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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

Ursula Nopp-Mayr, Iris Kempter, Gerald Muralt and Georg Gratzer

U. Nopp-Mayr, I. Kempter (iris.kempter@boku.ac.at) and G. Muralt, Inst. of Wildlife Biology and Game Management, Dept of Integrative Biology and Biodiversity Research, Univ. of Natural Resources and Life Sciences, Vienna, AU-1180 Vienna, Austria. – G. Gratzer, Inst. of Forest Ecology, Dept of Forest- and Soil Sciences, Univ. of Natural Resources and Life Sciences, Vienna, AU-1190 Vienna, Austria.

Predation of tree seeds can be a major factor structuring plant communities. We present a three year study on tree seed survival on experimental dishes in an old-growth forest in central Europe in Austria. We addressed species specific, spatial and temporal aspects of post-dispersal seed predation. Seeds of Norway spruce *Picea abies*, European beech *Fagus sylvatica*, and silver fir *Abies alba* were exposed on dishes in different types of exclosures which allowed access only to specific guilds of seed predators. Removal experiments were carried out in two old-growth forests and a managed forest (macro-sites), including micro-sites with and without cover of ground vegetation. We conducted the experiment in three consecutive years with a mast year of beech and spruce before the first year of the study. The seed removal experiments were combined with live trapping of small mammals being potential seed predators. Our experiments showed a distinctly different impact of different predator guilds on seed survival on the dishes with highest removal rates of seeds from dishes accessible for small mammals. We observed differing preferences of small mammals for the different tree species. Seed survival in different macro- and micro-habitats were highly variable with lower seed survival in old growth forests. In contrast to our assumption, and in contrast to the satiation hypothesis which assumes higher seed survival in and directly after mast years, seed survival was lower in the year following the mast year of beech when a population peak of small mammals occurred and higher in intermast periods when subsequently small mammal population crashed. This suggests a higher importance of sporadic masting shortly after mast years in intermast periods for establishment of forest trees provided that pollination efficiency is high enough in such years. Combined with the high seed mortality observed after the mast year, this corroborates the important role of seed predation for forest dynamics. An altered synchrony or asynchrony of masting of different tree species and changed masting frequencies through climate change may thus lead to strong and non-linear effects on forest dynamics.

Seed production of forest trees is an elementary process in forest ecosystem dynamics. It depends on a variety of interacting processes and mechanisms. Apart from endogenous aspects, i.e. specific reproduction strategies of tree species or provenances and the time lag since the last fruiting reflecting the internal resource status of trees, climatic and edaphic factors trigger seed production (Mencuccini et al. 1995, Piovesan and Adams 2001, Övergaard et al. 2007). The presence and quantity of seeds is not only a determinant of tree population dynamics: before and during seed dispersal, guilds of pre- and post-dispersal seed-consumers and pathogens may distinctly decrease the rate of effective seed deposition and germination (Janzen 1970, Howe and Smallwood 1982, Schupp 1988, Louda 1989). Seeds as important resource for consumers have a high potential for causing numerical responses in the seed consumers as well as their predators (Kager and Fietz 2009). Along with increased pollination efficiency for wind-pollinated plants, a strong coupling of seed production with frugivore dynamics is thought to be a driving factor for the evolution of interannual variations of seed production (Kelly and Sork 2002, Koenig et al. 2003, Kon et al. 2005). While small mammal populations might not reach or maintain high levels during intermast periods (Jensen 1985, Pucek et al. 1993), pronounced enhancement of nutrient-rich food supply in years with strongly increased seed production (mast years) can trigger increases in small mammal abundances rapidly (Pucek et al. 1993) but also lead to increased germination rates through satiation of the seed predators (Janzen 1971, Silvertown 1980, Jensen 1985, Borchert et al. 1989, McKone et al. 1998, Nilson 2000).

Before and after seed dispersal, different predators guilds consume seeds with specific responses to masting events. Invertebrates, birds, and certain small mammals (e.g. squirrels) frequently act as pre-dispersal seed predators, responding differently to excess food supply (Kelly et al. 2001). As demonstrated by Schnurr et al. (2002) and Plucinski and Hunter (2001), small mammals, being amongst the most effective post-dispersal seed predator guilds, may show species-specific responses on masting of different tree species. Thus, the occurrence of small mammal species as well as their degree of specialisation might influence the extent of seed consumption on the ground and subsequently tree population dynamics and eventually tree species coexistence. This creates the need for studying post-dispersal seed predation both by considering tree species-specific predation pressure (Kollmann et al. 1998) and population dynamics of potential seed predator guilds. Information on both aspects is largely lacking for European old growth forests, particularly for mountain forests. The need for understanding forest dynamics and its important drivers has become more pressing with climatic changes which influence masting intervals of trees. Several authors describe an increase of beech masting (both in terms of frequency of masting events and quantity of nuts) for large parts of Europe (Kantorowicz 2000, Hilton and Packham 2003, Litschauer and Konrad 2006, Schmidt 2006, Övergaard et al. 2007). The increase of mast years is attributed to changes in climate (in particular higher temperature and lower precipitation in July in the preceding year of a mast year) as well as to increased nitrogen status of the ecosystems due to nitrogen deposition (Schmidt 2006, Övergaard et al. 2007). Consequently, effects on mammalian seed predator populations as well as changes in the interspecific competition of tree species can be expected (Schnurr et al. 2002). The occurrence of predator guilds and their potential influence on seed survival seem to vary distinctly among different geographic regions and different forest ecosystems (Kelly et al. 2008). Several authors hold small mammals responsible for the major part of tree seed losses in northern temperate forests, whereas birds and arthropods are assumed to play an inferior role (Hulme and Borelli 1999, Schreiner et al. 2000). Recent studies however, corroborate the important role of invertebrates, particularly slugs as herbivores on tree seedlings (Pigot and Leather 2008).

To study fundamental processes of regeneration in forest ecosystems, old-growth forests lend themselves as study objects, providing conditions not impaired by recent or ancient human land use. In this paper, we present a study conducted in the largest remaining old-growth forest in central Europe, dealing with the removal of tree seeds due to different taxonomic groups of seed predators in consecutive years after a masting of European beech. Being part of a larger project dealing with regeneration dynamics and disturbances of this old-growth mountain forest in Austria, we observed removal rates of seeds of the main tree species on experimental dishes with different types of exclosures. Capturing a mast year for beech and spruce during a three years experimental study, we were able to address questions on the role of temporal variation in seed production and its effect on removal rates of seeds. We were aiming at characterising 1) species specific, 2) temporal, and 3) spatial aspects of post-dispersal seed removal. For the species specific aspects, we asked if survival rates of tree seeds on experimental dishes differ as a function of 1a) different guilds of seed predators, 1b) different tree species and if 1c) seed survival rates are correlated with small mammals´ trapping success. The temporal aspect was covered by the question if 2) seed survival rates change with increasing time lag from the mast year and for the spatial aspects we specifically asked the question if 3a) there are differences at a macro-habitat scale (three sample areas with different stand structure), and if 3b) at micro-habitat scales, seed survival rates differ with different ground vegetation cover as was observed in a number of studies dealing with small mammal seed predation (Alcántara et al. 2000, Schreiner et al. 2000, Kollman and Buschor 2002).

Material and methods

Study area

The study area is located in the Wilderness Area Dürrenstein (47°48' to 47°45'N, 15°01' to 15°07'E), which is part of the northern Limestone Alps of Lower Austria. The climate of the region is submaritime with long winter periods and short, cool summers. Mean annual temperature in the area is 3.9°C. January is the coldest month with an average temperature of –4.7°C and in July the mean temperature is 13.4°C. Annual precipitation can reach a maximum of 2300 mm and shows a bimodal pattern, reaching one maximum during the vegetation period in June/July and another one at wintertime. Snowfall occurs between October and May with continuous snow cover of about 200 days. The parent material of the area is composed of Dolomite and banked limestone, the soils are characterised by a mosaic of Rendzinas and relictic loams (Zukrigl et al. 1963). The Rothwald old-growth forest consists of a basin, surrounded by steep slopes. The forests in the basin were classified as *Asperulo–Abieti–Fagetum*, a higher altitude subtype of a Galio–odorati–Fagetum (Willner and Grabherr 2007). The forests on the slopes were described as *Adenostylo glabrae–Fagetum*. *Fagus sylvatica* dominates on all sites, particularly on the slopes. The co-dominant *P. abies* and *A. 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 sample areas were selected: two in an old-growth forest at altitudes of 1000 m and 1100 m for the small and large old-growth forest, respectively and one in a managed forest at 1050 m altitude. The sample area in the managed forest was located within a mature Norway spruce timber stand with a dominance of *P. abies* and admixed *F. sylvatica* and *A. alba*. These areas were chosen to represent the two main site types and associations of the old-growth forest (Zukrigl et al. 1963) and a comparable managed forest (Table 1).

Tree masting and seed rain

In 2003, *F. sylvatica, P. abies* and *A. alba* had a pronounced mast year. In the small old-growth forest an average of 301 beech seeds m^{-2}, 28 fir seeds m^{-2}, and 184 spruce seeds m^{-2} were recorded. In the large old-growth forest 406, 18 and 126 seeds m^{-2} of beech, fir, and spruce were recorded, respectively (Kutter 2007). *Fagus sylvatica* started dispersing seeds in the second half of September 2003, seed dispersal had a duration of eight weeks but 60% of the seeds were dispersed within two weeks, *A. alba* dispersed the seeds from mid September to late November with a peak in mid November while *P. abies* dispersed the seeds in late November and in spring 2004 (Kutter 2007) (exact date could not be determined because of snow coverage in the area and late accessibility).

Table 1. Characteristics of the sample areas (Kempter 2006).

	Small old-growth forest	Large old-growth forest	Managed forest
Stem density (number of Individuals per ha (± SD) with dbh > 10 cm)	342 (± 42)	259 (± 38)	---
Regeneration density (number of Individuals per ha (± SD) with dbh < = 10 cm	55 351 (± 4071)	30 752 (± 3315)	---
Regeneration cover	25–50%	---	< 5%
Canopy cover of ground surface	2/10–7/10	---	2/10–8/10
Deadwood cover percentage	15%	---	< 5%

Cafeteria experiments

For the post-dispersal seed removal experiments we exposed seeds of the main tree species, i.e. Norway spruce *Picea abies*, silver fir *Abies alba* and nuts of European beech *Fagus sylvatica*, on green or brown plastic dishes (12 cm ø) on a 4 × 3 grid (i.e. subplot) with approximately 1 m distances of the grid points (Schreiner et al. 2000). We installed 180 experimental dishes per year ($n_{total} = 540$). We placed five seeds per tree species per dish and dewinged seeds of silver fir and Norway spruce before exposure to reduce losses due to wind and to facilitate the identification of seeds originating from natural seed rain. The removal of wings is assumed to not cause differences in the probability of seeds being encountered by seed predators since this probability would not change with dislocations of seeds by wind. In 2006, no seeds of European beech could be found in nature and were not available, either. Thus, only seeds of Norway spruce and silver fir could be exposed. Four types of seed exposure were chosen (Kollmann et al. 1998, Castro et al. 1999, Schreiner et al. 2000): a) dishes, covered by a 1.3 × 1.3 cm wire mesh (13 cm ø, 10 cm height) allowing for access of invertebrates (mainly arthropods such as carabids, and weevils, or molluscs); b) dishes covered by a 3.0 × 3.0 cm wire mesh (13 cm ø, 10 cm height), offering access for invertebrates and small mammals, but not for birds; c) open dishes, being accessible for birds, small mammals, and invertebrates; d) dishes on a 30 cm plastic stick, exposing the seeds exclusively to birds. All but the last type of dishes were protected against wind and rain by a 14 × 14 cm transparent PVC screen, held about 10 cm above the ground by a plastic stick, which also fixed dish to the ground. We installed three replications per exposure type on each subplot, using a randomized block design for the designation of exposure types. At the two study areas in the old growth forest, three subplots were established on micro-sites covered by ground vegetation, shrubs or regeneration and three on open micro-sites. In the managed forest, only open micro-sites were available. We controlled the dishes on day 1, day 2 and day 9 after exposure. Controlling the dishes, we recorded the number of remaining seeds per tree species as well as signs of predation (empty coats) or of small mammal presence (gnawing signs, faecal pellets, and urine). Removed seeds were not substituted. In this paper, we define 'seed survival on experimental dishes' as the ratio of remaining seeds on the respective day of control related to the number of originally exposed seeds. Removal of seeds from the dishes is not per se perceived as predation of seeds, but as disappearance of experimentally exposed seeds.

Seeds of *F. sylvatica* are around 2 cm long and have a thousand seed weight of 160–240 g, *P. abies* seeds are 4–5 mm long, winged (length of the wing is 15 mm) and have a thousand seed weight of 7.7 g. Seeds of *A. alba* are 6–10 mm long with wings of 8-10 mm length and have a thousand seed weight of 35–55 g.

Small mammal trapping

To gain insight into the potential seed predator group of small mammals, live trapping was carried out with time intervals of several days between trapping and the cafeteria-experiments. We installed traps on a 15 × 15 m grid, with two traps per grid point and total sum of 50 traps per sample area. In 2004 and 2005, we used wooden box traps (17.0 × 7.0 × 5.0 cm) with a wire grating on the upper side. In 2006, both a wooden box trap and a plastic trap (38.7 × 6.0 × 8.0 cm) were installed per grid point for an accompanying study of their trapability. The traps were baited with butter cookies, peanut butter, and a piece of apple. Trapping occurred for two or three consecutive nights; 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 to the field at the point of capture.

Statistical analyses

As counts of remaining seeds on the experimental dishes followed a Poison distribution with variances greater than the mean (overdispersion) we used a GLM procedure (negative binomial regression; Hilbe 2011) for analysing rates of remaining seeds (link = log, criteria method = fisher scale, likelihood = full, contrast = pair wise). We run GLMs for each study year (2004–2006) and for day 1, 2 and 9 after exposure, respectively. We were considering two different combinations of factors:

a) Model a. Since only open micro-sites occurred in the managed forest, exclusively open subplots were taken for statistical analyses regarding the effects of treatment (i.e. predator guild/exposure type), tree species, and macro-habitat (i.e. sample areas) on seed survival.
b) Model b. Within the old-growth forest we analysed effects of treatment (i.e. predator guild/exposure type), tree species, macro-habitat (i.e. small and large old-growth forest), and micro-habitat (i.e. open subplots vs. subplots covered with ground vegetation, shrubs or regeneration) on seed survival.

For further modelling, we selected the factors having significant effects on seed survival on day 9 after exposure (excluding the bird dishes).

We compared seed survival in the consecutive years of investigation by non-parametric tests (Kruskal-Wallis test and Mann-Whitney test) and correlated trapping rates of potential seed predators, i.e. catches of murids, arvicolids, and glirids per 100 trapping nights with seed survival rates by Kendall's Tau. For analyses of trapping success we considered both newly and re-captured specimens as this measure better represents seed predation pressure than trapping success only expressed in newly caught individuals per 100 trapping nights.

For all data analyses, we used SPSS 15.0 for Windows.

Results

Small mammal trapping

Three species of potential seed predators (rodents) were caught in the study area during the study period 2004–2006, i.e. the yellow-necked mouse (*Apodemus flavicollis*, the bank vole *Myodes glareolus*, and the edible dormouse *Glis glis*. The trapping success distinctly changed in the years after masting of European beech in autumn 2003, showing a pronounced peak in 2004 followed by a collapse in 2005 (Table 2). In the managed forest, every night a predator manipulated the traps in 2004. Thus, we could only observe the presence of small mammals in the traps (i.e. faecal pellets and gnawing signs on the baits), but not determine their genera and species. Signs of small mammal presence indicated a similar proportion of entered traps compared to the intact traps on the other sample areas, but trapping rates of rodent species could not be determined.

Seed survival on experimental dishes

On dishes accessible for small mammals and invertebrates and on dishes with open access we observed variable seed survival rates on day 9 after exposure regarding the tree species and the year. In 2004, no beech seeds remained on the dishes in any sample area at all and mean survival rates of spruce seeds were very low, too (maximum of 9% in the managed forest) (Table 3). Only fir seeds gained higher survival rates ranging from 28% up to 82%. In the following years, seed survival rates were high in the managed forest (87–100%) but very diverse in the old-growth forest. In 2005, mean survival rates of spruce and fir seeds were high but for beech seeds the average survival rate only ranged from 16% up to 29%. In 2006, when no beech seeds were available, the average survival rate of fir seeds was high again (92–100%) while mean survival rates of spruce seeds were much lower (12–28%) (Table 3).

Dishes on 30 cm-sticks, constructed to allow mainly birds for seed predation, were in several cases entered by small mammals in 2004 (indicated by indirect signs of small mammal presence such as gnawing signs, faecal pellets, and urine). For data analyses of this treatment, we considered only dishes without indirect signs of small mammals (i.e. 38 out of 45 dishes). Mean seed survival rates on the bird dishes varied to a large extent between areas, years, and tree species. In general, they were high in the managed forest in all years and lowest in the old-growth forest in 2005 (Table 3).

Table 2. Trapping rates of rodent species (newly and re-captured specimens per 100 trapping nights) on the three sample areas within the three study years.

	2004	2005	2006
Small old-growth forest	68.7	0.0	8.0
Large old-growth forest	62.0	7.0	4.7
Managed forest	---	1.0	0.7

In 2004, rodents captured exclosures of small mammals (i.e. dishes with close meshed wire grating) in several cases (4 out of 45 dishes). In the following years, small mammals did not enter close meshed exclosures. For data analyses, we considered only functioning small mammal exclosures. In 2004, on these dishes, only accessible for invertebrates, mean survival rates of seeds were again highest in the managed forest and lower in the old-growth forest. In 2005 and 2006 the average survival rate of seeds was high on every sample area and ranged between 91% and 100% (Table 3).

In the small mammals peak year 2004, Wald's χ^2 was significant for the variables treatment (i.e. predator guild), tree species, and macro-habitat on day 1, 2 and 9 after exposure of the seeds but never for the variable micro-habitat (i.e. vegetation cover) (Table 4, 5). In 2005, Wald's χ^2 was significant for the variables treatment on day 1 after exposure (model a and b) and on day 9 (model b) and for the variable macro-habitat on day 1 after exposure (model a) (Table 4, 5). In 2006, Wald's χ^2 was significant for the variables treatment, tree species, and micro-habitat on day 9 after exposure (model b) (Table 5).

Species specific aspects of seed removal

According to the negative binomial regression models for 2004, seed survival rates were significantly enhanced on dishes accessible only for invertebrates in both, model a and b regarding the seed predator guilds (Table 6, 7). In 2005 and 2006 seed survival rates were significantly higher on dishes not accessible for small mammals only in model b (Table 7). In other words, only exclosures of small mammals showed a positive effect on seed survival on the dishes, particularly in the year of high small mammal abundances.

Both model a and b (Table 6, 7) illustrate that the tree species had a significant effect on survival rates of seeds: Fir seeds gained the highest regression coefficients in both model types in 2004, representing higher survival rates of these seeds. For the following years, only model b showed significant regression coefficients indicating again higher survival rates of fir seeds respectively lower survival rates of beech seeds in both years (Table 7).

Trapping success, measured in newly captured and re-captured specimens per 100 trapping nights, was correlated with seed survival on dishes accessible for small mammals for each sample area and tree species using nonparametric tests (Kendall's Tau). Correlations were only calculated, where data of both trapping and survival rates of the three years of study were available (i.e. spruce and fir seed survival in the small and large old-growth forest). In all but one cases, trapping rates significantly negatively correlated with seed survival rates on the dishes accessible for small mammals. Only in the large old-growth forest, survival of fir seeds did not correlate with trapping success.

Temporal aspects of seed removal

Apart from one single exception (see below) seed survival rates of all three tree species on day 9 after exposure on the

Table 3. Mean survival rates of spruce, fir, and beech seeds (mean percentage ± SD) within sample areas, study years and treatments (subplots covered with vegetation and open subplots are summarized). Date of control = day 9 after exposure, except for the bird-dishes (s. below).

		2004			2005			2006[b]	
Sample area	Treatment/access for	Beech	Spruce	Fir	Beech	Spruce	Fir	Spruce	Fir
Small old-growth forest	Small mammals, invertebrates	0.0 ± 0.0	0.0 ± 0.0	27.8 ± 12.9	18.7 ± 11.9	93.3 ± 8.4	95.0 ± 6.4	15.6 ± 25.5	92.2 ± 9.8
	Invertebrates	16.7 ± 40.8	34.4 ± 37.8	96.1 ± 4.4	100.0 ± 0.0	98.9 ± 2.7	98.3 ± 3.3	93.3 ± 7.3	100.0 ± 0.0
	Birds[a]	98.3 ± 4.1	100.0 ± 0.0	100.0 ± 0.0	30.7 ± 16.1	1.1 ± 2.7	8.3 ± 10.0	97.8 ± 5.4	97.8 ± 3.4
	Open access	0.0 ± 0.0	1.1 ± 2.7	38.9 ± 11.5	18.7 ± 15.9	80.0 ± 39.3	95.0 ± 6.4	12.2 ± 19.1	92.2 ± 7.8
Large old-growth forest	Small mammals, invertebrates	0.0 ± 0.0	1.1 ± 2.7	66.8 ± 13.2	29.4 ± 16.1	87.2 ± 10.8	96.7 ± 5.6	27.8 ± 31.1	100.0 ± 0.0
	Invertebrates	60.7 ± 49.0	76.0 ± 27.5	88.9 ± 24.1	98.9 ± 2.7	92.2 ± 8.9	96.9 ± 3.4	97.8 ± 3.4	100.0 ± 0.0
	Birds[a]	41.7 ± 37.7	47.2 ± 45.2	100.0 ± 0.0	26.7 ± 33.5	3.3 ± 8.2	8.9 ± 18.7	100.0 ± 0.0	100.0 ± 0.0
	Open access	0.0 ± 0.0	0.0 ± 0.0	61.1 ± 16.6	15.6 ± 10.9	80.0 ± 21.5	83.3 ± 12.5	27.8 ± 39.0	97.8 ± 5.4
Managed forest	Small mammals, invertebrates	0.0 ± 0.0	0.0 ± 0.0	44.4 ± 13.9	95.6 ± 3.8	91.1 ± 15.4	100.0 ± 0.0	95.6 ± 3.8	100.0 ± 0.0
	Invertebrates	100.0 ± 0.0	91.1 ± 7.7	95.6 ± 7.7	97.8 ± 3.8	97.8 ± 3.8	100.0 ± 0.0	97.8 ± 3.8	91.1 ± 10.2
	Birds[a]	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	97.8 ± 3.8
	Open access	0.0 ± 0.0	8.9 ± 10.2	82.2 ± 20.4	95.6 ± 7.7	88.9 ± 19.2	86.7 ± 17.6	97.8 ± 3.8	100.0 ± 0.0

[a] date of control = day 1 after exposure. (As the bird-dishes were not equipped with a PVC screen accumulation of rainwater occurred with time (particularly in 2004). Thus, only day 1 after exposure could be considered for data analyses.)

[b] in 2006, no seeds of European beech were exposed.

dishes accessible for small mammals and invertebrates differed between the years. Seed survival rates of spruce, fir and beech were significantly lower in the year right after beech masting in autumn 2003 (i.e. 2004, with a small mammal gradation) compared to the following year (2005). In the second year after the small mammals population peak (2006), spruce seeds survived to a lower degree on the dishes accessible for rodents compared to the year of population breakdown (2005). For fir seeds, no significant differences between the survival rates in 2005 and 2006 could be observed. Only in the managed forest, survival of spruce seeds showed no difference between the years (Kruskal-Wallis test, $\chi^2 = 5.862$, DF = 2, p = 0.053).

Seed survival in the small mammal exclosures did not vary with time-lag from the masting year (exception: spruce and beech seeds in the small old-growth forest, with lowest survival rates in 2004).

Spatial aspects of seed removal

According to the negative binomial regression models (model a and b), only in 2004 the macro-habitat (i.e. different forest types) had an effect on seed survival rates with a significant negative regression coefficient in the small old-growth forest (Table 6, 7). This means that in the year with high small mammals abundances less seeds exposed in the small old-growth forest remained on the dishes.

Only one model yielded significant regression coefficients for the variable micro-habitat (i.e. cover of ground vegetation): In 2006, exposure of seeds on open micro-sites had a positive effect on seed survival. In all other models regression coefficients for the micro-site were non-significant (Table 7).

Discussion

Species specific aspects of seed removal

In the year of highest abundance of small mammals (2004), seed survival rates of all three tree species were higher on the small mammal exclosures, whereas on the dishes accessible for small mammals nearly all spruce and beech seeds were removed within a few days. Thus, in most cases seeds were removed by small mammals before other potential seed predators, such as arthropods or birds, were able to remove them. In the years after the small mammal gradation (2005, 2006) seed survival rates on the small mammal exclosures were never below 90%, indicating that invertebrates have low to moderate influence on average post-dispersal seed loss (cf. Nystrand and Granström 2000). Seed removal from open dishes and from wide wire mesh dishes was approximately equal (Schreiner et al. 2000). This again indicates that substantial parts of seeds are removed by small mammals rapidly and are consequently no longer available for other guilds of predators (such as birds or ungulates) (Borchert et al. 1989, Haas and Heske 2005, Iob and Vieira 2008).

Within the negative binomial regression models, the variable 'treatment' (i.e. the type of exclosure) had a significant influence on seed survival in 10 out of 18 models, namely in all models in the year of small mammal population peak and in all b-models (old growth forest) for day 9 after exposure. Within these models, an exclosure of small mammals

Table 4. Model a: Wald's χ^2 test values of the factors treatment, tree species and macro-habitat in a negative binomial regression model for seed survival for all three study years (only open subplots without vegetation cover are included in this model).

	2004			2005			2006[c]		
Variable	Day 1	Day 2	Day 9	Day 1	Day 2	Day 9	Day 1	Day 2	Day 9
Treatment[a]	**125.414*****	**196.266*** **	**162.964*** **	**27.238*** **	0.011	0.412	0.003	0.059	0.983
Tree species	**75.620*** **	**142.150*** **	**209.120*** **	0.345	0.013	0.530	0.003	0.148	1.295
Macro-habitat[b]	**7.093* **	**14.579** **	**33.935*** **	**12.651** **	0.021	0.409	0.005	0.227	0.840

parameters that were significant at $p \leq 0.05$ are in bold, p-values are represented as follows: $*p \leq 0.05/**p \leq 0.01/***p \leq 0.001$.
[a]day 2 and 9: treatment without bird-dishes.
[b]old-growth forest (small and large) and managed forest.
[c]in 2006, no seeds of European beech were exposed.

again led to a higher survival of tree seeds. Summing up, our experiments demonstrated that the three predator guilds tested have a distinctly different impact on seed survival on the experimental dishes (with the most important effect of small mammals). This shows that assertions on correlations between predator guilds and seed losses in forest ecosystems need to take species or at least guild specific population dynamics into account (see also Choquenot and Ruscoe 2000, Nystrand and Granström 2000). Furthermore, as shown by Hulme (1996), seed exploitation by small mammals depends on the probability of encounter. Again, it has to be mentioned that removal of seeds does not necessarily imply that these seeds have been killed but seeds could have been cached (Jansen et al. 2004, Vander Wall et al. 2005). In a survey of germinants along three 1 m wide and strip transects with a total length of 960 m in 2004, only a total of two beech germinants, one fir germinant and five spruce germinants were found (Kutter 2007). This indicates that caching, even if it occurred in the studied sites, did not lead to seedling establishment.

At micro-sites not frequently explored by rodents other seed predators than small mammals gain more importance. This is also congruent with our observations at intact bird dishes, where seeds were removed within one day to a notable degree, e.g. to approximately 60% in the large old-growth forest in 2004 (Castro et al. 1999). However, seed survival rates on the bird dishes varied to a large extent between areas, years, and tree species. This variable predation pattern might be caused by a higher mobility and a larger foraging range of these seed predators.

Apart from the potential seed predators addressed in the cafeteria-experiment, other predator guilds may contribute to seed losses in the study areas. For example, faeces of the brown bear *Ursus arctos arctos* with plenty seed coats of beech were found in the study area in 2004. It is also known that roe deer *Capreolus capreolus* and red deer *Cervus elaphus* feed on seeds of many forest trees (Baskin and Danell 2003). Within northern temperate old-growth forests, abundances of ruminating ungulates are frequently rather low compared to managed forests as both food supply and habitat attractiveness are poorer. Thus, consumption rates of seeds of ungulates will seldom reach those of small mammals (particularly during gradation years). As this might not be true for the consumption of tree seedlings, we also conducted a study on early browsing in the study area (Nopp-Mayr et al. unpubl.).

In several negative binomial regression models, the variable 'tree species' had a significant influence on seed survival. Particularly in 2004, all type a-models and type b-models included this variable. Thereby, fir always gained positive regression coefficients, indicating higher survival of these tree seeds on the dishes. Higher survival rates in a year with high rodent predation pressure clearly indicates a lower preference of fir seeds by this predator group compared to spruce and beech (Schreiner et al. 2000, Jedrzejewska and Jedrzejewska 1998), and a lower probability of being predated even after masting of beech. Thus, other factors but not synchrony of masting between fir and beech and predation by small mammals might be a major determinant in regeneration ecology of fir in the study area. Contrary, spruce seeds experienced a lower level of survival in 2006 when no beech seeds were available (both in nature and in the experiment) compared to 2005, although small mammal populations did not change significantly between these two years. As demonstrated by Holt and Kotler (1987) or Kitzberger et al. (2007), predators may only feed on given prey when the density of preferred prey does not reach specific thresholds (i.e. apparent mutualism between alternative prey induced by predator selectivity). Our study indicates a preference ranking of tree seeds by small mammals in this study which might results from different seed size and palatability: beech > spruce > fir.

Table 5. Model b: Wald's χ^2 test values of the factors treatment, tree species, macro-habitat and micro-habitat (i.e. vegetation cover) in a negative binomial regression model for seed survival for all three study years.

	2004			2005			2006[c]		
Variable	Day 1	Day 2	Day 9	Day 1	Day 2	Day 9	Day 1	Day 2	Day 9
Treatment[a]	**227.696*** **	**388.901*** **	**257.450*** **	**129.116*** **	0.093	**6.073* **	0.310	0.560	**18.273*** **
Tree species	**154.147*** **	**302.105*** **	**280.359*** **	5.675	0.123	4.508	0.262	1.087	**29.662*** **
Macro-habitat[b]	1.632	1.212	**11.720** **	0.458	0.056	0.096	0.396	1.249	1.561
Vegetation cover	0.003	0.000	1.726	1.942	0.011	0.336	0.230	0.177	**7.396** **

parameters that were significant at $p \leq 0.05$ are in bold, p-values are represented as follows: $*p \leq 0.05/**p \leq 0.01/***p \leq 0.001$.
[a]day 2 and 9: treatment without bird-dishes.
[b]only old-growth forest (small and large).
[c]in 2006, no seeds of European beech were exposed.

Table 6. Model a. Regression coefficients of negative binomial regression models for the years 2004, 2005 and 2006 with seed survival on day 9 after exposure as dependent variable and treatment, tree species and macro-habitat as independent variables (only open subplots without vegetation cover are included in these models).

		Regression coefficient		
Variable		2004	2005	2006
Access for	small mammals, invertebrates	-0.453	0.087	-0.163
	invertebrates	**3.150*****	0.232	0.235
	open access	0[a]	0[a]	0[a]
Tree species	spruce	**0.740***	0.249	-0.388
	fir	**4.191*****	0.257	0[a]
	beech	0[a]	0[a]	---[b]
Macro-habitat	small old-growth forest	**-1.829*****	-0.107	-0.372
	large old-growth forest	-0.342	-0.231	-0.165
	managed forest	0[a]	0[a]	0[a]

parameters that were significant at p ≤ 0.05 are in bold, p-values are represented as follows:
*p ≤ 0.05/**p ≤ 0.01/***p ≤ 0.001.
[a] 0 because parameter is redundant.
[b] in 2006, no seeds of European beech were exposed.

For fir, we noted a significant relationship between trapping rates and seed survival. The higher the number of caught specimens, the lower was the recorded seed survival. For spruce seeds, we only observed a significant negative correlation in the small old-growth forest, but not in the large old-growth forest.

Temporal aspects of seed removal

The small mammal abundances showed a peak in 2004, the year with high abundance of seeds (note that seeds were dispersed in autumn 2003 and spring 2004) and a pronounced crash in the following year (Jędrzejewska and Jędrzejewska 1998, Wittmer et al. 2007). This indicates that tree seeds are a critical source of nutrition for small mammals in the studied old growth mountain forests. Based on this, we expected significant changes in the exploitation rate of seeds. Indeed, seed survival rates differed significantly in the consecutive years after masting of beech. In all but one cases, seed survival on experimental dishes was significantly lower during times of high seed abundance (autumn 2003 and spring 2004), when the population peak of small mammals was recorded and higher, when small mammal populations crashed. The observed low level of seed survival was not only a local phenomenon, but could also be observed in the Limestone Alps National Park, Upper Austria, where an analogous study was conducted (Nopp-Mayr unpubl.). There again, spruce and beech seeds were exploited to about 90% and 100% in September 2004 within nine days after exposure, respectively. In the Carpathians, a similar lack of tree regeneration from the mast year 2003 was observed (Szwagrzyk unpubl.).

These results are in contradiction with the satiation hypothesis which postulates higher survival rates of seeds in and directly after mast years caused by a delayed response of the frugivor population densities to a sudden increase in resources (Kelly and Sullivan 1997, Kon et al. 2005). Given that seeds are a critical resource for the seed predators in our study area, we interpret this as a result of the ability of small mammals to respond quickly to the increased resource availability in autumn of the mast year 2003 and 2004. Small mammals are able to reproduce into late autumn and already reproduce under the thick and long lasting snow cover in late spring (snow melt in the study area usually occurs in late May, Gratzer unpubl.) (Niethammer and Krapp 1978, 1982). Their population size is thus already large in early summer of the years subsequent to the masting and creates the observed strong pressure on the seed resources. For spruce, we recorded significantly lower survival rates in the last year of investigation, where only fir and spruce seeds were exposed on the dishes (see above) and where beech seeds were not available. The observed higher seed survival after sporadic masting in intermast periods indicates that, given that pollination efficiency is high enough, such events may play a more important role for regeneration than previously assumed. Taking the ratio of full beechnuts as a proxy for successful pollination (Nilsson and Wästljung 1987, Schmidt 2006), data from the study area show that beech pollination efficiency was 43–67% in years of sporadic masting (Gratzer unpubl.).

Table 7. Model b. Regression coefficients of negative binomial regression models for the years 2004, 2005 and 2006 with seed survival on day 9 after exposure as dependent variable and treatment, tree species, macro-habitat and vegetation cover as independent variables (the managed forest is excluded in these models).

		Regression coefficient		
Variable		2004	2005	2006
Access for	small mammals, invertebrates	-0.136	0.388	-0.103
	invertebrates	**3.710*****	**0.810***	**1.209*****
	open access	0[a]	0[a]	0[a]
Tree species	spruce	**0.669***	0.524	**-1.580*****
	fir	**4.273*****	**0.680***	0[a]
	beech	0[a]	0[a]	---[b]
Macro-habitat	small old-growth forest	**-0,785****	0.085	-0.359
	large old-growth forest	0[a]	0[a]	0[a]
Vegetation cover	no	-0.300	0.162	**0.776****
	yes	0[a]	0[a]	0[a]

parameters that were significant at p ≤ 0.05 are in bold, p-values are represented as follows:
*p ≤ 0.05/**p ≤ 0.01/*** p ≤ 0.001.
[a] 0 because parameter is redundant.
[b] in 2006, no seeds of European beech were exposed.

Spatial aspects of seed removal

Within the two parts of the old-growth forest, higher densities of forest regeneration occur in the small old-growth forest compared to the large old-growth forest (Kempter 2006). As demonstrated by several authors (Alcántara et al. 2000, Schreiner et al. 2000, Kollman and Buschor 2002) small mammals are assumed to prefer richly structured forests with a dense cover of ground vegetation (avoidance of predators) resulting in higher rates of seed predation or seed hoarding there. Within the negative binomial regression models, we only found significant positive effects of open micro-sites on seed survival on the experimental dishes in 2006 for day 9 after exposure. Apparently, the high population pressure and the resulting bottleneck in food supply in the peak year of the small mammal populations forced rodents to feed also on micro-sites, which would be avoided in years of low to moderate abundances.

Our experiments revealed highly variable patterns of tree seed survival on the experimental dishes regarding the habitat situation. In 2004, seeds disappeared to a significantly differing extent between the three study areas. We found differences not only between old-growth forest areas and managed forest areas (type a-models), but also between the small and the large old-growth forest (type b-models). Within these models, exposure of seeds in the small old-growth forest led to significant lower survival rates. The macro habitat effect can thus be assumed to reflect differences in microhabitat at coarser scales where no neighbourhood of dense patches is available. In the years after the post-masting year, the macro-habitat had no significant effect on seed survival rates on the dishes.

Conclusion

Successful germination is but one of a number of critical processes in the early life phases of trees and transition probabilities into later life phases are influenced by a number of biotic and abiotic factors (Gratzer et al. 2004). The results presented in this study contribute to an understanding of the causes of an almost complete failure of a mast year in terms of tree establishment (Gratzer unpubl., Kutter 2007). We suggest that the satiation hypothesis which explains the evolution of masting does not explain the temporal dynamics of seed predation in our study areas for all masting events (Nilson 2000). Contrary, from the higher survival rates of seeds on experimental dishes in intermast periods, we conclude that sporadic masting may play a more important role for tree population dynamics than previously thought, provided that pollination efficiency is not too low for successful pollination. Tree species differences in susceptibility for seed predation were strong. Although seeds of silver fir are larger than those of spruce, their high content of tannins prevents them from being exploited to a large extent in situ (cf. Wang and Chen 2008). In the study area, both in the year after masting and during the following intermasting period, beech and spruce seeds were removed rapidly and substantially. There is also a substitution effect of seed predation which is indicated by the increased spruce seed predation in a year without beech seeds.

This indicates that establishment patterns of trees might be altered distinctly by changing timing and synchrony of masting of different tree species and by the capacity of certain seed predators to respond on changing resource supply. Considering the results of Litschauer and Konrad (2006), who recorded shortened time periods between full masting of beech, enhanced predation pressure on tree seeds as well as changed competition between tree species might be expected in the future.

Seed removal experiments were frequently conducted in the past in the northern hemisphere (Alcántara et al. 2000, Nystrand and Granström 2000, Schreiner et al. 2000), but they mainly took place in managed forests. The comparisons of seed predation in managed forests and in old-growth forests suggests that seed removal patterns and their attribution to certain seed predator guilds are less complex in managed forests which allow for an easier interpretation of causal relations.

Within the old-growth forests, temporal and spatial effects are more complex and interpretation of results has to be more cautious. Considering this fact and potential changes of tree masting due to climate change, future research demands in old-growth forests become obvious. Thereby, methodical improvements of cafeteria experiments as well as research on seed fate after removal will be necessary (Forget and Wenny 2005) as seed removal from experimental dishes should not be equalled with seed mortality (Sone et al. 2002). By combining seed fate experiments (Gómez et al. 2008), studies on seed caching and directed caching including the role of different microsites with experiments on seedling browsing, knowledge on regeneration dynamics in old-growth forests might be improved.

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