

## RESEARCH PAPER

# Negative and positive interactions among plants: effects of competitors and litter on seedling emergence and growth of forest and grassland species

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## Keywords

*Campanula*; competition; facilitation; *Galium*; germination; oak (*Quercus robur* L.); plant recruitment; plant–plant interactions; *Poa*; *Rumex*; seedling biomass; seedling emergence.

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## ABSTRACT

Living plant neighbours, but also their dead aboveground remains (*i.e.* litter), may individually exert negative or positive effects on plant recruitment. Although living plants and litter co-occur in most ecosystems, few studies have addressed their combined effects, and conclusions are ambivalent. Therefore, we examined the response in terms of seedling emergence and growth of herbaceous grassland and forest species to different litter types and amounts and the presence of competitors. We conducted a pot experiment testing the effects of litter type (grass, oak), litter amount (low, medium, high) and interspecific competition (presence or absence of four *Festuca arundinacea* individuals) on seedling emergence and biomass of four congeneric pairs of hemicryptophytes from two habitat types (woodland, grassland). Interactions between litter and competition were weak. Litter presence increased competitor biomass. It also had positive effects on seedling emergence at low litter amounts and negative effects at high litter amounts, while competition had no effect on seedling emergence. Seedling biomass was negatively affected by the presence of competitors, and this effect was stronger in combination with high amounts of litter. Litter affected seedling emergence while competition determined the biomass of the emerged individuals, both affecting early stages of seedling recruitment. High litter accumulation also reduced seedling biomass, but this effect seemed to be additive to competitor effects. This suggests that live and dead plant mass can affect species recruitment in natural systems, but the mechanisms by which they operate and their timing differ.

## INTRODUCTION

At large scales, plant communities are mainly structured by climatic conditions (Walther *et al.* 2002; Krebs 2009), while at smaller scales biotic interactions and microsite conditions seem to prevail (Huston 1999; Lortie *et al.* 2004). Abiotic conditions, such as soil moisture or light availability, have been intensively studied, showing that high stress may change the relations among individuals and lead to an increase or decrease in abundance of certain species (Holmgren *et al.* 1997; Grime 2001). Studies on biotic relations have focused on negative interactions among species. Competition has been considered the most significant biotic factor structuring plant communities (Bertness & Callaway 1994; Keddy 2001). More recently, facilitation has been increasingly acknowledged as another facet of plant–plant relations, which may change the abundance of plant species through effects of neighbours (*e.g.* nurse plants) on microsite conditions (Bruno *et al.* 2003; Michalet *et al.* 2006; Maestre *et al.* 2009). The relative importance of positive and negative interactions may change over time. Plant individuals may be more sensitive to negative interaction dur-

ing a certain developmental or phenological stage. In these periods, positive interactions will assure a certain level of development, however, during ontogeny relations may shift from facilitation to competition (Parish & Bazzaz 1985; Miriti 2006). Similarly, the presence of a neighbouring individual may be negative under favourable environmental conditions and change to a positive interaction when environmental conditions become more stressful (Bertness & Callaway 1994; Holmgren *et al.* 1997; Brooker & Callaghan 1998; Gómez-Aparicio *et al.* 2004; Resco de Dios *et al.* 2014). Here, we evaluated the role of before- and after-death plant interactions as factors exerting positive and/or negative interactions on seeds and seedlings.

After-death plant material, such as litter, may have positive or negative effects on seed germination and recruitment, depending on litter amount (Loydi *et al.* 2013). The presence of a thick litter layer may reduce seedling emergence, while moderate or low amounts of litter may enhance emergence (*e.g.* Xiong *et al.* 2001; Donath & Eckstein 2012; Schmiede *et al.* 2013; Mollard *et al.* 2014). Also, the origin of the litter layer may have different effects depending on its physical structure: a more interwoven thread-like structure, such as grass litter,

may have a more negative effect on emergence than the presence of a layer of litter composed of small flat pieces, such as that from deciduous tree leaves (Donath & Eckstein 2008). But species response to these different litter types may also vary with the species' origin. Grassland species seem to be more adapted and more tolerant to grass litter than to woodland litter, and *vice versa* (Qusted & Eriksson 2006; Donath & Eckstein 2008). Moreover, litter effects also depend on environmental conditions, changing the effect of litter on emergence and establishment. It has been shown that litter reduces evaporation from the soil and the temperature amplitude (Deutsch *et al.* 2010; Loydi *et al.* 2014b), which have positive effects during dry periods, in areas of high insolation or with high temperatures (Facelli & Pickett 1991; Loydi *et al.* 2013). Similarly, litter releases nutrients to the soil that may increase seedling growth (Myers *et al.* 1997; Berg 2000) but it can also release allelochemicals during decomposition, which may reduce seed germination (*e.g.* Inderjit *et al.* 2008; Ruprecht *et al.* 2008). However, grass litter seems to have low allelochemical effects (Loydi *et al.* 2014a).

On the other hand, living plants, co-occurring with litter from the same or other species, will compete with seeds and seedlings and reduce their establishment (Fenner & Thompson 2005). Presence of established vegetation will cause a reduction in the available space, alter light interception and availability of water and nutrients (Keddy 2001). This will reduce the capacity of seedlings to grow and establish. But this negative effect may change in the case of extreme conditions. Particularly, with low water supply or high temperatures, the presence of a plant canopy may reduce water evaporation and increase soil humidity, thus, exerting a positive effect on seed germination and promoting seedling growth (Gómez-Aparicio *et al.* 2004; Eckstein 2005; Janeček & Lepš 2005; Fayolle *et al.* 2009; Schmiede *et al.* 2013). Also, established vegetation will interact with litter, and the mix of these two factors may change the final outcome of their specific negative and positive effects (Bonanomi *et al.* 2013). It seems that low amounts of litter may improve microsite conditions, thereby increasing seedling growth even when competitors are present (Violle *et al.* 2006). Additionally, there may be an indirect positive effect of litter on seedling emergence and growth, if litter cover reduces growth and biomass of competitors (Török *et al.* 2012; Schmiede *et al.* 2013). In contrast, high litter amounts may exert negative effects that add to the negative effects of competition, particularly under moist conditions (Foster 1999).

Different factors may influence seed germination, seedling emergence, growth, survival and reproduction (*e.g.* Eckstein 2005; Renne *et al.* 2006; Fayolle *et al.* 2009). Current knowledge suggests that competitors, but not litter, affect seedling growth after emergence (Foster 1999; Violle *et al.* 2006; Nyanumba & Cahill 2012). But it is not clear whether litter and competition exert differential (interactive) or similar (additive) effects on early life stages and which of these factors is more important for germination and seedling emergence. Therefore, we performed a pot experiment testing the effects of litter type, litter amount and interspecific competition on species from two habitat types. We specifically addressed the following hypotheses:

1 The effects of litter, competition and their interaction differ between two phases of recruitment, *i.e.* seedling emergence and growth. Whereas litter will be more important than

competition for seedling emergence, competition will have stronger effects on seedling growth.

- 2 Litter will exert an indirect positive effect on seedling emergence and biomass by reducing competitor biomass.
- 3 The presence of litter will improve microsite conditions (*i.e.* increase soil nutrients and reduce temperature amplitude) for seedling emergence. The magnitude and direction of the litter effect will vary with litter amount.
- 4 Grassland species are adapted to higher competition levels and thus are less affected by the presence of competitors than are woodland species. With respect to different litter types, species will perform better with the litter of their original habitat type.

## MATERIAL AND METHODS

### Studied species

Four genera of perennial hemicryptophytes and two species within each genus were used. The species have similar morphology but differ with respect to their habitat preference, *i.e.* each species either occurs in deciduous woodlands/forests or grassland habitats (Table 1). Except for *Rumex sanguineus*, which was collected from field populations, seeds were obtained from a commercial supplier of regional seeds (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany). An initial germination test under glasshouse conditions showed that all species had a germination potential of more than 50% (Table 1).

### Experimental design

A full factorial pot experiment was conducted in a common garden near Giessen, Germany, (50°32' N, 8°41.3' E, 172 m a.s.l.) to study the effect of genus (factor levels ( $k$ ) = 4), original habitat ( $k$  = 2, grassland *versus* woodland), litter type ( $k$  = 2, grass litter *versus* oak litter), litter amount ( $k$  = 3, low/medium/high) and interspecific competition ( $k$  = 2, with and without presence of competitors) on seedling emergence and biomass per pot. Each genus  $\times$  habitat combination was represented by one species. For each species we prepared 60 pots of 4 l (with an upper surface of 16  $\times$  16 cm) for each litter type  $\times$  litter

**Table 1.** Habitat, family, mass per seed (mg) and germination percentage of the study species under glasshouse conditions.

original habitat	family	species	mass per seed (mg)	germination (%)
grassland	Campanulaceae	<i>Campanula rapuncululus</i>	0.03	56.0
		Poaceae	<i>Poa pratensis</i>	0.3
	Polygonaceae	<i>Rumex acetosa</i>	0.8	72.4
		Rubiaceae	<i>Galium wirtgenii</i>	0.4
	woodland	Campanulaceae	<i>Campanula trachelium</i>	0.2
Poaceae			<i>Poa nemoralis</i>	0.2
Polygonaceae		<i>Rumex sanguineus</i>	1.1	68.8
		Rubiaceae	<i>Galium sylvaticum</i>	1.3

amount  $\times$  competition combination ( $2 \times 3 \times 2 = 12$  combinations), each replicated five times. In addition, for each species we prepared ten control pots without litter: five with competitors and five without competitors. The experiment consisted of 560 pots in total.

We sowed 50 seeds of one species in each pot for all studied species (Table 1). Seeds were evenly scattered over the soil surface. Afterwards, we manually applied different litter types and amounts to each pot. For this we collected dry grass litter from mesic unfertilised grasslands lacking any of the studied species, and leaves of oak (*Quercus robur* L.) from a deciduous forest. Grassland litter was a low-diversity species mixture, dominated by the grasses *Poa pratensis*, *Agrostis stolonifera*, *Arrhenatherum elatius* and *Dactylis glomerata*. We used only oak leaves in the woodland litter treatments to minimise potential effects of particle size and chemical composition that may arise from using a mixture of tree species. Since litter may affect seed germination through the interception of light at ground level, we adjusted the applied amounts of grass and oak litter to similar levels of light reduction (cf. Donath & Eckstein 2008). Consequently, the amounts of litter applied in the current experiment were 5, 10 and 20 g of grass litter and 1.25, 2.5 and 5 g of oak litter per pot, denoted as low, medium and high litter amounts hereafter. These amounts correspond to an initial relative PAR below the litter of about 10%, 1% and 0.1%, respectively, of the incident radiation above the litter layer. The levels of grass litter applied, i.e.  $200 \text{ g}\cdot\text{m}^{-2}$ ,  $400 \text{ g}\cdot\text{m}^{-2}$  and  $800 \text{ g}\cdot\text{m}^{-2}$ , respectively, are within the range of low- to high-productive grasslands (Donath *et al.* 2004). Levels of oak litter manipulation, i.e.  $50 \text{ g}\cdot\text{m}^{-2}$ ,  $100 \text{ g}\cdot\text{m}^{-2}$  and  $200 \text{ g}\cdot\text{m}^{-2}$ , respectively, are within the range found in deciduous forests (Sydes & Grime 1981; Ellenberg 1986; Wilke *et al.* 1993). Our experimental design also allows comparisons between treatments with the same litter amount of different litter types (5 g of grass litter versus 5 g of oak litter).

The competition treatment consisted of four individuals of *Festuca arundinacea* per pot (hereafter referred to by genus), which is a common species in mesic grasslands in Central Europe. Well-developed *Festuca* seedlings (four to five leaves) were transplanted to the pots at the time of sowing and after application of the litter.

All pots were filled with commercial potting soil (Fruhstorfer Erde, Type P; Industrie-Erdenwerke Archut, Lauterbach, Germany) composed of a mixture of peat, clay and humus (pH-CaCl<sub>2</sub> 5.7, 188 mg·l<sup>-1</sup> N, 136 mg·l<sup>-1</sup> P<sub>2</sub>O<sub>5</sub> and 206 mg·l<sup>-1</sup> K<sub>2</sub>O). Pots were saturated with water twice a week and maintained constantly moist throughout the whole experiment. To accomplish this, we watered all pots with the same amount of water when the soil in the treatment without litter was superficially dry. Seeds were sown on 27 February 2012. This allowed enough time for cold stratification of the seeds, which is important for successful germination. Germination started in mid-April. Seedlings emerging above the litter layer were counted on 16 April, 15 May and 25 June. Since a very low (<3%) mortality was observed during the experiment, we assume that percentage of emerged seedling at the end of the experiment represents cumulative emergence. The emergence peak was similar for each pair of congeneric species. Established seedlings and *Festuca* aboveground biomass were collected at the end of the experiment, cleaned, dried for 48 h at 70 °C and weighed.

To study the effect of litter on microsite conditions, we prepared 42 pots with the same size, potting soil and treatments at the same time as the experiment described above, but no seeds were added. In this case, we prepared three replicates per treatment combination and control. In these pots we estimated soil supply rates for nitrate (NO<sub>3</sub><sup>-</sup>-N), ammonium (NH<sub>4</sub><sup>+</sup>-N), phosphorus (P), potassium (K), sulphur (S), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B) and aluminium (Al) using PRS probes (Western Ag Innovations, Saskatoon, SK, Canada). PRS probes consist of an ion-exchange membrane that adsorbs ions through electrostatic attraction, simulating a plant root. Two anion and two cation probes were buried in the top 5 cm of soil at a 45° angle for a 4-week period (25 June to 21 July 2012). This period coincides with the last month of soil resource-driven seedling growth before biomass harvesting from the pots. After removal, the PRS probes were washed with deionised water and returned to Western Ag Innovations for analysis of adsorbed ions: amounts of NO<sub>3</sub><sup>-</sup>-N and NH<sub>4</sub><sup>+</sup>-N were estimated by an automated colorimetry flow injection analysis system and all other ions by inductively-coupled argon plasma (ICP) spectrophotometry (Hangs *et al.* 2004). Additionally, we measured mean daily temperature and amplitude (difference between maximum and minimum daily temperatures) below the litter layer using temperature loggers (Tinytalk with internal sensor; Gemini Dataloggers, Chichester, UK) in one pot of each treatment combination (n = 14). At the end of the experiment *Festuca* above- and belowground biomass was collected, cleaned, dried for 48 h at 70 °C and weighed.

### Statistical analysis

To analyse the effect of competition, habitat type, litter amounts and types, and species identity on cumulated seedling emergence and biomass per pot we performed a mixed effect factorial ANOVA. Since the main objective of our study was to test interactions between litter amount and type and competitors, for the statistical analyses we excluded the controls (i.e. pot without litter). A preliminary analysis using response ratios showed that inclusion of these controls only provides information about the effect of litter, which can be found elsewhere (e.g. Loydi *et al.* 2013).

Before analysis, we transformed the data using the Box-Cox transformation whenever necessary (Legendre & Legendre 1998). We selected species pairs from the same genus but from different habitats. Since our main objective was to analyse the response of species from different habitats to litter and competition, we considered genus as a random effect in the analyses, since it represents a random sample of all possible genera that could be employed in the experiment (Underwood 1997). Species was not used as a variable itself because the combination of factors genus and habitat sufficiently defines the different species used. All other factors were considered fixed. For F-ratio calculation in the ANOVA analyses, we used the error terms according to Underwood (1997). Additionally, to detect treatment effects at the species level we performed separate three-way ANOVAs (i.e. litter amount  $\times$  litter type  $\times$  competition) for each species. The same procedures were followed to analyse the effect of genus, habitat and litter amount and type on *Festuca* aboveground biomass. In the second experiment, nutrient

adsorption by the PRS probes, mean daily temperature and thermal amplitude were analysed with a three-way ANOVA (*i.e.* litter amount  $\times$  litter type  $\times$  competition). *Festuca* above- and belowground biomass was compared using a paired *t*-test. Additionally, we calculated the relative competition intensity index (RCI index) for each species and all combinations of litter type and litter amount, including the controls, as follows (Weigelt & Jolliffe 2003):

$$\text{RCI} = \frac{\bar{X}_C - \bar{X}_F}{\bar{X}_C}$$

where  $\bar{X}_C$  is the mean value (*i.e.* accumulated germination or biomass per pot) for the treatment without *Festuca*, and  $\bar{X}_F$  is the mean value for the treatments with *Festuca*. RCI value was multiplied by  $-1$ . Consequently RCI varies between  $-1$  and  $1$ , when the presence of *Festuca* had a negative or a positive effect, respectively.

As a measure for the relative contribution of each factor and their interactions to the total variability on accumulated seedling emergence and biomass per pot, we used the ratio of the sum of squares of the factor or interaction of interest to the total sum of squares (*i.e.* for all factors, their interactions and the error). In all cases, for fixed effect factors Tukey *post-hoc* tests were performed. For all random effect factors (*i.e.* genus and all genus  $\times$  factor interactions), *post-hoc* tests were not performed, since their results may change with any other random selection of genera, and they therefore do not explain the outcome of the fixed effect factors considered in the experiment (Underwood 1997; Quinn & Keough 2002). All statistical analyses were performed using Statistica (version 10.0; StatSoft Inc, Tulsa, OK, USA).

## RESULTS

### Effects of litter and competition on seedling emergence and biomass (Hypothesis 1)

Average seedling emergence ranged from  $24 \pm 2\%$  to  $57 \pm 2\%$  (mean  $\pm$  SE,  $n = 60$ ) across all treatment combinations, with minimum values per pot of zero (*Campanula rapunculus* and *R. sanguineus*) and maximum values of  $>80\%$  (*Galium wirtgenii* and *Rumex acetosa*). For emergence, litter amount accounted for the highest percentage explained variance (45%; Table 2). Low litter amounts showed significantly higher seedling emergence ( $50.7 \pm 1.2\%$ ) than medium litter amounts ( $44.9 \pm 1.2\%$ ), and both were statistically different from high litter amounts ( $26.6 \pm 1.4\%$ ). Competition had no main effect on seedling emergence (Table 2) and, considering each species separately, competition had only minor effects on one species (*P. pratensis*; see Fig. 1). The mean RCI index (*i.e.* across species) for the effects of competition on seedling emergence had a value of  $-0.07$  when litter was absent, positive values (*i.e.* positive effect of *Festuca*) when oak litter or low amounts of grass litter were present (from 0.02 to 0.11) and negative values at medium or high amounts of grass litter ( $-0.07$  and  $-0.28$ , respectively). For details on RCI index for each species see Table S1.

For biomass, there was a strong effect of competition, explaining 68% of the variance (Table 2): presence of *Festuca*

significantly reduced biomass per pot ( $1.25 \pm 0.08$  and  $0.11 \pm 0.01$  g.pot $^{-1}$ , without and with competitors, respectively). This effect was consistent for all studied species (Figure S1). Also, biomass was higher at low and medium litter amounts compared to high litter amounts (significant Litter amount effect in Table 2). For biomass, mean RCI index for the effects of competition on pot biomass was  $-0.89$  in the absence of litter, slightly more negative values were obtained when litter was present (between  $-0.89$  and  $-0.92$ ). For details of RCI index for each species see Table S2.

### Effect of litter on *Festuca* biomass per pot (Hypothesis 2)

In the first experiment, the presence of different amounts of litter affected the development of *Festuca* individuals (Table S3). They showed higher aboveground biomass values when they were growing in pots with increasing amounts of litter ( $F_{2,6} = 16.43$ ,  $P < 0.01$ ; Fig. 2).

In the second experiment, *Festuca* belowground biomass was six-fold higher than aboveground biomass ( $11.9 \pm 5.6$  g.pot $^{-1}$  and  $2.0 \pm 0.06$  g.pot $^{-1}$ , respectively; paired *t*-test = 8.89,  $df = 17$ ,  $P < 0.01$ ). Belowground biomass showed no difference among litter types ( $F_{1,12} = 0.54$ ,  $P > 0.45$ ), litter amounts ( $F_{2,12} = 0.21$ ,  $P > 0.85$ ) or their interaction ( $F_{2,12} = 0.37$ ,  $P > 0.70$ ). Aboveground biomass followed the same pattern as in the first experiment, *i.e.* higher biomass with grass litter ( $F_{1,12} = 6.45$ ,  $P < 0.05$ ) and with higher litter amounts ( $F_{2,12} = 5.30$ ,  $P < 0.05$ ).

### Microsite conditions (Hypothesis 3)

In general, the presence of different litter types had no effect on available nutrients, except for Ca and Mg, which had higher adsorption values under oak litter than under grass litter ( $F_{1,24} = 12.6$ ,  $P < 0.01$  and  $F_{1,24} = 5.0$ ,  $P < 0.05$ , respectively). Potassium had higher adsorption values under high amounts of grass litter ( $F_{2,24} = 26.2$ ,  $P < 0.01$ ). On the other hand, most of the analysed nutrients (except Mg, B and Al) had lower adsorption values (*i.e.* lower availability) when competition was present ( $P < 0.05$ ), but there were no differences among litter amounts or litter types ( $P > 0.05$ ).

Analysis of temperature showed that mean daily temperature was not affected by any of the considered factors. Nonetheless, across litter types, daily temperature amplitudes were significantly lower under high litter amounts than under medium or low litter amounts ( $F_{2,732} = 38.4$ ,  $P < 0.01$ ). Presence of competitors also reduced temperature amplitude ( $F_{1,732} = 14.8$ ,  $P < 0.01$ ) at low litter amounts (Fig. S2). Litter type had no effect on temperature amplitude. However, daily temperature amplitude between pots covered by the same amount (*i.e.* 5 g) of litter was higher under grass litter than under oak litter (low grass *versus* high oak amounts; Tukey = litter amount  $\times$  litter type,  $P < 0.05$ ).

### Effects of litter type and species' original habitat (Hypothesis 4)

Across species, emergence was significantly higher from beneath oak litter ( $42.2 \pm 1.1\%$ ) than from beneath grass litter ( $39.2 \pm 1.3\%$ ; Table 2). Low amounts of grass litter showed higher emergence than low amounts of oak litter, but high amounts of grass litter reduced emergence more strongly than

**Table 2.** Results of ANOVA on the effects of Genus, Habitat, Litter type, Litter amount and Competition on cumulative seedling emergence and biomass per pot.

source of variation	effect type	MS <sub>error</sub>	df	seedling emergence			biomass per pot		
				MS	P	%exp	MS	P	%exp
Genus [G]	R	Residual	3	404.3	0.071	14.93	85.7	0.152	13.93
Habitat [H]	F	G*H	1	57.4	0.722	2.12	1.4	0.879	0.22
Litter Type [LT]	F	G*LT	1	<b>80.0</b>	<b>0.005</b>	<b>2.95</b>	0.0	0.990	0.00
Litter Amount [LA]	F	G*LA	2	<b>1224.9</b>	<b>0.002</b>	<b>45.24</b>	<b>25.3</b>	<b>0.025</b>	<b>4.10</b>
Competition [C]	F	G*C	1	0.9	0.845	0.03	<b>419.0</b>	<b>0.007</b>	<b>68.08</b>
G*H	R	Residual	3	<b>374.7</b>	<b>&lt;0.001</b>	<b>13.84</b>	<b>49.3</b>	<b>&lt;0.001</b>	<b>8.01</b>
G*LT	R	Residual	3	1.4	0.777	0.05	1.6	0.739	0.26
G*LA	R	Residual	6	<b>56.2</b>	<b>&lt;0.001</b>	<b>2.08</b>	3.5	0.476	0.57
G*C	R	Residual	3	<b>20.9</b>	<b>0.001</b>	<b>0.77</b>	9.1	0.066	1.48
H*LT	F	G*H*LT	1	4.7	0.743	0.17	0.3	0.358	0.05
H*LA	F	G*H*LA	2	5.2	0.821	0.19	1.0	0.796	0.16
H*C	F	G*H*C	1	9.2	0.233	0.34	2.6	0.428	0.43
LT*LA	F	G*LT*LA	2	<b>320.8</b>	<b>&lt;0.001</b>	<b>11.85</b>	2.3	0.096	0.37
LT*C	F	G*LT*C	1	15.1	0.077	0.56	0.0	0.658	0.00
LA*C	F	G*LA*C	2	5.1	0.592	0.19	0.2	0.749	0.04
G*H*LT	R	Residual	3	<b>36.6</b>	<b>&lt;0.001</b>	<b>1.35</b>	0.3	0.975	0.04
G*H*LA	R	Residual	6	<b>25.4</b>	<b>&lt;0.001</b>	<b>0.94</b>	4.1	0.366	0.67
G*H*C	R	Residual	3	4.2	0.347	0.15	3.2	0.473	0.51
G*LT*LA	R	Residual	6	<b>8.0</b>	<b>0.049</b>	<b>0.30</b>	0.6	0.984	0.10
G*LT*C	R	Residual	3	2.1	0.635	0.08	0.1	0.993	0.02
G*LA*C	R	Residual	6	<b>9.0</b>	<b>0.028</b>	<b>0.33</b>	0.7	0.979	0.12
H*LT*LA	F	G*H*LT*LA	2	4.9	0.478	0.18	0.1	0.911	0.02
H*LT*C	F	G*H*LT*C	1	0.7	0.486	0.03	0.0	0.651	0.00
H*LA*C	F	G*H*LA*C	2	1.2	0.579	0.05	0.1	0.899	0.01
LT*LA*C	F	G*LT*LA*C	2	12.8	0.058	0.47	0.2	0.876	0.03
G*H*LT*LA	R	Residual	6	5.9	0.158	0.22	1.0	0.952	0.16
G*H*LT*C	R	Residual	3	1.1	0.823	0.04	0.1	0.997	0.01
G*H*LA*C	R	Residual	6	2.1	0.771	0.08	0.6	0.988	0.09
G*LT*LA*C	R	Residual	6	2.7	0.635	0.10	1.3	0.916	0.21
H*LT*LA*C	F	G*H*LT*LA*C	2	2.2	0.611	0.08	1.2	0.106	0.20
G*H*LT*LA*C	R	Residual	6	4.0	0.378	0.15	0.4	0.997	0.06
Residual			384	3.8		0.14	0.4		0.06

%exp = percentage explained variance; df = degrees of freedom; F = fixed; MS = mean square; P = error probability; R = random.

Significant effects ( $P < 0.05$ ) are given in bold.

MS<sub>error</sub> according to Underwood (1997).

high amounts of oak litter (Fig. 3a). However, considering the same amount (5 g) of grass and oak litter (low grass *versus* high oak amounts), seedling emergence was higher under grass litter than under oak litter ( $55.2 \pm 1.4$  *versus*  $34.6 \pm 1.8\%$ , respectively; Fig. 3a). Seedling biomass was not affected by the different litter types (Fig. 3b).

Species from different habitats responded similarly to litter presence. For seedling emergence or biomass there was no difference between grassland and forest species (Table 2). However, *Festuca* plants had a higher aboveground biomass when competing with forest species than with grassland species ( $1.47 \pm 0.05$  and  $1.24 \pm 0.05$  g·pot<sup>-1</sup>, respectively;  $F_{1,3} = 45.90$ ,  $P < 0.01$ ).

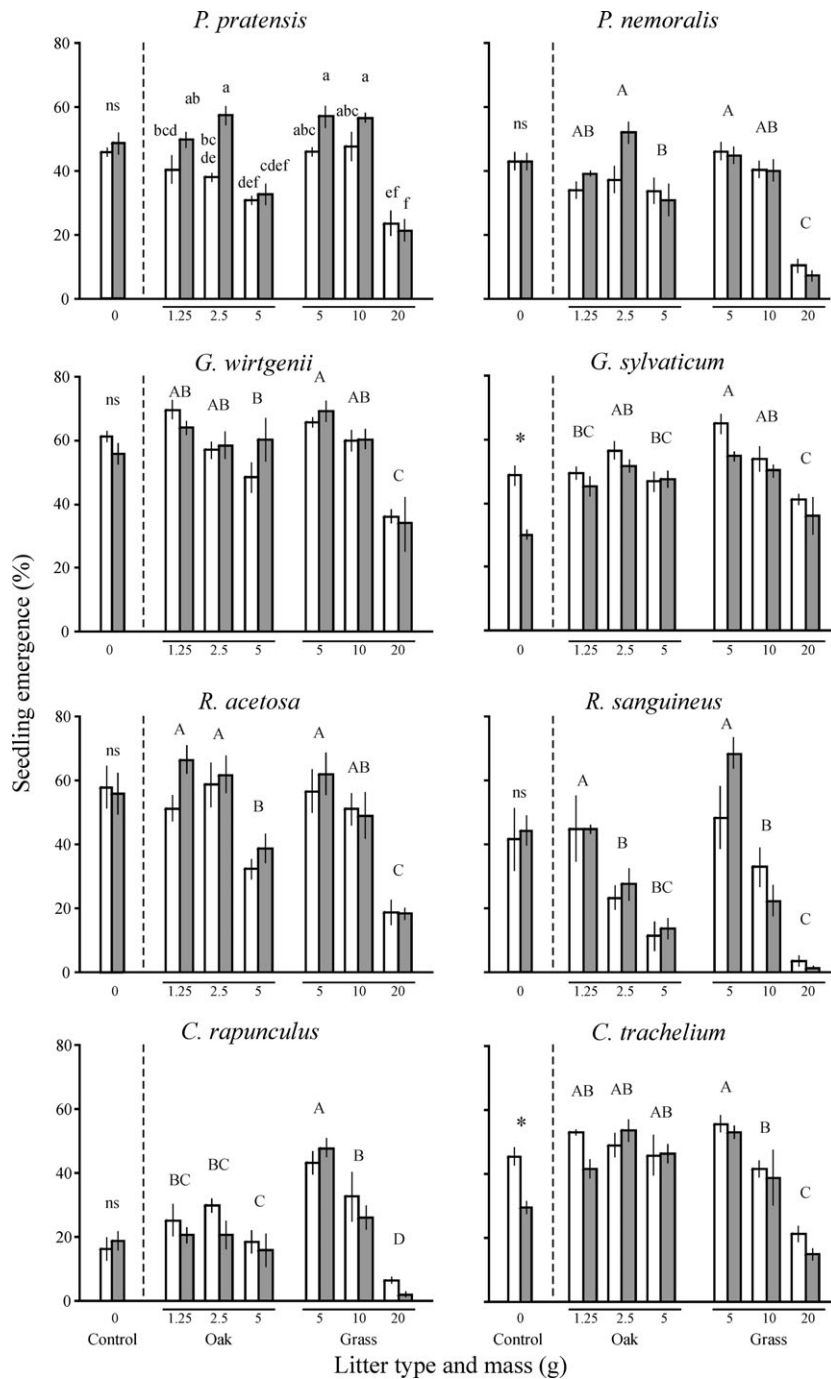
## DISCUSSION

Our results showed that competitive effects through established grasses and after-death effects through litter exert different control mechanisms during various phases of recruitment. While litter plays a major role for seedling emergence, interspecific competition was the most important factor for seedling bio-

mass, but had no main effect on seedling emergence. Moreover, the amount of litter is a strong modulator of emergence, changing from a positive effect at low litter amounts to a negative effect at high litter amounts. High litter amounts have an additive effect with competition, further reducing seedling biomass.

### Relative effects of litter and competition on seedling emergence and biomass (Hypothesis 1)

The presence of competitors changed the effects of litter on seedling establishment. We found that the negative effects of competition on seedling biomass were stronger in combination with high amounts of grass litter. This indicates that the penetration of a thick and dense grass litter cover exhausts the resources of a seedling, which in turn reduces its competitive ability. Violle *et al.* (2006) found similar results, showing that litter had a positive effect on emergence, while seedling growth was also affected by the presence of competitors. However, in their case, litter seemed to modulate the effect of competition, increasing biomass and seed production of annual species. Nonetheless, these effects change rapidly after emergence, and

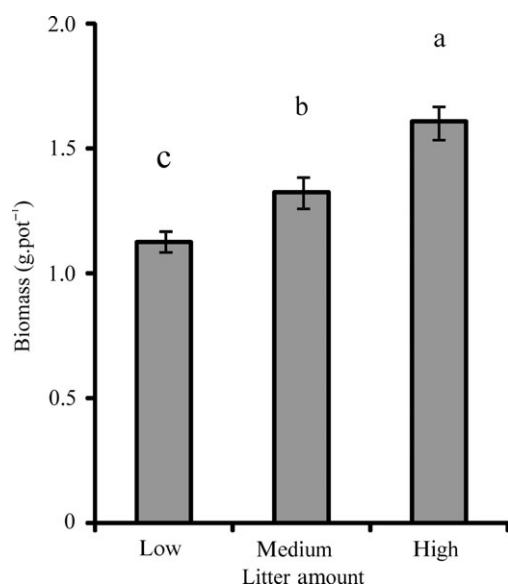


**Fig. 1.** Percentage cumulative seedling emergence of grassland (left panels) and woodland (right panels) species under different litter types and amounts, and with presence (grey bars) or absence (white bars) of competitors. Data are means  $\pm$  1 SE ( $n = 5$ ). Difference between control pots is shown ( $t$ -test) but was not considered in the main statistical analysis (see Material and Methods). Different letters indicate significant differences among means of transformed data ( $P < 0.05$ ). We used capital letters for the litter type  $\times$  litter amount interaction when interactions with competition were not significant and lowercase letters for litter type  $\times$  litter amount  $\times$  competition interaction (only *Poa pratensis*). Abbreviations of genera: *P* = *Poa*, *G* = *Galium*, *R* = *Rumex*, *C* = *Campanula*.

competition with established vegetation becomes a crucial determinant of seedling growth. Similarly, Fayolle *et al.* (2009) showed that facilitation in the recruitment of herbaceous species is related to habitat amelioration by established vegetation, enhancing emergence of seedlings; but afterwards, the presence of competitors may limit seedling growth, showing a clear change in the interaction direction throughout the recruitment phase of seedlings.

In the present experiment, competition through *Festuca* strongly reduced seedling biomass, while effects on emergence were weak. The overriding effect of competition on biomass could partly be explained through the relatively high competitor density (four individuals of *Festuca* per pot equals  $>150$

individuals.m<sup>-2</sup>). Given the restricted volume of the pots (4 l), *Festuca* roots occupied most of the pot space shortly after transplantation (A. Loydi, personal observation), which in turn reduced space for the development of the sown seedlings. Consequently, very low RCI values for biomass of about  $-0.90$  (Table S3) indicate that the presence of *Festuca* reduced seedling biomass by 90%. Additionally, high biomass allocation to *Festuca* roots in all treatments will further increase below-ground competition intensity, since reducing the rooting space in the pots will reduce the shoot biomass or growth rate of the sown individuals, even when enough water and nutrients are supplied (Booth *et al.* 2003). However, the outcome of the experiment might have changed if competitors were not



**Fig. 2.** *Festuca* aboveground biomass per pot under different litter amounts, averaged across species and litter types. Data are means  $\pm$  SE ( $n = 80$ ). Different letters indicate significant differences among means of transformed data ( $P < 0.05$ ).

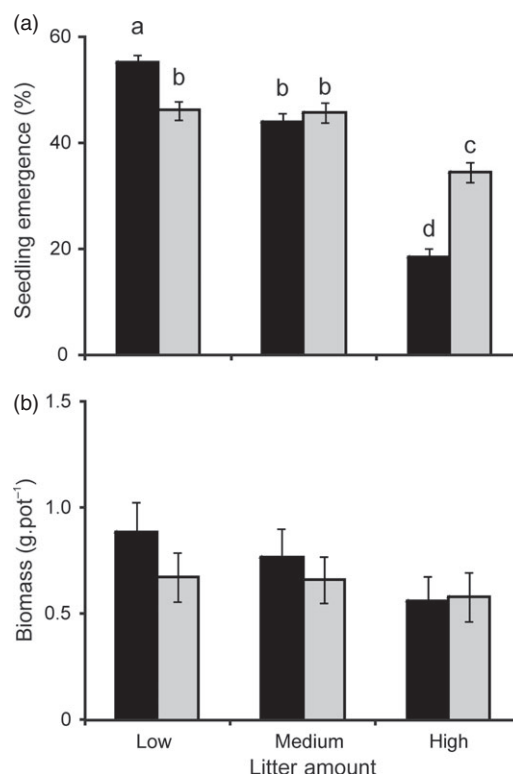
transplanted into the pots but sown with the rest of the seeds. In this case, initial competition would be low since only young seedlings are present and the effect of competitors on germination cannot be evaluated. The opposite may have occurred if *Festuca* individuals transplanted to the pots were larger than those used here. However, at least in the case of seedling emergence, we assume this effect was small since germination is mainly triggered by water availability and temperature regimes.

#### Indirect effect of litter on *Festuca* biomass (Hypothesis 2)

In contrast to our expectation, litter increased biomass of *Festuca* individuals. The individuals were transplanted to the pots, so they did not experience the negative effects of litter during germination. However, the maintenance of soil moisture by litter (Eckstein & Donath 2005; Deutsch *et al.* 2010) and the amelioration of extreme temperature (Donath & Eckstein 2010) probably results in better growth of individuals that are rooting beneath a litter layer (Foster 1999). Litter accumulation may promote the growth of established perennial species, such as *Festuca arundinacea*, increasing competition intensity. Under field conditions, this will not impact seedling emergence *per se* at low to medium litter amounts, but might during subsequent establishment, since established vegetation may benefit from litter accumulation, whereas species reproducing through seeds may fail to establish. In this case, the long-term survival of species could be threatened, even after successful germination, through increasing competition intensity when litter is present.

#### Effects on microsite conditions (Hypothesis 3)

In our study, presence of litter only increased Ca, Mg and K content. The former two are more frequent under tree litter (Sayer 2006), while the latter is not a structural component of plant litter, and higher K adsorption with grass litter may be



**Fig. 3.** Percentage cumulative emergence (a) and biomass per pot (b) of seedling under grass (black bars) or oak (grey bars) litter and with different litter amounts (see Material and Methods), averaged across species and competition treatments. Data are means  $\pm$  SE ( $n = 80$ ). Different letters indicate significant differences among means of transformed data ( $P < 0.05$ ).

related only to higher litter quantities (Blair 1988). However, the availability of nutrients under different amounts of litter did not differ between treatments when competitors were present, indicating that litter presence did not reduce competition intensity for soil nutrients in the short term, as we expected. Moreover, competitors reduced available nutrients, showing that even if litter releases nutrients, these will be taken up by established vegetation and will not be available for developing seedlings. However, litter did reduce temperature amplitude, and this reduction was higher with increasing amounts of litter, while the presence of competitors had a similar effect, probably through shading the soil surface (Eckstein 2005; Fayolle *et al.* 2009). Thus, low litter amounts may have the same effect as a vegetation canopy (*e.g.* Janeček & Lepš 2005; Kruk *et al.* 2006) with respect to temperature amplitude, thus improving microclimate conditions.

Temperature changes trigger loss of seed dormancy (*e.g.* Thompson & Grime 1983; Baskin & Baskin 2001) whereas soil moisture is decisive for germination and seedling emergence (Baskin & Baskin 2001; Ludewig *et al.* 2014). Pots in the present experiment were regularly watered, while positive microclimatic and nutritional effects of litter were weak; therefore, potential effects of litter on soil water availability were probably negligible. Consequently, positive effects of litter on seedling emergence were only found for low litter amounts, whereas negative mechanical effects dominated at high litter amounts (Egawa & Tsuyuzaki 2013). High litter amounts reduce emergence, probably because mortality increases as a consequence

of resource depletion associated with the difficulties in penetrating a thick litter layer (Donath & Eckstein 2008; Schmiede *et al.* 2013).

#### Differences among litter type and species' original habitat (Hypothesis 4)

Considering the same amount of grass and oak litter (5 g), the latter had stronger negative effects on emergence and seedling biomass. Since litter thickness was similar (<3 cm; A. Loydi, personal observation), probably the structure of oak litter, *i.e.* larger particle sizes (as whole deciduous tree leaves), may translate into stronger negative effects on vegetation than small particles (Xiong *et al.* 2001).

We found no differences between grassland and woodland species. We expected that adaptation to habitat-specific conditions, such as the presence of higher belowground competition in grasslands (Lamb *et al.* 2007), might lead to differences in competitive abilities of related species from different habitats. However, the relatively high intensity of competition in our experiment probably reduced the chance of detecting different responses among species of grassland and woodland. Nonetheless, higher *Festuca* biomass in the presence of woodland species compared to grassland species suggests that the latter may be able to cope better with competition from established vegetation, but more studies are needed.

#### CONCLUSIONS

We showed that although competition and litter seem to interact, this interaction was weak and these two factors play different roles for recruitment. While litter affected the early stage of seedling recruitment (emergence), competition crucially determined the size (biomass) reached by those individuals that successfully emerged from beneath the litter layer, and therefore their long-term survival and establishment success. Both factors will lead to similar results (*i.e.* reducing seedling recruitment), but our data suggest that the mechanisms through which they operate, and the phases they affect, differ. Litter is an important component of plant communities (Berg 1986; Aerts 1997; Xiong & Nilsson 1997), but is also actively used as a restoration tool in many restoration

projects (Kiehl *et al.* 2010; Schmiede *et al.* 2012). In the present scenarios of land-use change, accumulation of litter is expected to increase in underused natural grasslands and abandoned fields (Quétier *et al.* 2007; Egawa & Tsuyuzaki 2013). This may challenge the maintenance of grassland diversity, since increased competition intensity when litter is present may reduce the establishment of less-competitive species. Because of the high conservation value of European grasslands (Critchley *et al.* 2004; Hodgson *et al.* 2005), litter-mediated mechanisms and processes should be incorporated in future scenarios of global change and in grassland degradation and restoration.

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#### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Relative competition intensity (RCI) index on accumulated germination for the study species at all combinations of litter type  $\times$  litter amount.

**Table S2.** Relative competition intensity (RCI) index on pot biomass for the study species for all combinations of litter type  $\times$  litter amount.

**Table S3.** Results of ANOVA on the effects of genus, habitat, litter type, litter amount and competition on *Festuca* biomass per pot.

**Figure S1.** Biomass per pot of grassland (left panels) and woodland (right panels) species under different litter types and amounts and with presence (grey bars) or absence (white bars) of competitors.

**Figure S2.** Mean daily temperature amplitude under different litter amounts with presence (grey bars) or absence (white bars) of competitors, averaged across litter types.

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