The effect of the dominant grass Festuca rupicola on the establishment of rare forbs in semi-dry grasslands

Article *in* Folia Geobotanica · September 2017

DOI: 10.1007/s12224-017-9298-8

Folia Geobot
DOI 10.1007/s12224-017-9298-8

The effect of the dominant grass *Festuca rupicola* on the establishment of rare forbs in semi-dry grasslands

Monika Partzsch · Maria Faulhaber · Tim Meier

Received: 22 February 2016 / Accepted: 12 June 2017

Abstract Establishment is the most sensitive process in the life-cycle of plant species, and each stage – from germination to survival and growth – can be affected by environmental factors and plant traits. We hypothesized that the dominant tussock grass *Festuca rupicola* negatively affects forb establishment in semi-dry grasslands where it has recently expanded into. Moreover, we expected that seedling recruitment is affected by grass density and seed size, with larger seeded forbs being more successful in areas of higher grass density. In a garden experiment, we sowed seven forb individuals of differing seed size (smallest to largest: *Veronica spicata* < *Dianthus carthusianorum* < *Plantago media* < *Biscutella laevigata* < *Filipendula vulgaris* < *Scabiosa ochroleuca* < *Sanguisorba minor*) into pots with zero, one, two and three grass individuals, and assessed germination, survival and growth over one year. As expected, increasing grass density negatively affected germination, survival and growth of forbs; however, contrary to our expectation, seed size did not influence any of parameters measured. The response of each individual species varied from zero or weak to strong with respect to grass density. *Festuca rupicola* therefore acts as a strong competitor against the establishment of forbs, irrespective of their seed size, and its spread lowers species diversity in semi-dry grasslands.

Keywords Garden experiment · Seed size · Seedling recruitment · Species competition · Species dynamics

Electronic supplementary material The online version of this article (doi:10.1007/s12224-017-9298-8) contains supplementary material, which is available to authorized users.

M. Partzsch (✉) · M. Faulhaber · T. Meier
Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchtor 1, D-06118 Halle (Saale), Germany
e-mail: monika.partzsch@botanik.uni-halle.de

Introduction

The establishment stage of plants is known to be a very sensitive and important 'bottleneck' in a species' life-cycle (Jongejans et al. 2006; Jorritsma-Wienk et al. 2006), which includes germination and survival of seedlings and juveniles (Gross 1984; Tessier et al. 2000). A species is regarded as having become successfully established when it successfully passes through ontogenetic development and becomes capable of reproduction (Mahn 1996; Kowarik 2003). Successful establishment is limited by both biotic and abiotic conditions and their interactions, which vary greatly in space and time together with environmental conditions (Münzbergová 2004). In addition to prevailing environmental factors, the process of establishment can be affected by particular plant traits.

In the competitive hierarchy of semi-dry grasslands, monocotyledonous species such as grasses are stronger competitors than forbs (Del-Val and Crawley 2005). The general change in traditional land-use patterns in Europe involving nitrogen (N) deposition and the abandonment of grazing over the last few decades has enhanced the competitive capacity of grass species. The expansion of different grass species, such as *Arrhenatherum elatius* (Dostálek and Frantík 2012), *Bromus erectus* (Bornkamm 2006),

Published online: 09 September 2017

Festuca rupicola (Partzsch 2000) or *Stipa lessingiana* (Enyedi et al. 2008), has led to the transformation of formerly species-rich dry and semi-dry grasslands into species-poor grasslands across the continent (Habel et al. 2013).

Seed germination and seedling survival can be strongly inhibited by environmental factors such as living biomass and litter concentration (Jutila and Grace 2002; Donath and Eckstein 2010; Miglécz et al. 2013), both of which increase with productivity across grasslands (Galvánek and Lepš 2012). Regeneration niches are necessary for some species, not only for germination, but also to improve growth potential and allow for the establishment of self-perpetuating, viable populations (Vítová and Lepš 2011). Certain types of disturbance, such as traditional land use by mowing and grazing or small mammal activity, can create gaps for regeneration, which can increase the rate of seedling recruitment (Watt and Gibson 1988; Bullock et al. 1994, Kladivová and Münzbergová 2016) or alter competitive interactions between plants (Goldberg and Werner 1983; Partzsch 2011). However, regeneration in more productive grasslands is more gap-dependent than it is in less productive grasslands (Zobel et al. 2000), where gaps are of minor importance and physical hazards and pathogens control seedling recruitment to a greater extent than competition by neighbouring plants (Ryser 1993). In comparing seedling survival across different grassland types (i.e. dry, mesic and wet), Eckstein (2005) found facilitative effects of vegetation cover in dry grasslands. While the two steps of establishment are rarely separated, they can be affected differently by environmental conditions (Jorritsma-Wienk et al. 2006). Conditions suitable for germination or recruitment can be unsuitable for seedling survival and growth (Schupp 1995; Fenner and Thompson 2005). For example, while vegetation cover can protect seed germination and seedling recruitment against climatic extremes (Knappová et al. 2013), the long-term survival and growth of juveniles and adults can be hampered by competition from the resident vegetation (Howard and Goldberg 2001).

Plant traits such as seed size, dormancy, germination percentage, dispersal, growth form, life form and life span are central components of a plant's life-history (Harper 1977; Fenner and Thompson 2005), and their importance to the fitness of the species is widely accepted (Grubb 1977; Higgins and Richardson 1999). Positive correlations between seed size and germination have been revealed in various studies and differentiated with regard to relationships between individuals of a single species (Vera 1997; Weis 1982), between plant families (Poaceae, Wu and Du 2007; Brassicaeae, Miglécz et al. 2013) and between a broad range of different various grassland species (Silvertown 1981; Jakobsson and Eriksson 2000). However, there are also a number of reports that reveal no correlation between germination and seed size (Eriksson 1999), and one that reveals a negative correlation (Counts and Lee 1991).

In general, seedling recruitment is enhanced by disturbance, with the greatest effect being reported for small-seeded species (Eriksson and Eriksson 1997) while relative recruitment in undisturbed swards can increase with increased seed size (Jakobsson and Eriksson 2000). Some studies associate small-seeded species germination with higher light demand and report them to be more sensitive to increasing vegetation density (Milberg et al. 2000; Jensen and Gutekunst 2003; Koutsovoulou et al. 2013). Large-seeded species are more likely to show increased seedling establishment than small-seeded species because their seedlings tend to have better survival potential and show lower mortality (Moles and Westoby 2002). They also provide more reserves for growth, support etiolation in shaded conditions and help overcome unfavourable climate conditions (Grime and Jeffrey 1965; Gross 1984; Leishman and Westoby 1994), but they need longer germination time (Eriksson and Eriksson 1997) and are often dormant (Fenner and Thompson 2005). In addition, large-seeded species perform better under particularly adverse conditions (such as shade, drought or herbivory) and can show higher survival rates through early seedling establishment than smaller-seeded species (Moles and Westoby 2004). Larger seeds enable quick initial growth, which is an important characteristic for establishment within closed turf (Grime and Jeffrey 1965; Gross 1984).

In formerly species-rich, dry and semi-dry grassland communities with low productivity in central Germany, biodiversity has declined, and particularly over the last 25 years. Following political changes in 1990 and the subsequent abandonment of grazing dominated land-use practices, interactions between species changed dramatically. This trend led to the proliferation of more species-poor stands dominated by the grass *Festuca rupicola* and a decline in the abundance of several forbs (Partzsch 2000), while the lack of grazing and trampling by sheep strongly reduced biomass removal and the potential for regeneration gaps (Smith and Rushton 1994).

For the present study, we simulated different levels of vegetation openness, by incorporating differing densities of *F. rupicola*, and assessed effects on seed germination, seedling survival and growth characteristics in seven typical yet rare xerothermic grassland forbs differing in seed mass (hereafter referred to seed size). In preliminary germination experiments, we found that the perennial species *Biscutella laevigata*, *Dianthus carthusianorum*, *Filipendula vulgaris*, *Plantago media*, *Sanguisorba minor*, *Scabiosa ochroleuca* and *Veronica spicata* developed non-dormant seeds, the smallest and lightest of which originated from *V. spicata* and the largest and heaviest from *S. minor*. Accordingly, the selected species create a seed size gradient for perennial forbs of xerothermic plant communities from central Germany. We tested the following hypotheses: (i) Germination and survival of the forbs are negatively affected by increasing density of the expanding grass *F. rupicola*; and (ii) Larger seeded species are more successful in germination, survival and growth than smaller seeded species.

Material and methods

Study species and collection

For our study, we selected perennial hemicryptophytes from different plant families typical of semi-dry grassland communities (Festuco-Brometea Class according to Zurich-Montpellier system; Ellenberg and Leuschner 2010) of central Germany (Table S1). Species were selected that showed a germination capacity exceeding 70% in a pilot trial (six weeks in climate chambers at 20°C / day and 10°C / night). Diaspores (dispersal units such as fruits and seeds; hereafter seeds) of selected species spanned three orders of magnitude: *V. spicata* (0.08 mg), *D. carthusianorum* (0.42 mg), *P. media* (0.61 mg), *B. laevigata* (0.92 mg), *F. vulgaris* (1.25 mg), *S. ochroleuca* (1.75 mg) and *S. minor* (8.72 mg). The species are distributed mainly across submeridional to southern temperate Europe (Jäger 2011). The forbs generally occur at low abundance, and none of the species attains values more than 1% of total vegetation cover (Partzsch 2000) in their respective grassland communities. *Dianthus carthusianorum*, *B. laevigata* and *V. spicata* are protected by law (and the latter two are listed as *endangered* on the Red List of Saxony-Anhalt (Frank et al. 2004). By contrast, the perennial tussock grass *Festuca rupicola* is highly frequent and its abundance has increased from approximately 25% to more than 90% of vegetation cover in the last few decades (Partzsch 2000).

Mature seeds of all species, including *F. rupicola*, were collected from semi-dry grasslands in the surroundings of Halle/Saale (51°48′ N, 11°97′ E) in summer 2009, 2011 and 2012. The seeds were pooled from 10 to 15 individuals from five to eight populations of each species. Seeds were dry-stored until the following summer when the garden experiment was established. The climate of the dry region of central Germany is characterized by a mean annual temperature of 9.2°C and a mean annual precipitation of 473 mm (Döring and Borg 2008).

Garden experiment

The experiments were conducted in different years in order to avoid any singular effects of extreme weather conditions on germination, survival or growth. At the beginning of February 2010, 2012 and 2013, seeds of *F. rupicola* were sown into small plastic pots in a compost-sand mixture (2:3, pH 7.0) and cultivated in an unheated greenhouse. In May, the young plants were transferred to larger pots (diameter: 22 cm; height: 19 cm), filled with the same compost-sand mixture and placed outdoors at the Halle Botanical Garden. Four different treatments were used: (1) without any *F. rupicola* individuals (F0); (2) with one *F. rupicola* individual (F1); (3) with two *F. rupicola* individuals (F2), and (4) with three *F. rupicola* individuals (F3). The pots were watered as required and weeds were removed on emergence. Before the start of the experiment, the *F. rupicola* individuals were grown into well developed tussocks (diameter: 17–21 cm), but no litter layer developed during the period. In August, 20 seeds per pot of the forbs (2010: *D. carthusianorum*, *S. ochroleuca*; 2012: *B. laevigata;* 2013: *F. vulgaris*, *P. media*, *S. minor*, *V. spicata*) were separately sown into the pots with different densities of *F. rupicola* (six replications per treatment and species; 168 pots in total).

We assessed germination (% of germinated seedlings per sown seeds), length of survival and survival (% of seedlings which survive until end of the experiment). Monitoring of the developing seedlings was performed every one to two weeks. Each seedling was marked and plant height was measured along with leaf number and flower number and number of flower heads or flowering stems (growth characteristics). Pots were placed randomly and their positions were changed every two weeks. The final measurements in each year were taken at the end of October and the first measurements in the following year were taken in April. The separate experiments were ceased in August 2011, 2013 and 2014 (after ca 12 months), at which point all aboveground biomass was harvested, dried at 80°C for eight hours and weighed. During the growth period, *F. rupicola* developed dense, compact tussocks, with pot yields varying across the years: One individual yielded 19.82 ± 3.01 g, two yielded 23.84 ± 4.72 g, and three yielded 28.66 ± 5.34 g. Total *F. rupicola* yield significantly increased between treatments F1, F2 and F3 (ANOVA: $F = 11.686$, $P < 0.001$) and reflected vegetation density.

Data analysis

The values of germination and survival percentages were arcsin-transformed to meet ANOVA assumptions. Visual inspection of the raw data, a non-significant Kolmogorov-Smirnov-test and a Bartlett's test confirmed that there were no serious deviations from the ANOVA assumptions. We conducted analysis with 3,360 seeds that were sown initially (20 seeds per forb × 7 forbs × 4 grass densities × 6 replications). We used the mean of the measured parameters per pot. Statistical analyses were performed using SPSS 21.0 (2015).

In order to test the general patterns between forb germination and survival and grass density we assessed mixed-effect models with germination and survival percentages set as dependent variables and density of the dominant grass set as a fixed factor. Forb species and experiment year were set as random variables, with species being nested within year. One-way ANOVAs were calculated to determine differences in germination and survival for the individual species separately between the four grass densities (F0, F1, F2, F3). The relationships between germination and survival with seed size were determined using the Pearson correlation coefficient and tested for significance.

The survival of the seven forbs in relation to the grass densities over the whole period of the experiment (350 to 370 days) was calculated using survival analyses in accordance with Kaplan-Meier, with the resulting values indicating the proportion of survived vs dead seedlings for the duration of the experiment. Significant differences between the surviving individuals depending on grass density were estimated using a log-rank test following Cox-Mantel and using χ^2 values.

The values of the growth characteristics for the surviving individuals were compared with parametric one-way ANOVAs and Tukey's post hoc tests ($P < 0.05$) using treatment as a fixed factor for examining the differences between F0, F1, F2 and F3 on the dependent variables of above-ground biomass, plant height and number of leaves. The relationship between above-ground biomass of the adults and the seed size were determined using the Pearson correlation coefficient and tested for significance.

Results

Germination

Germination of the seven semi-dry grassland forbs was dependent on grass density and it significantly decreased with increasing number of grass individuals in the pots ($F = 5.959$, $P < 0.001$; Fig. 1a). The relationship was not affected by year of experiment (i.e. the random factor of species nested within year, $P = 0.091$); however, individual forbs differed in germination percentages, with the highest proportion of germinated seeds being recorded for *D. carthusianorum* and the lowest for *P. media* (Fig. 2). When analysing individual species separately, no difference in germination in relation to grass density was found, except for *P. media*, which germinated significantly better in the pots without grass. There was no correlation between germination percentage and seed size ($R = -0.033$, $P = 0.869$).

Survival

Survival differed between the seven forbs, with most seedlings dying in the first 50 to 60 days after germination (Fig. 3). Nearly all of the surviving seedlings of *V. spicata*, *D. carthusianorum*, *F. vulgaris* and *S. minor* persisted until the following summer, while those of *B. laevigata* and *S. ochroleuca* showed strong reductions in seedling numbers after winter. The emerged seedlings of *P. media* survived less than 50 days in pots with grass individuals, but all seedlings in the pots without grass survived until the end of the experiment.

At the end of the experiment, the survival of forb seedlings depended on grass density and significantly

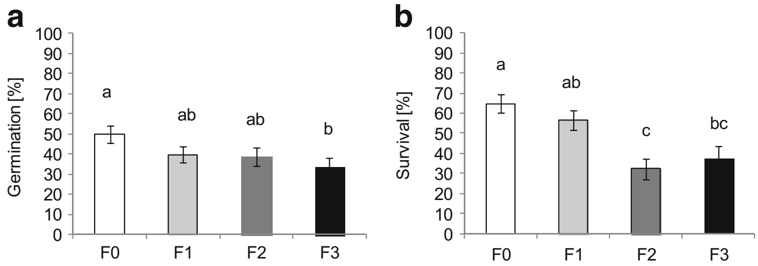

Fig. 1 Percentages of germination (**a**) and survival (**b**) of seven semi-dry grassland forb species in four treatments with differing densities of the grass *Festuca rupicola* (means + *SE*; F0 – no grass individuals, F1 – one grass individual, F2 – two grass individuals, F3 – three grass individuals)

decreased with increasing number of grass individuals in the pots ($F = 9.004$, $P < 0.0001$; Fig. 1b). Survival was not affected by year in which the experiment was performed (the random factor of species nested within year, $P = 0.227$).

When analysing individual species separately, we can see that seedling survival in *V. spicata* and *D. carthusianorum* did not differ significantly between grass densities (Fig. S1), while other species showed significant differences in seedling survival between the four grass densities. In *P. media*, all seedlings died quickly in the pots with grass but survived in the pots without grass. Similarly, survival was higher in the pots without grass than in pots with grass for *B. laevigata*, *F. vulgaris* and *S. minor*. However, *S. ochroleuca* showed lowest survival in F0, which significantly increased with increasing grass density. There was no correlation between survival percentage and seed size among the seven forbs ($R = 0.178$, $P = 0.365$).

Growth characteristics

Growth characteristics of the seven forbs were very similar in the treatments with differing grass densities. The surviving individuals attained much higher above-ground biomass, plant height and number of leaves in

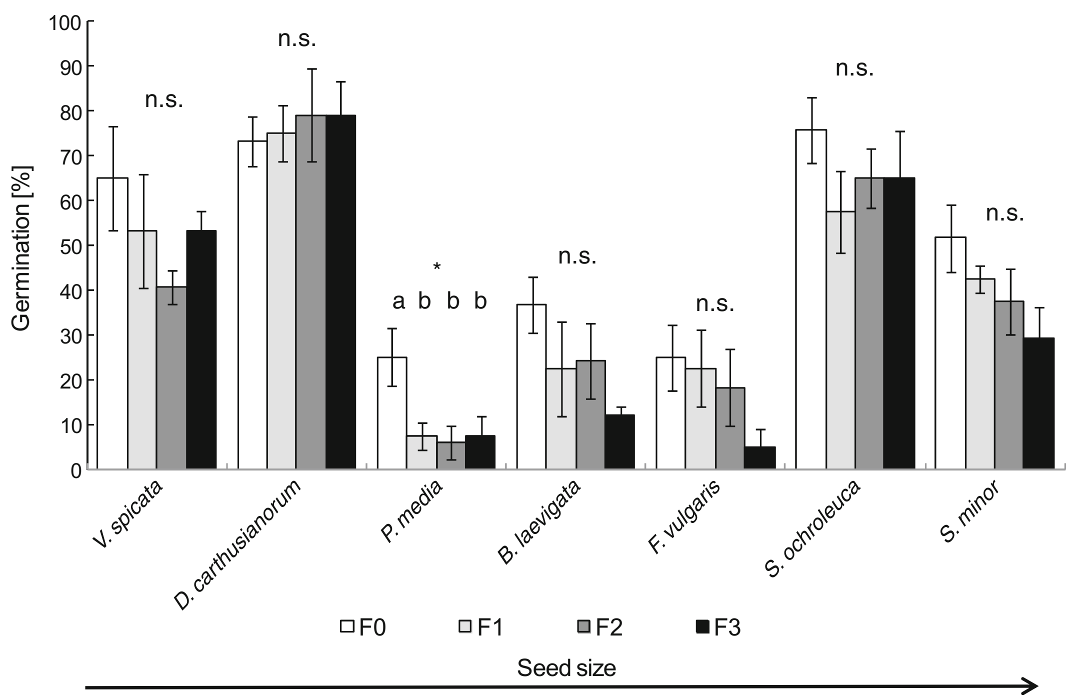

Fig. 2 Germination percentages of individual semi-dry grassland forb species in four treatments with differing densities of the grass *Festuca rupicola* (means + *SE*; F0 – no grass individuals, F1 – one grass individual, F2 – two grass individuals, F3 – three grass individuals)

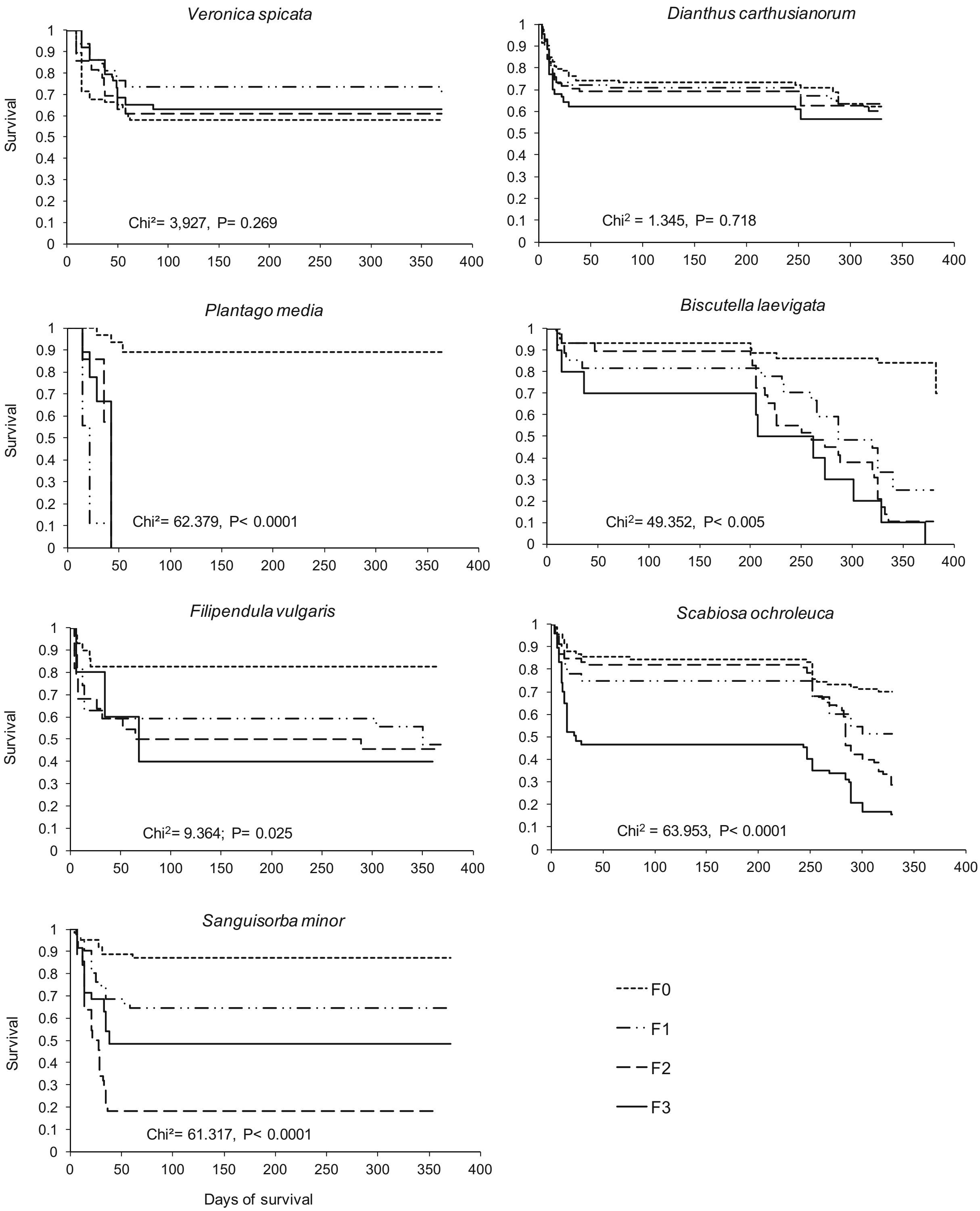

Fig. 3 Survival of seven forb species in four treatments with differing densities of the grass *Festuca rupicola* (F0 – no grass individuals, F1 – one grass individual, F2 – two grass individuals, F3 – three grass individuals) over the duration of the experiment

pots without grass than in the pots with grass (Table 1, Table S2). All forbs produced reproductive organs such as flowers (*D. carthusianorum*), flower heads (*S. minor* and *S. ochroleuca*) or flowering stems (*B. laevigata*, *F. vulgaris*, *P. media* and *V. spicata*), but only in the treatment without grass. In all the treatments with grass, above-ground biomass was negligible, as the forbs remained at the seedling stage, even beyond the 350 to 370 day period of the experiment. A significant positive correlation was recorded between the above-ground biomass of the adult individuals (those surviving in treatment without grass) and seed size across all species ($R = 0.630$, $P < 0.0001$).

Discussion

We found significant suppression of the first stage of establishment in all forbs. Germination was reduced by about 15% with increased grass density (from F0 to F3), but the individual species were affected differently: Germination was reduced in *P. media*, but not in the other six species. In general, established vegetation is characterized as a cryptic form of competition (Grace 1999), whereby living biomass and litter strongly inhibit germination and seedling survival (Jutila and Grace 2002; Donath and Eckstein 2010; Miglécz et al. 2013). In our study, the resident vegetation exerted competitive effects on germination and recruitment in all species. However, neighbouring plants can often *facilitate* seedling recruitment and growth by serving as *nurse plants* (Franco and Nobel 1988; Eckstein 2005), i.e. by improving environmental conditions such as enhancing air humidity, preventing extreme temperature fluctuations, improving soil properties or reducing mechanical or herbivorous damage (Holmgren et al. 1997; Brooker et al. 2008). Knappová et al. (2013) found a facilitative effect of resident vegetation on germination in semi-dry grassland species during an unusually dry spring, whereas in a more typical spring with average precipitation, the competitive effects of the same species prevailed. A positive effect of May and July precipitation on seedling survival has also been recorded (Bakker et al. 2003; Dickson and Foster 2011), suggesting that recruitment reacts differently to varying light levels in dry and wet years. It is therefore likely that the effect of resident vegetation on germination and seedling recruitment is related to moisture and light (Eckstein 2005; Knappová et al. 2013). In accordance, light favouring erect plant structures in a salt marsh dominated by *Juncus gerardii* and *Triglochin maritimum* facilitated recruitment in the natural vegetation (Ludewig et al. 2015). In our study, it seems that *S. ochroleuca* survival, but not germination, was facilitated in pots with two or three grass individuals. However, in our experiment, the species only developed a negligible amount of litter, and it consequently cannot be considered as an important factor controlling germination in our species.

Disturbance of the vegetation cover, mostly in connection with land use, can have positive effects on species germination and recruitment (Kladivová and Münzbergová 2016). In our experiment, we simulated the abandonment of grazing under varying densities of the grass *F. rupicola* and found that the second stage of establishment, which includes survival and growth of seedlings and juveniles (Jorritsma-Wienk et al. 2006), strongly declined with increasing grass density. Most of the forb individuals died within the first 50 days after germination in the warm and hot periods of the year. In *V. spicata*, *D. carthusianorum*, *F. vulgaris* and *S. minor*, nearly all seedlings survived the winter period and were likely to have survived into the following year. However, *B. laevigata* und *S. ochroleuca* showed strongly reduced seedling numbers the following year. We found that the survival of all species decreased by nearly a half between the plots without grass (survival 65%) and those with increasing grass densities (survival 32%). A number of similar studies have shown high levels of seedling mortality, with some reaching 100% (Vítová and Lepš 2011; Knappová et al. 2013; Kladivová and Münzbergová 2016), as was found in our study for *P. media* and *B. laevigata*. Jakobsson and Eriksson (2000) reported that only 16 of 45 semi-dry grassland species showed significantly better recruitment in disturbed places, but for the species *F. vulgaris* and *P. media*, which were also tested in our study, they did not find significantly better recruitment between disturbed and undisturbed swards. Similar results were recorded in an oligotrophic wet meadow, where recruitment decreased between treatments with gaps to mown and undisturbed plots (Kotorová and Lepš 1999). According to our results, there were considerable differences in seedling recruitment sensitivity between the tested species.

Interestingly, in our study, the surviving forbs only developed into adult flowering individuals in the pots without grass, and they became fully established the following year. This suggests that between forb

Table 1 ANOVAs of growth parameters (above-ground biomass, plant height and number of leaves per individual) of subsisting individuals of seven forb species at the end of the experiment. Species are ordered by increasing seed size.

		Biomass		Plant height		Number of leaves	
Species	*D.f.*	*F*	*P*	*F*	*P*	*F*	*P*
Veronica spicata	3	1,125.749	< 0.0001	13.179	< 0.0001	12.041	< 0.001
Dianthus carthusianorum	3	26.732	< 0.0001	40.893	< 0.0001	75.069	< 0.0001
Plantago media	–	–	–	–	–	–	–
Biscutella laevigata	3	5.091	< 0.05	24.17	< 0.0001	21.892	< 0.0001
Filipendula vulgaris	3	313.885	< 0.0001	276.08	< 0.0001	27.735	< 0.0001
Scabiosa ochroleuca	3	174.904	< 0.0001	250.303	< 0.0001	87.472	< 0.0001
Sanguisorba minor	3	894.301	< 0.0001	121.88	< 0.0001	25.086	< 0.0001

individuals (with the exception of *S. ochroleuca*), there is little or no intraspecific competition, and the release from interspecific competition by the tussock grass promotes growth and accelerated maturity in all seven forbs. Knappová et al. (2013) investigated establishment in disturbed and undisturbed semi-dry grassland vegetation and found that only a half of the 35 sown species flowered in the following two years, while three other species failed to establish. The study also tested three species that were included in our study: *Filipendula vulgaris* showed low levels of germination without flowering in disturbed and undisturbed plots in year one; in the following year, the species neither germinated nor became fully established. *Scabiosa ochroleuca* and *S. minor* were able to reach the flowering stage in both years, but only in the disturbed plots. Elsewhere, Gross (1984) found that the growth of six more ruderal grassland species were significantly lower under vegetation cover compared with non-competitive cover types, such as with litter or bare.

Elsewhere, the chance of plant survival has been shown to increase with seedling size (Villar-Salvador et al. 2012), which can be a good proxy of survival probability into adulthood (Kladivová and Münzbergová 2016). In our study, in the pots with grass, the forb seedlings were very small (between 0.5 and 5 cm) after one year, with a low number of leaves (between 2 and 10) and very low above-ground biomass (between 1.2 and 12.8 mg), which was similar to the effect found by Knappová et al. (2013) for small plant size and individuals in undisturbed plots. Münzbergová (2004) found continuously declining seedling numbers with grass density over three consecutive years, while in our study, forbs grown with grass did not develop into flowering individuals and were expected to die in the following years. In other treatments with grass, the strongly delayed growth of the forbs reflected the strong interspecific competition ability of *F. rupicola* (Partzsch 2011; Partzsch et al. 2011). Increasing grass density also had negative effects on the grass itself, i.e. the resultant total biomass was not proportionate to the number of grass seedlings planted. Overall, the results indicate that *F. rupicola* acts as a strong competitor against adolescent forb species. However, Ryser (1993) found that in a seedling establishment experiment on limestone grassland (Mesobrometum), the survival of *Arabis hirsuta* and *Primula veris* in microsites with vegetation was significantly higher than in sites without vegetation, while *Plantago lanceolata*, *S. minor* and *Medicago lupulina* established well in both sites. The study concluded that physical hazards control seedling establishment to a greater extent than competition by neighbouring plants, which we could not confirm with our results, perhaps due to the higher density of tussocks of *F. rupicola* in our study compared to that of the corresponding grass *Bromus erectus* in the former study.

In addition to environmental factors, establishment is understood to be strongly affected by particular plant traits such as seed size. Both germination and survival of the small-seeded species *V. spicata* and *D. carthusianorum* was not affected by grass density, while different effects were recorded for the other species. The larger-seeded species *B. laevigata*, *F. vulgaris*, *S. ochroleuca* and *S. minor* showed no differences in germination, but their survival declined significantly with increasing grass density. Only *P. media* showed significantly better germination and survival in pots without grass. However, we did not find any significant correlation between seed size and germination or forb survival. This finding does not correspond with the widely described positive relationship between seed size and germination and survival (e.g. Silvertown 1981; Jakobsson and Eriksson 2000; Moles and Westoby 2002; Wu and Du 2007; Miglécz et al. 2013). However, our results correspond with Knappová et al. (2013), who did not find any relationship between germination and seed size in semi-dry grassland species, which suggests that several antagonistic mechanisms neutralize the effects of seed size. Other studies found positive correlations between seed size and seedling recruitment in competition-influenced plots compared to gap plots in wet meadows (Křenová and Lepš 1996; Kotorová and Lepš 1999). This suggests that the effect of seed size on seedling establishment is connected with particular habitat characteristics, and it is more likely that seed size evolves as a life-history trait along with plant size, life span, juvenile survival rate and time to reproduction (Moles and Westoby 2006).

However, we found a significant positive correlation between biomass of the adult individuals and seed size. Larger seeds provide more reserves for growth, support etiolation in shaded conditions and help overcome unfavourable climate conditions (Grime and Jeffrey 1965; Gross 1984; Leishman and Westoby 1994), suggesting that seedling and juvenile growth is promoted by increased nutrient storage in seeds.

Variation in establishment success, especially in the second stage of survival and growth, can be explained by differing morphology among plant species (Xiong et al. 2001). In our study, the growth form of all species (with the exception of *P. media*), was a half-rosette. *Veronica spicata* and *D. carthusianorum* develop smaller half-rosettes and thin, less branching, flowering stems that are able to pass between the grass tussocks. *Biscutella laevigata*, *F. vulgaris*, *S. minor* and *S. ochroleuca* develop more robust, half-rosettes with large unfledged or bipinnate leaves and strongly branched flowering stems that need more space, which results in grass representing a significant obstacle to growth. *Plantago media* develops compact full rosettes with broad leaves, which are likewise more adversely affected by grass. However, depending on their growth morphologies, species need specific spatial niches to facilitate regeneration among the resident vegetation. In accordance with Jensen and Gutekunst (2003), we conclude that success in germination and seedling survival and growth is more a species-specific trait, and that seed size is not generally a good predictor of establishment capacity (Leishman 1999).

Conclusion

We found that the stages of establishment, germination and survival, are sensitive in different ways to vegetation density or particular plant traits. Under field conditions, there are a lot of uncontrolled factors, such as spatial variation in vegetation cover, soil and moisture, neighbour effects, seed predation or fungal infection. While our garden experiment could not fully reflect the complex environmental conditions of the open field, the results provide some insight into the factors affecting germination and survival in seven forbs with differing plant traits when grown among varying densities of grass.

The establishment of forbs is hampered by increased neighbouring vegetation density, whereby survival and growth are much more strongly negatively affected than germination. As such, the successful restoration of species-rich, semi-dry grasslands would be facilitated by the reintroduction of traditional land-use practices such as grazing at low-intensity, as sheep are able to hamper competitiveness through grazing the more dominant grass species (Partzsch 2011; Dostálek and Frantík 2012; Kladivová and Münzbergová 2016). Moreover, through trampling and biomass removal, herbivores create gaps that serve as important regeneration niches for other plant species (Watt and Gibson 1988; Bullock et al. 1994; Nystuen et al. 2014).

Acknowledgements We are very thankful to the editor-in-chief, the associated editor and the two anonymous referees for their helpful comments, all of which helped to make the manuscript more constructive. We also thank Isabell Hensen and Anselm Krumbiegel for their helpful remarks on the first version of our manuscript, and Christine Voigt for her technical help, and Daniel McCluskey for checking our English.

References

Bakker JD, Wilson SD, Christian JM, Li XD, Ambrose LG, Waddington J (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecol Applic* 13:137–153

Bornkamm R (2006) Fifty years vegetation development of a xerothermic calcareous grassland in Central Europe after heavy disturbance. *Flora* 201:249–267

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travies JMJ, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz CL, Saccone P, Schiffers K, Seifan M, Touzard B, Michalet R (2008) Facilitation in plant communities: the past, the present, and the future. *J Ecol* 96:18–34

Bullock JM, Hill CB, Dale MP, Silvertown J (1994) An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *J Appl Ecol* 31:493–507

Counts RL, Lee PF (1991) Germination and early seedling growth in some northern wild rice (*Zizania palustris*) populations differing in seed mass. *Canad J Bot* 69:689–696

Del-Val E, Crawley MJ (2005) What limits herb biomass in grasslands: competition of herbivory? *Oecologia* 142:202–211

Dickson TL, Foster BL (2011) Fertilization decreases plant biodiversity even when light is not limiting. *Ecol Letters* 14:380–388

Donath TW, Eckstein RL (2010) Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. *Pl Ecol* 207:257–268

Döring J, Borg H (2008) Ist das Klima von Halle (Saale) noch "normal"? Betrachtungen anhand der Temperatur- und Niederschlagsreihe von 1851 bis heute. *Hercynia NF* 41:3–21

Dostálek J, Frantík T (2012) The impact of different grazing periods in dry grassland on the expansive grass *Arrhenatherum elatius* L. and on woody species. *Environm Managem* 49:855–861

Eckstein RL (2005) Differential effects of interspecific interactions and water availability on survival, growth and fecundity of three congeneric grassland herbs. *New Phytol* 166:525–536

Ellenberg H, Leuschner C (2010) *Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht.* Ulmer-Verlag, Stuttgart

Enyedi ZK, Ruprecht E, Deák M (2008) Long-term effects of the abandonment of grazing on steppe-like grasslands. *Appl Veg Sci* 11:53–60

Eriksson O (1999) Seed mass variation and its effect on germination and seedling performance in the clonal herb *Convallaria majalis*. *Acta Oecol* 20:61–66

Eriksson A, Eriksson OE (1997) Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. *Nordic J Bot* 17:469-482

Franco AC, Nobel PS (1988) Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida. Ecol* 69: 1731–1740

Frank D, Herdam H, Hilbig W, Jage H, John HG, Kison HU, Korsch H, Stolle J. (2004) Rote Liste der Farn- und Blütenpflanzengesellschaften des Landes Sachsen-Anhalt. *Ber Landesamtes f Umweltschutz Sachsen-Anh* 39:91–110

Fenner M, Thompson K (2005) *The ecology of seeds.* Cambridge University Press, Cambridge

Galvánek D, Lepš J (2012) The effect of management on productivity, litter accumulation and seedling recruitment in a Carpathian mountain grassland. *Pl Ecol* 213:523–533

Goldberg DE, Werner PA (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.) *Oecologia* 60:149–155

Grace JB (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspect Pl Ecol Evol Syst* 2:1–28

Grime JP, Jeffrey DW (1965) Seedling establishment in vertical gradients of sunlight. *J Ecol* 53:621–642

Gross KL (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J Ecol* 72: 369–387

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

Habel JC, Dengler J, Janišová M, Török P, Wellstein C, Wiezik M (2013) European grassland ecosystems: threatened hotspots of biodiversity. *Biodivers & Conservation* 22:2131–2138

Harper JL (1977) *Population biology of plants.* Academic Press, London

Higgins SL, Richardson DM (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *Amer Naturalist* 153:464–475

Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975

Howard TG, Goldberg DE (2001) Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* 82:979–990

Jakobsson A, Eriksson (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88:794–502

Jäger EJ (ed) (2011) *Exkursionsflora von Deutschland*, founded by Rothmaler W, Gefäßpflanzen: Grundband. Spektrum Akad. Verlag, Heidelberg

Jensen K, Gutekunst K (2003) Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic Appl Ecol* 4:579–587

Jongejans E, Soons MB, de Kroon H (2006) Bottlenecks and spatiotemporal variation in the sexual reproduction pathway of perennial meadow plants. *Basic Appl Ecol* 7:71–81

Jorritsma-Wienk LD, Ameloot E, Lenssen JPM, de Kroon H (2006) Differential responses of germination and seedling establishment in populations of *Tragopogon pratensis* (Asteraceae). *Pl Biol* 9:109–115

Jutila HM, Grace JB (2002) Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *J Ecol* 90:291–302

Kladivová A, Münzbergová Z (2016) Interacting effects of grazing and habitat conditions on seedling recruitment and establishment. *J Veg Sci* 27:834–843

Knappová J, Knapp M, Münzbergová Z (2013) Spatio-temporal variation in contrasting effects of resident vegetation on establishment, growth and reproduction of dry grassland plants: implications for seed addition experiments. *PLOS ONE* 8:e65879

Kotorová I, Lepš J (1999) Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *J Veg Sci* 10:175–186

Koutsovoulou K, Daws MI, Thanos CA (2013) Campanulaceae: a family with small seeds that require light for germination. *Ann Bot (Oxford)* 113:135–146

Kowarik I (2003) *Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa.* Ulmer, Stuttgart

Křenová Z, Lepš J (1996) Regeneration of a *Gentiana pneumonanthe* population in an oligotrophic wet meadow. *J Veg Sci* 7:107–112

Leishman MR (1999) How well do plant traits correlate with establishment ability? Evidence from a study of 16 calcareous grassland species. *New Phytol* 141:487–496

Leishman MR, Westoby M (1994) The role of large seed size in shaded conditions: experimental evidence. *Funct Ecol* 8: 205–214

Ludewig K., Wanner A, Jensen K (2015) Recolonization and facilitation in Baltic salt marsh vegetation. *Ann Bot Fenn* 52:181–191

Mahn EG (1996) Einfluß spontaner und gelenkter Sukzessionsprozesse in Braunkohlentagebaulandschaften auf die Entwicklung einer ressourcenangepaßten Vegetationsstruktur. *Hercynia NF* 30:5–12

Miglécz T, Tóthmérész B, Valkó O, Kelemen A, Török P (2013) Effects of litter on seedling establishment: an indoorexperiment with short-lived Brassicaceae species. *Pl Ecol* 214:189–193

Milberg P, Andersson L, Thompson K (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Sci Res* 10:99–104

Moles AT, Westoby M (2002) Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99:241–248

Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. *J Ecol* 92:372–383

Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. *Oikos* 113:91–105

Münzbergová Z (2004) Effect of spatial scale on factors limiting species distributions in dry grassland fragments. *J Ecol* 92: 854–867

Nystuen KO, Evju M, Rusch GM, Graae BJ, Eide NE (2014) Rodent population dynamics affect seedling recruitment in alpine habitats. *J Veg Sci* 25:1004–1014

Partzsch M (2000) Die Porphyrkuppenlandschaft des unteren Saaletals – Strukturwandel ihrer Vegetation in den letzten vier Jahrzehnten. *Tuexenia* 20:153–187

Partzsch M (2011) Does land-use change affect the interactions between two dry grassland species? *Flora* 206:550–558

Partzsch M, Piesch C, Hensen I (2011) A comparative study of germination biology and plant performance in two dry grassland species. *Folia Geobot* 46:35–48

Ryser P (1993) Influences of neighbouring plants on seedling establishment in limestone grassland. *J Veg Sci* 4:195–202

Schupp EW (1995) Seed-seedlings conflicts, habitat choice, and pattern of plant recruitment. *Amer J Bot* 82:99–409

Silvertown JW (1981) Seed size, life span, and germination date as coadapted features of plant life history. *Amer Naturalist* 118: 860–864

Smith RS, Rushton SP (1994) The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *J Appl Ecol* 31:13–24

SPSS (2015) *SPSS for Windows 21.0*. SPSS, Chicago

Tessier M, Cloaguen JC, Lefeuvre JC (2000) Factors affecting the population dynamics of *Suaeda maritima* at initial stages of development. *Pl Ecol* 147:193–203

Thompson K, Bakker JP, Bekker RM (1997) *The soil seed banks of north west Europe: methodology, density and longevity*. Cambridge University Press, Cambridge

Vera ML (1997) Effects of altitude and seed mass on germination and seedling survival of heathland plants in north Spain. *Pl Ecol* 133:101–106

Villar-Salvador P, Puértolas J, Cuesta B, Peñuelas JL, Uscola M, Heredia-Guerrero N, Rey Benayas JM (2012) Increase in size and nitrogen concentration enhances seedling survival in Mediterranean plantations. Insights from an ecophysiological conceptual model of plant survival. *New Forests* 43:755–770

Vítová A, Lepš J (2011) Experimental assessment of dispersal and habitat limitation in an oligotrophic wet meadow. *Pl Ecol* 212:1234–1242

Watt TA, Gibson CWD (1988) The effects of sheep grazing on seedling establishment and survival in grassland. *Pl Ecol* 78: 91–98

Weis IM (1982) The effect of propagule size on germination and seedling growth in *Mirabilis hirsuta*. *Canad J Bot* 60:1868–1874

Wu G, Du G (2007) Germination is related to seed mass in grasses (Poaceae) of the eastern Quinhai-Tibetan Plateau, China. *Nordic J Bot* 25:361–365

Xiong S, Nilsson C, Johansson ME (2001) Effects of litter accumulation on riparian vegetation: importance of particle size. *J Veg Sci* 12:231–236

Zobel M, Otsus M, Liira J, Moora M, Möls T (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecol* 81:3274–3282