. Herbivores like small mammals, which influence tree regeneration densities in specific years, might not do so in other years. The same might be true for phytopathogens, which may have driven mortality in the first year of the study in the total exclosures, but appeared less important than herbivore effects in the second year. As shown in a separate study, phytopathogens generally have a high potential for causing mortality in seedlings in the study area (Szwagrzyk et al. in prep.). Contrary to our findings, the impacts of mammalian herbivores in general and of ungulates in particular was temporally consistent in other studies (e.g. Gómez et al. 2003; Kuijper et al. 2010a).

Vertebrate herbivores caused distinct losses of fir in the second year of study. In his review on seedling herbivory, Hanley (1998) highlighted both the prominent impact of invertebrates on mortality in early plant life stages and the frequent underestimation of rodent and invertebrate herbivory. In our study, consumption rates did not stringently differ between the treatments and did not vary consistently with small mammal abundances. Consequently, feeding pressure on tree seedlings might not be simply correlated with small mammal abundances. Since open access plots did not show highest mortality rates, ungulate herbivory can be ruled out as prime mortality cause. Forests in the study area in general and the study plots have high canopy cover and have lower habitat quality as compared to areas of large windthrow disturbances at similar sites where ungulate browsing inhibits tree regeneration (Pröll et al. 2014).

Nystrand and Granström (2000) observed considerable losses of juvenile seedlings in Swedish boreal forests due to attacks of slugs (*Arion subfuscus*), which attacked seedlings immediately after germination. Reviewing the literature on seedling herbivory Hanley (1998) highlights the major role of molluscs as seedling herbivores in temperate plant communities. This was also found in our study where mortality rates in treatments only accessible to non-vertebrates were high for fir and beech.

The better performance of ZINB compared to the corresponding NB models indicated a significant impact of specific factors on the survival of entire seedling clusters per treatment plot. Again, this survival was driven by distinct factors in different years. In 2005, spruce showed the highest survival of complete seedling clusters, whereas fir and—to a lower degree—beech obviously had more problems to survive transplantation as entire cluster. As fir seedlings have distinctly longer tap-roots than spruce (cf. Knapp and Smith 1982), their
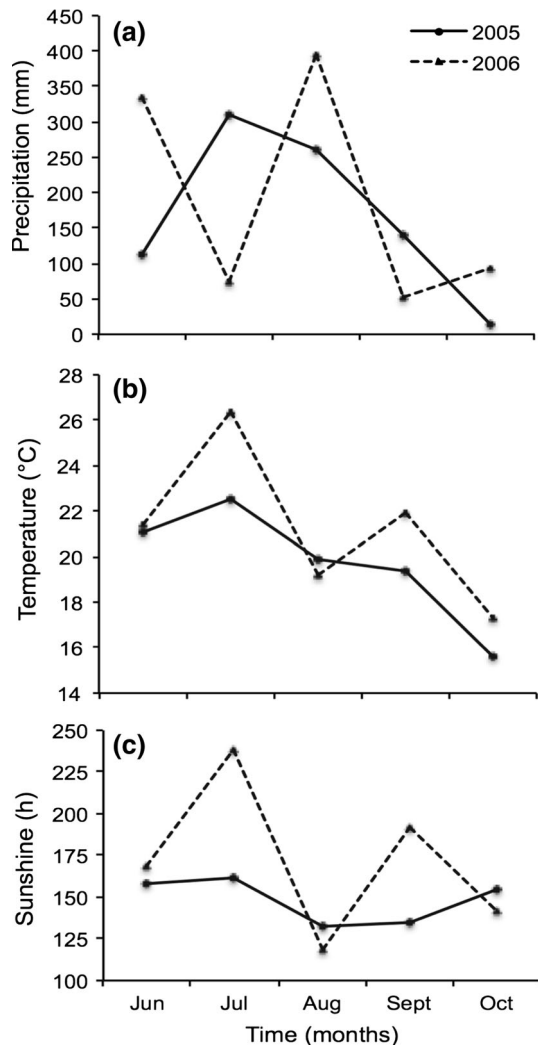
Fig. 2 Climate data for the study area from June to October in 2005 and 2006, respectively: total precipitation (mm) per month (**a**) Average temperature (°C) of all daily maxima (**b**) Total sunshine (h) per month (**c**). (*Source* ZAMG)

vulnerability to transplantation-induced injuries might be higher. Thus, the probability of mechanic damages of at least one plant within a whole cluster of transplants might have lead to lower survival of complete plant clusters for fir in our study.

Impact of forest types on seedling losses

The independent variable "experimental site" significantly influenced the probability of seedling losses in both year's submodels. Thereby, seedlings in LOF faced the highest probability of dying (2005 and 2006) and the lowest probability in MF (2005). Probabilities of seedling losses also significantly differed between the large and the small old-growth forest (SOF). Thus, seedling mortality in our study may not be reduced to a simple contrast "old-growth forests" vs. "managed forest". This result is in line with results of our seed predation

study, where spatial differences in seed removal could not be simply attributed to the degree of human intervention (Nopp-Mayr et al. 2012). Nystrand and Granström (2000) also observed a large between-site variation in seedling predation with no strong relation to forest site types. However, the latter authors found strong effects of logging operations on predation patterns, implying opportunities for reducing damages in the course of silvicultural management. As shown in Tables 1 and 3, the experimental sites of our study differed in terms of small mammal capture rates as well as densities of forest regeneration and regeneration cover, offering different micro-sites for potential herbivores and different growing conditions for early-stage seedlings. Ground vegetation cover as well as regeneration cover might improve habitat suitability for small mammals, as they provide both food and shelter against predators. On the other hand, seedling survival might also be positively influenced by accompanying vegetation (positive plant–plant interaction), in case that microclimate is harmonized by conspecifics and other plants (e.g. Ameztegui and Coll 2013).

Contrary to other studies of early regeneration development (e.g. Royo and Carson 2008; Caccia et al. 2009) seedling losses were higher in case of a low cover understorey vegetation (reflected by higher regression coefficients in LOF compared to SOF). It has been shown that a higher feeding pressure on seeds and seedlings might occur under dense ground or understorey vegetation (i.e. vegetation with a diameter at breast-height (dbh) ≤ 10 cm; Kikuzawa 1988; Caccia et al. 2009) as rodents and also some deer species preferably forage in these habitat patches offering hiding cover against visually oriented predators (Jacob and Brown 2000; Sullivan et al. 2007). According to Herrera (1995) shrub canopies may allow for an escape of seeds and seedlings from vertebrate herbivores thus exerting facilitative functions to tree regeneration although this effect is usually combined with abiotic effects, particularly in severe environments (Gómez-Aparicio et al. 2008). However, cover of shrubs or tree regeneration had no effect on seed removal in an earlier study (Nopp-Mayr et al. 2012). Similarly, Gómez et al. (2003) found no effect of microhabitat (in terms of understorey cover) on predation intensity of *Quercus sp.* seedlings. This is also in line with Bertness and Callaway's (1994) model of lower incidence of positive interactions in mesic habitats with moderate herbivore pressures as compared to severe habitat conditions and high herbivore pressures.

On our experimental sites, a medley of small mammal densities, plant-animal and plant–plant interactions may account for observed differences in seedling loss rates between study sites and study years. In 2005 and 2006, small mammal captures rates were higher in LOF compared to SOF (Table 3). In LOF, low regeneration cover and vegetation cover provided poorer food supply for small mammals and potentially lower facilitating effects for planted seedlings. This might in turn have

caused higher seedling loss rates in LOF compared to SOF. The lowest seedling loss rates in the MF compared to the other old-growth sites in 2005 may have been caused by higher disturbance through anthropogenic activity.

Seedling losses—a matter of tree species?

Both years count submodels yielded significant effects of tree species on the probability of seedling losses. In both cases, probabilities of seedling losses were highest for fir, lowest for spruce and (in 2005) intermediate for beech. Seedling mortality of tree species at early life-stages depends on various extrinsic and intrinsic biotic as well as abiotic factors including e.g. intra- and interspecific plant competition, shade, cold and drought tolerance, feeding preferences of herbivores, pathogen inoculation pressure or microsite and weather conditions (e.g. Ameztegui and Coll 2013; Čater and Levanič 2013; Kobe et al. 1995).

As shown by several authors (e.g. Dullinger et al. 2004; Holtmeier and Broll 2005), species-specific responses of plants to combinations of abiotic and biotic factors can be found at fine temporal and spatial scales. Moreover, micro-site conditions like micro-topography may modify effects of climate on plant survival (Diaci 2002; Dovčiac et al. 2003; Scherrer and Körner 2011; Simon et al. 2011; Ameztegui and Coll 2013). In our study, micro-site conditions varied to some degree between the experimental plots, but were in general more or less standardized by our experimental design (i.e. comparable micro-relief to ensure a proper fixing of exclosures on the ground). Thus, micro-site conditions are not expected to explain species-specific losses of tree seedlings.

Tree seedlings show species-specific adaptability to new environments after transplantation (Burschel and Huss 1997), resulting in an increased mortality rate within a short time period (Kawaletz et al. 2014). In our case, fir seedlings seemed to be more vulnerable to transplantation-induced mortality at first sight, but temporal mortality patterns did support this impression: Mortality did not predominantly occur within the first weeks after planting but was rather equally distributed over the whole study period. Thus, additional or other factors than the transplantation shock must be held responsible for observed species-specific seedling mortality. This is reflected in model "2006", where the factors "treatment" and "tree species" were included as interaction term, indicating that fir seedlings died to a higher extent on ungulate/hare exclosures and open access plots than in the total exclosures. Fir seedling mortality also tended to be higher on open access plots compared to spruce seedling mortality within the same treatment. This is in line with other studies (e.g. Motta 1996; Heuze et al. 2005), where fir was particularly subjected to browsing. However, our study provides evidence that deer or hare browsing were not major mortality factors for fir seedlings and that feeding of small mammals and invertebrates might be as well decisive for losses of for fir plants at early life stages.

Against our expectations, beech seedlings were not subjected to high browsing mortality, although they still had their cotyledon at the time of planting. Obviously, this feature did not improve the nutritional value of the plantlets to an extent that would have resulted in higher feeding preference by herbivores compared to conifer seedlings. Zimmermann (2009), investigating in situ germinated current year seedlings of deciduous tree species grown under a spruce canopy and protected with a gauze against vertebrate herbivory, observed distinctly lower losses of beech seedlings due to slug herbivory than for other deciduous tree species (like ash, sycamore, hornbeam, or elm). For beech seedlings, only 2 % of losses were caused by feeding of slugs (mainly on the hypocotyl) compared to 20–40 % for elm (Zimmermann 2009). In general, feeding preferences of herbivores can be seen as a function of nutritional values of feeding plants, their taste and palatability, which is in turn determined by the production and allocation of structural carbo-hydrates (like cellulose, lignin), non-structural carbo-hydrates (like sugar and starch; Dietze et al. 2014), tannins and other secondary metabolites. However, feeding preferences of different herbivores in terms of nutritional values or palatability of tree seedlings has not been comprehensively investigated, yet.

According to Rupf and Zeyrer (1961), favourable pH-ranges for successful germination and subsequent growth of seedlings are lower for spruce and fir (4.5–5.5) than for beech (5.0–6.0). In our study, neither the substrate in the seedling nursery nor on the experimental forest sites are expected to cause specific responses of tree species in terms of species-specific mortality patterns. But even if the substrate had caused different mortality of seedlings, tree species specific mortality rates would have been different (i.e. spruce/fir vs. beech) than observations in our study (i.e. fir vs. beech vs. spruce).

Merging the results with respect to the treatments, the higher vulnerability of transplanted fir seedlings as compared to beech and spruce seedlings can be deduced as well as a stronger effect of vertebrate herbivores on fir than on beech and spruce.

Feeding specialisation, seasonal availability of food, population dynamics of herbivores (rodents in particular) and different palatability of tree species might be key factors driving the proportion of tree species in mammalian herbivore diet (Massei et al. 2000; Vehviläinen and Koricheva 2006). Apart from the trees species, seedling size seems to be an influential factor in selective herbivory (see Hanley 1998). Thus, several interacting factors such as genotypic resistence, phenolic content, seedling size and developmental status (with or without cotyledon) as well as species diversity and microhabitat structure, acting on a stage set by interannual weather variations might be held responsible for highly variable feeding patterns of mammalian and invertebrate herbivores regarding specific tree species (Hulme 1996; O'Reilly-Wapstra et al. 2004; Vehviläinen and Koricheva 2006).

References

Ameztegui A, Coll L (2013) Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients. For Ecol Manage 303:25–34. doi:10.1016/j.foreco.2013.04.011

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193. doi:10.1016/0169-5347(94)90088-4

Boege K, Marquis RJ (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends Ecol Evol 20:441–448. doi:10.1016/j.tree.2005.05.001

Bogon K (1990) Landschnecken. Biologie—Ökologie—Biotopschutz. Natur-Verlag, Augsburg, Germany

Bryant JP, Chapin FS III, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368

Burschel P, Huss J (1997) Grundriß des Waldbaus. Pareys Studientexte 49, Berlin, Germany

Caccia FD, Chaneton EJ, Kitzberger T (2009) Direct and indirect effects of understorey bamboo shape tree regeneration niches in a mixed temperate forest. Oecologia 161:771–780. doi:10.1007/s00442-009-1412-z

Čater M, Levanič T (2013) Response of *Fagus sylvatica* L. and *Abies alba* Mill. in different silvicultural systems of the high Dinaric karst. For Ecol Manage 289:278–288. doi:10.1016/j.foreco.2012.10.021

Cavieres L, Fajardo A (2005) Browsing by guanaco on forest gaps in Tierra del Fuego, Chile. For Ecol Manage 204:237–248. doi:10.1016/j.foreco.2004.09.004

Coley PD, Barone JA (1996) Herbivory and plant defences in tropical forests. Annu Rev Ecol Syst 27:305–335. doi:10.1146/annurev.ecolsys.27.1.305

Crawley MJ (1997) Plant-herbivore dynamics. In: Crawley MJ (ed) Plant Ecology. Blackwell Sciences Ltd., Oxford, pp 401–474

Crawley MJ, Harral JE (2001) Scale dependence in plant biodiversity. Science 291:864–868. doi:10.1126/science.291.5505.864

Diaci J (2002) Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian Alps. For Ecol Manage 161:27–38

Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R (2014) Nonstructural carbon in woody plants. Annu Rev Plant Biol 65:667–687. doi:10.1146/annurev-arplant-050213-040054

Dorren LKA, Berger F, Imeson AC, Maier B, Rey F (2004) Integrity, stability and management of protection forests in the European Alps. For Ecol Manage 195:165–176. doi:10.1016/j.foreco.2004.02.057

Dovčiac M, Reich PB, Frelich LE (2003) Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. Can J For Res 33:1892–1904. doi:10.1139/X03-115

Dullinger S, Dirnböck T, Grabherr G (2004) Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invisibility. J Ecol 92:241–252. doi:10.1111/j.0022-0477.2004.00872.x

Ellenberg H (1992) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot 18:9–166

Feber RE, Brereton TM, Warren MS, Oates M (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. Forestry 74:271–276. doi:10.1093/forestry/74.3.271

Fenner M, Hanley ME, Lawrence R (1999) Comparison of seedling and adult palatability in annual and perennial plants. Funct Ecol 13:546–551. doi:10.1046/j.1365-2435.1999.00346.x

Fisichelli NA, Frelich LE, Reich PB (2013) Climate and interrelated tree regeneration drivers in mixed temperate–boreal forests. Landsc Ecol 28:149–159. doi:10.1007/s10980-012-9827-z

Gómez J, García D, Zamora RR (2003) Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. For Ecol Manage 180:125–134. doi:10.1016/S0378-1127(02)00608-4

Gómez-Aparicio L, Pérez-Ramos IM, Mendoza I, Matías L, Quero JL, Castro J, Zamora R, Maranón T (2008) Oak seedling survival and growth along resource gradients in Mediterranean forests: implications for regeneration in current and future environmental scenarios. Oikos 117:1683–1699. doi:10.1111/j.1600-0706.2008.16814.x

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Hanley ME (1998) Seedling herbivory, community composition and plant life history traits. Perspect Plant Ecol 1:191–205. doi:10.1078/1433-8391-00058

Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM (2007) Plant structural traits and their role in anti-herbivore defence. Perspect Plant Ecol 8:157–178. doi:10.1016/j.ppees.2007.01.001

Heikkilä R, Härkönen S (1996) Moose browsing in young Scots pine stands in relation to forest management. For Ecol Manage 88:179–186. doi:10.1016/S0378-1127(96)03823-6

Herrera J (1995) Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.). For Ecol Manage 76:197–201. doi:10.1016/0378-1127(95)03566-S

Herrera J, Jordano P, Guitián J, Traveset A (1998) Reassessment of principles and relationship to pollination and seed dispersal. Am Nat 152:576–594

Heuze P, Schnitzler A, Klein F (2005) Is browsing a major factor of silver fir decline in the Vosges Mountains of France? For Ecol Manage 217:219–228

Hewitt N, Kellman M (2004) Factors influencing tree colonization in fragmented forests: an experimental study of introduced seeds and seedlings. For Ecol Manage 191:39–59. doi:10.1016/j.foreco.2003.11.003

Hilbe JM (2011) Negative binomial regression. Cambridge University Press, Cambridge

Holtmeier F-K, Broll G (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecol Biogeogr 14:395–410. doi:10.1111/j.1466-822X.2005.00168.x

Homolka M, Heroldova M (2003) Impact of large herbivores on mountain forest stands in the Beskydy Mountains. Forest Ecol Manage 181:119–129. doi:10.1016/S0378-1127(03)00121-X

Hulme PE (1996) Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? J Ecol 84:853–861

Illius AW, Gordon IJ (1987) The allometry of food intake in grazing ruminants. J Anim Ecol 56:989–999

Ito H, Hino T (2005) How do deer affect tree seedlings on a dwarf bamboo-dominated forest floor? Ecol Res 20:121–128. doi:10.1007/s11284-004-0023-8

Jacob J, Brown JS (2000) Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos 91:131–138. doi:10.1034/j.1600-0706.2000.910112.x

Kabeya D, Sakai S (2003) The role of roots and cotyledons as storage organs in early stages of establishment in *Quercus crispula*: a quantitative analysis of the nonstructural carbohydrate in cotyledons and roots. Ann Bot 92:537–545. doi:10.1093/aob/mcg165

Kantorowicz W (2000) Half a century of seed years in major tree species of Poland. Silvae Genet 49:245–249

Kawaletz H, Mölder I, Zerbe S, Annighöfer P, Terwei P, Ammer C (2013) Exotic tree seedlings are much more competitive than natives but show underyielding when growing together. J Plant Ecol 6:305–315

Kawaletz H, Mölder I, Annighöfer P, Terwei P, Zerbe S, Ammer C (2014) Pot experiments with woody species—a review. Forestry 87:482–491. doi:10.1093/forestry/cpu017

Kelly D, Sork VL (2002) mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–447

Kempter I, Nopp-Mayr U (2013) Langzeit-Monitoring von Kleinsäugern im Wildnisgebiet Dürrenstein. Silva Fera 2:94–99

Kikuzawa K (1988) Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest. For Ecol Manage 25:1–8. doi:10.1016/0378-1127(88)90129-6

Knapp AK, Smith WK (1982) Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Can J Bot 60:2753–2761. doi:10.1139/b82-337

Kobe RK, Pacala SW, Silander JA, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. Ecol Appl 5:517–532

Krapp F (2003) Handbuch der Säugetiere Europas, Bd. 3/II, Hasentiere. AULA Verlag GmbH, Wiebelsheim, Germany

Kuijper DPJ, Cromsight JPGM, Jędrzejewska B, Miscicki S, Churski M, Jędrzejewski W, Kweczlich I (2010a) Bottom-up versus top-down control of tree regeneration in the Bialowieza Primeval Forest, Poland. J Ecol 98:888–899. doi:10.1111/j.1365-2745.2010.01656.x

Kuijper DPJ, Jędrzejewska B, Brzeziecki B, Churski M, Jędrzejewski W, Zybura H (2010b) Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. J Veg Sci 21:1082–1098. doi:10.1111/j.1654-1103.2010.01217.x

Kupferschmid AD, Wasem U, Bugman H (2014) Light availability and ungulate browsing determine growth, height and mortality of *Abies alba* saplings. For Ecol Manage 318:359–369. doi:10.1016/j.foreco.2014.01.027

Kutter M (2007) Dispersal ecology of the dominant woody species (*Fagus sylvatica, Picea abies, Abies alba*) in the old growth forest Rothwald. Thesis, Dept. of Forest- and Soil Sciences, Univ. of Natural Resources and Life Sciences, Vienna, Austria

Leditznig C, Pekny R (2009) Die Säugetiere des Wildnisgebietes Dürrenstein. Schutzgebietsverwaltung Wildnisgebiet Dürrenstein, Scheibbs

Lyly M, Klemola T, Koivisto E, Huitu O, Oksanen L, Korpimäki E (2014) Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings. Oecologia 174:271–281. doi:10.1007/s00442-013-2761-1

Martinez J-JY, Wool D (2003) Differential response of trees and shrubs to browsing and pruning: the effects on Pistacia growth and gall-inducing aphids. Plant Ecol 169:285–294. doi:10.1023/A:1026085307964

Massei G, Hartley SE, Bacon PJ (2000) Chemical and morphological variation of Mediterranean woody evergreen species: do plants respond to ungulate browsing? J Veg Sci 11:1–8. doi:10.2307/3236768

McArthur C, Marsh NR, Close DC, Walsh A, Paterson S, Fitzgerald H, Davies NW (2003) Nursery conditions affect seedling chemistry, morphology and herbivore preferences for Eucalyptus nitens. For Ecol Manage 176:585–594. doi:10.1016/S0378-1127(02)00315-8

McNeil A, Carlson JK, Beerkircher LR (2009) Shark depredation rates in pelagic longline fisheries: a case study from the Northwest Atlantic. ICES J Mar Sci 66:708–719. doi:10.1093/icesjms/fsp022

McShea WJ, Rappole JH (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conserv Biol 14:1161–1170. doi:10.1046/j.1523-1739.2000.99210.x

Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the western Italian Alps. For Ecol Manage 88:93–98

Munier A, Hermanutz L, Jacobs JD, Lewis K (2010) The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. Plant Ecol 210:19–30. doi:10.1007/s11258-010-9724-y

Niethammer J, Krapp F (1978) Handbuch der Säugetiere Europas, Bd. 1, Nagetiere I. Akademische Gesellschaft Wiesbaden, Germany

Niethammer J, Krapp F (1982) Handbuch der Säugetiere Europas, Bd. 2/1, Nagetiere II. Akademische Gesellschaft Wiesbaden, Germany

Niethammer J, Krapp F (1986) Handbuch der Säugetiere Europas, Bd. 2/, Paarhufer. Akademische Gesellschaft Wiesbaden, Germany

Nopp-Mayr U, Kempter I, Muralt G, Gratzer G (2012) Seed survival on experimental dishes in a central European old-growth mixed-species forest—effects of predator guilds, tree masting and small mammal population dynamics. Oikos 121:337–346. doi:10.1111/j.1600-0706.2011.19099.x

Nystrand O, Granström A (2000) Predation on *Pinus sylvestris* seeds and juvenile seedlings in Swedish boreal forest in relation to stand disturbance by logging. J Appl Ecol 37:449–463. doi:10.1046/j.1365-2664.2000.00505.x

O'Reilly-Wapstra JM, McArthur C, Potts BM (2004) Linking plant genotype, plant defensive chemistry and mammal browsing in a Eucalyptus species. Funct Ecol 18:677–684. doi:10.1111/j.0269-8463.2004.00887.x

O'Reilly-Wapstra JM, Iason GR, Thoss V (2007) The role of genetic and chemical variation of *Pinus sylvestris* seedlings in influencing slug herbivory. Oecologia 152:82–91. doi:10.1007/s00442-006-0628-4

Övergaard R, Gemmel P, Karlsson M (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. Forestry 80:555–565. doi:10.1093/forestry/cpm020

Pietrzykowski E, McArthur C, Fitzgerald H, Goodwin A (2003) Influence of patch characteristics on browsing of tree seedlings by mammalian herbivores. J Appl Ecol 40:458–469. doi:10.1046/j.1365-2664.2003.00809.x

Pröll G, Darabant A, Gratzer G, Katzensteiner K (2014) Unfavourable microsites, competing vegetation and browsing restrict post-disturbance tree regeneration on extreme sites in the Northern Calcareous Alps. DOI, Eur J Forest Res (online first). doi:10.1007/s10342-014-0851-1

Pucek Z, Jedrzejewski W, Jedrzejewska B, Pucek M (1993) Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. Acta Theriol 38:199–232

Ravolainen VT, Brathen KA, Yoccoz NG, Nguyen JK, Ims RA (2014) Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. J Appl Ecol 51:234–241. doi:10.1111/1365-2554.12180

Reimoser F (1991) Verbiss-Kontrollgatter—Eine Methode zur objektiven Erfassung des Einflusses von Schalenwild und Weidevieh auf die Waldverjüngung (System Vorarlberg). Holzwirtschaft 47:11–15

Riipi M, Lempa K, Haukioja E, Ossipov V, Pihlaja K (2005) Effects of simulated winter browsing on mountain birch foliar chemistry and on the performance of insect herbivores. Oikos 111:221–234. doi:10.1111/j.0030-1299.2005.13781.x

Royo AA, Carson WP (2008) Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. Can J For Res 38:1634–1645. doi:10.1139/X07-247

Rupf H, Zeyrer M (1961) Der Forstpflanzengarten: Ein Lehrbuch für Schule und Praxis zur rationellen Anzucht von Forstpflanzen. BLV, Munich

Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J Biogeogr 38:406–416. doi:10.1111/j.1365-2699.2010.02407.x

Siemann E, Rogers WE (2003) Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84:1489–1505. doi:10.1890/0012-9658(2003)084[1489:HDRLAS]2.0.CO;2

Simon A, Gratzer G, Sieghart M (2011) The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. For Ecol Manage 262:1289–1297. doi:10.1016/j.foreco.2011.06.028

Splechtna K (2001) Wildnisgebiet Dürrenstein—Albert Rothschild Bergwaldreservat: Skizzen einer Nutzungsgeschichte. In: Gossow H (ed) LIFE-Projekt Wildnisgebiet Dürrenstein—Managementplan. Amt der Niederösterreichischen Landesregierung, Abteilung Naturschutz, pp 75–81

Stancioiu PT, OHara KL (2006) Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. Eur J Forest Res 125:151–162. doi:10.1007/s10342-005-0069-3

Sullivan T, Sullivan D, Lindgren P, Ransome D (2007) Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest IV. Relative habitat use by mammalian herbivores. For Ecol Manage 240:32–41. doi:10.1016/j.foreco.2006.11.020

Suominen O, Persson I-L, Danell K, Bergström R, Pastor J (2008) Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. Ecography 31:636–645. doi:10.1111/j.0906-7590.2008.05480.x

Tripler C, Canham C, Inouye R, Schnurr J (2002) Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. Oecologia 133:517–524. doi:10.1007/s00442-002-1046-x

Vehviläinen H, Koricheva J (2006) Moose and vole browsing patterns in experimentally assembled pure and mixed forest stands. Ecography 29:497–506. doi:10.1111/j.0906-7590.2006.04457.x

Vuong QH (1989) Likelihood ratio tests for model selection and non-nested hypotheses. Econometrica 57:307–333

Willner W, Grabherr G (eds) (2007) Die Wälder und Gebüsche Österreichs. Elsevier, Spektrum Akademischer Verlag, Munich

Zimmermann, K (2009) Keimverhalten und Sämlingsentwicklung mehrerer Laubbaumarten bei unterschiedlicher Samenlagerung unter seminatürlichen Bedingungen und in einem buchendominierten Laubmischbestand eines Kalkstandortes. Schriftenreihe Freiburger Forstliche Forschung 14. Freiburg (Breisgau), Germany

Zukrigl K, Eckhart G, Nather J (1963) Standortskundliche und waldbauliche Untersuchungen in Urwaldresten der niederösterreichischen Kalkalpen. Mitt. forstl BVA Mariabrunn 62. Mariabrunn, Austria