

# Experimental evidence for root competition effects on community evenness in one of two phytometer species

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## Abstract

### Aims

Plant–plant interactions, being positive or negative, are recognized to be key factors in structuring plant communities. However, it is thought that root competition may be less important than shoot competition due to greater size symmetry belowground. Because direct experimental tests on the importance of root competition are scarce, we aim at elucidating whether root competition may have direct or indirect effects on community structure. Indirect effects may occur by altering the overall size asymmetry of competition through root–shoot competitive interactions.

### Methods

We used a phytometer approach to examine the effects of root, shoot and total competition intensity and importance on evenness of experimental plant communities. Thereby two different phytometer species, *Festuca brevipila* and *Dianthus carthusianorum*, were grown in small communities of six grassland species over three levels of light and water availability, interacting with neighbouring shoots, roots, both or not at all.

### Important Findings

We found variation in community evenness to be best explained if root and shoot (but not total) competition were considered. However, the effects were species specific: in *Dianthus* communities increasing root competition increased plant community evenness, while in *Festuca* communities shoot competition was the driving force of this evenness response. Competition intensities were influenced by environmental conditions in *Dianthus*, but not in *Festuca* phytometer plants. While we found no evidence for root–shoot interactions for neither phytometer species root competition in *Dianthus* communities led to increased allocation to shoots, thereby increasing the potential ability to perform in size-asymmetric competition for light. Our experiment demonstrates the potential role of root competition in structuring plant communities.

**Keywords:** plant–plant interactions, root and shoot competition, intensity vs. importance, experimental plant communities, asymmetry of competition

Received: 17 May 2017, Revised: 7 June 2018, Accepted: 4 July 2018

## INTRODUCTION

Plant–plant interactions, being positive or negative, are recognized to be key factors in structuring plant communities (Keddy 1989, reviewed by Brooker *et al.* 2008). However, and despite a long history of research on this topic, the predictability of how plant–plant interactions change along environmental gradients of resources and productivity is still low (Soliveres *et al.* 2015). According to Grime's theory (Grime

1973) and confirmed by some experimental studies, competitive interactions, both above- and belowground, prevail in productive environments and decrease in importance with increasing stress (Brooker *et al.* 2008; Gaucherand *et al.* 2006; Kunstler *et al.* 2011; Maalouf *et al.* 2012; Michalet *et al.* 2006). Moreover, there is growing evidence that in harsh, extreme conditions plant–plant interactions are not important at all for community structure relative to the effect of other environmental drivers such as abiotic conditions (Maalouf *et al.* 2012;

Malkinson and Tielbörger 2010; Michalet *et al.* 2006; Mitchell *et al.* 2009). It is the severity of the abiotic environment that determines community structure, overriding any plant–plant interaction. Other studies consider competition, the key factor (of constantly high importance) along the entire gradient (Tilman 1988). They only distinguish between above- and belowground competition with aboveground competition being more intense in productive habitats and belowground competition being more intense in unproductive, resource-poor habitats (Tilman 1988).

Indeed, experimental evidence is ambiguous. The strength of belowground competition has been shown to decrease (Casper and Jackson 1997; Lamb *et al.* 2008; Schenk 2006), increase (Bartelheimer *et al.* 2010; Lamb *et al.* 2007) or to be invariant (Belcher *et al.* 1995; Lamb *et al.* 2007) along gradients of water or nutrients. However, a few studies suggest that belowground competition, no matter how intense, is less important in determining the structure and diversity of plant communities while aboveground competition is assumed to be the decisive factor (DeMalach *et al.* 2016; Hautier *et al.* 2009; Lamb *et al.* 2009; Rajaniemi *et al.* 2003). These studies postulate that the difference is due to a lack of positive feedback mechanisms in size-symmetric belowground competition (Lamb and Cahill 2008; Lamb *et al.* 2009). Aboveground competition for light is size-asymmetric, i.e. larger plants can pre-empt light benefitting disproportionately relative to their size creating a positive feedback, eventually leading to competitive exclusion (Schwinning and Weiner 1998). In contrast, belowground competition, which is largely for water, nitrogen and phosphorus, is presumably size symmetric, i.e. resource capture is proportional to a plant's size (Cahill and Casper 2000; Schwinning and Weiner 1998). Competition among plants likely occurs above- and belowground simultaneously. Root competition, though, has been shown to potentially influence community structure indirectly *via* root–shoot interactions. They occur if root competition alters the ability of a plant to compete for aboveground resources (Lamb *et al.* 2009; Li *et al.* 2011; Mariotte *et al.* 2012). However, these interactions vary greatly depending on the environment, species and growth phases (Cahill 2002; Kiær *et al.* 2013; Song *et al.* 2006, 2012). Co-occurring species can differ in their competitive response (Gaucherand *et al.* 2006; Liancourt *et al.* 2005; Maestre *et al.* 2009; Michalet 2007). Thus, the identity of the phytometer species used to measure competition may strongly affect the conclusions of competition experiments. The only experimental study explicitly examining root competition effects on community structure, finding no direct effect of belowground competition on community structure, was restricted to one species (Lamb *et al.* 2009). In addition, it is rarely considered how the importance of belowground interactions changes over environmental gradients. Schenk (2006) hypothesized that negative effects of root competition could be potentially more important under resource-rich conditions. However, so far this has not been reported. Additionally, studies on the relationship

between intensity and importance of plant–plant interactions show generally no distinct pattern, being either correlated or not (Brooker *et al.* 2005; Le Bagousse-Pinguet *et al.* 2014; Maalouf *et al.* 2012; Welden and Slauson 1986).

In contrast to the exploration of variations in plant–plant interactions along environmental gradients, the relationship between the intensity and importance of competition and community structure, i.e. diversity, has not gained much attention yet. The majority of studies found that plant–plant interactions did not have an effect on taxonomic diversity (Lamb and Cahill 2008; Lamb *et al.* 2009; Mitchell *et al.* 2009) nor on phylogenetic diversity (Bennett *et al.* 2013) (but see Le Bagousse-Pinguet *et al.* 2014). Therein, even fewer studies explicitly considered below- and aboveground competition (Lamb *et al.* 2009). We therefore conducted an experiment using two different phytometer species from a semi-natural dry grassland community to grow within a community of five different grassland species. We separated root, shoot and total competition intensity and importance over two gradients, aboveground for light and belowground for water, to ask: (i) Do competition intensity and importance vary across environmental conditions? (ii) Do shoot and root competitions interact? (iii) Do root, shoot or total competition intensity and importance, i.e. the role of plant–plant interactions compared to the role of abiotic factors, influence community structure? and (iv) Is this dependent upon the phytometer species used?

## METHODS

### Species

We chose two perennial phytometer species characteristic for steppe-like, nutrient-poor and dry grasslands typical in the north-eastern part of the federal state of Brandenburg, Germany, *Dianthus carthusianorum* L. and *Festuca brevipila* Tracey. Both species are similar in growth form, building tussocks, with grass-like leaves and share the same Ellenberg values, but they differ in occurrence frequency (*Festuca* is a typical matrix species) and belong to different plant families (Caryophyllaceae and Poaceae). They were planted into the centre of a mixture of five species, which co-occur in their natural habitats (Table 1) plus either *Dianthus* or *Festuca* (if not used as phytometer), so that the communities consisted of three grasses and forbs each. Species were selected based upon available seeds, germination records, being perennial, non-leguminous and not building up spacers.

### Experimental design

#### Competition treatments

Phytometer plants were exposed to one of the four competition treatments: no neighbours, shoots of neighbours, roots of neighbours or shoots and roots of neighbours. Root competition by neighbouring plants was excluded by planting the phytometer plants into root exclusion tubes (PVC tubes of 4.5 cm diameter covered at the bottom with gaze to allow

**Table 1:** species used and sources of seeds used in the experiment

Species	Family	Seed source
<i>Dianthus carthusianorum</i>	Caryophyllaceae	Hillsides at the River Oder near Mallnow
<i>Festuca brevipila</i>	Poaceae	Rieger-Hoffmann
<i>Hieracium umbellatum</i>	Asteraceae	Hillsides at the River Oder near Mallnow
<i>Solidago virgaurea</i>	Asteraceae	Hillsides at the River Oder near Mallnow
<i>Arrhenatherum elatius</i>	Poaceae	Rieger-Hoffmann
<i>Dactylis glomerata</i>	Poaceae	Rieger-Hoffmann
<i>Pimpinella nigra</i> (a)	Apiaceae	Hillsides at the River Oder near Mallnow
<i>Filipendula vulgaris</i> (a)	Rosaceae	Hillsides at the River Oder near Mallnow

Seeds of forbs had been collected in the field while seeds of grasses had to be obtained by a commercial seed supplier (Rieger-Hoffmann) due to limited germination of available seeds. (a) Due to limitations in germination of *S. virgaurea*, in some pots we planted individuals of *P. nigra* or *F. vulgaris* as sixth species.

water flow while preventing roots to grow through), and shoot competition was excluded by using wire mesh cones with 1-cm<sup>2</sup> mesh size around focal phytometer individuals.

### Abiotic treatments

We applied two independent environmental gradients to gain high environmental variation. Aboveground we set up three levels of light availability (100% (high), 80% (medium) and 20% (low) light availability) by using shade cloths. Both phytometer species most probably originate in dry woods in our region and occur also in grassland-wood border zones (M Ristow (personal communication)) making it reasonable to explore also high level of light interception. Light levels were applied in four blocks each (see below). Belowground we set up three levels of water supply as water is the most limiting resource in the dry grasslands typical for the phytometer species (Moeslund et al. 2013). All pots were watered by use of a nozzle every second day. One-third of the pots was additionally watered with 50 ml every second day, and another third with 100 ml of water every second day. We intended to set up a target water content in three levels ('low', 'medium' and 'high') to include a range of 5–15 Vol%. Due to lower evaporation, in low light conditions, the additional water in the medium and high water level treatment was restricted to 25 and 50 ml, respectively. Pots were covered with rain shelter if necessary. Necessity was surveyed by carefully observing rain radar and sky.

Phytometer individuals were planted into the centre of five neighbouring plants, so that each community consisted of six individuals from different species (see above). The combination of four competition treatments, three light levels, three water levels, two phytometer species and four replications each resulted in 288 pots with 1 728 plants, placed in 12 blocks.

Seedlings were transplanted into pots (13 × 13 × 13 cm) filled with a 50:50 mixture of sand and steamed compost soil on 20 June 2011. Pots were placed outdoors in the Botanical Garden Potsdam. The final application of abiotic treatments started 2 weeks later after seedlings had consolidated.

### Measurements and indices of plant–plant interactions and community structure

Harvest took place 13 weeks after the start of the experimental treatments, between 10 and 24 October 2011. Each individual plant (phytometer and community) was measured for its height (highest point in cm) and clipped for determination of aboveground biomass at the soil surface. Roots of all plants were extracted by washing and manual separation under water, taking particular thoroughness for the phytometer species. Separation was feasible as both phytometer species have distinguishable roots, being particularly darker than roots of competing species. Biomass was dried at 85°C for 12 h after harvest and again for 3 h before weighing.

We assessed the intensity of competition, i.e. the degree to which competition reduces plant performance below the physiological maximum achievable in a given environment, as competitive response of the phytometer species. The importance of competition, i.e. the change in performance of a target species due to neighbours compared with the effect of other community drivers such as abiotic conditions, was calculated as importance index in Seifan et al. (2010). Both indices are commonly used measures in plant competition studies. The intensity of root, shoot and total competition within the community was measured as competitive response of the phytometer plant  $\ln(XN/NN)$  (Cahill 1999), with NN representing total phytometer plant biomass when grown without competition of neighbours and XN total phytometer plant biomass when grown in competition with neighbouring plants. To distinguish between root, shoot and total competition intensity, XN was total phytometer plant biomass when (i) grown with the roots, but not shoots of neighbours for calculation of belowground (root) competitive response (RCR), (ii) grown with the shoots, but not roots, of neighbours for calculation of aboveground (shoot) competitive response (SCR) and (iii) grown with the shoots and roots of neighbours for calculation of total competitive response (TCR). The importance of interactions was calculated as the index  $I_{\text{Imp}}$  in Seifan et al. (2010):

$$I_{\text{Imp}} = N_{\text{Imp}} / (|N_{\text{Imp}}| + |E_{\text{Imp}}|)$$

with  $N_{\text{Imp}}$  (the contribution of biotic interactions to phytometer plant performance) =  $XN - NN$  and  $E_{\text{Imp}}$  (the contribution of the abiotic environment to phytometer plant performance) =  $NN - P_{\text{max}}$ , with  $P_{\text{max}}$  being the maximal phytometer plant biomass over all scenarios. To distinguish between root, shoot and total competition importance, XN was used as stated above for competition intensity. Negative values of competitive response and  $I_{\text{Imp}}$  indicate competition, whereas positive values indicate facilitation. An increase in either of the indices therefore means that competition becomes weaker.

As measure of community structure evenness was used because species richness was same for all pots and the number of dead individuals at the end of the experiment comparably low. Evenness was calculated as Simpson's Reciprocal Diversity ( $1/D$ ) based on total plant biomasses divided by the number of species (Lamb *et al.* 2009). Simpson's  $D$  equals  $\sum (n/N)^2$ , with  $n$  being the individual total plant biomass and  $N$  the total pot biomass. For these analyses, individual biomasses were used from treatments with root and shoot competition per environmental scenario per block, as root and shoot exclusion devices may alter growth of surrounding plants (Lamb *et al.* 2009; McPhee and Aarssen 2001).

To test whether root and shoot competition do interact, we generated a new variable,  $TCR_{\text{predicted}}$ , as the sum of SCR and RCR per environmental treatment and block, and compared this value to the measured total competition intensity TCR. If  $TCR_{\text{predicted}}$  does not significantly differ from the measured TCR, root and shoot competition are additive, i.e. they do not interact to affect plant growth (see Cahill 2002 for a detailed description).

### Statistical Analysis

All statistical analyses were conducted using R version 3.0.3. (R development core team, <http://cran.r-project.org>).

To analyse performance of interaction indices in dependence of environmental conditions of phytometer plants, we performed linear mixed-effects models, including total biomass of neighbouring roots, shoots or whole plants (depending on the respective response variable: root, shoot or total competition intensity or importance) in interaction with light and water level. Biomasses were ln-transformed to meet assumptions of normality and equal variance. Interactions of root and shoot competition on phytometer plant performance were analysed by comparing TCR and  $TCR_{\text{predicted}}$  with Wilcoxon's rank sum test for the different abiotic scenarios. Correlations between interaction indices were calculated as Pearson's correlation coefficient.

To analyse effects of plant interactions on community biomass evenness, we also performed linear mixed-effects models with either intensity or importance of competition ( $I_{\text{imp}}$ ) as predictors separately for the different competition components (root, shoot or total). To account for differences in productivity, we included ln-transformed total pot biomass as predictor of evenness in each analyses and the ln-transformed proportion of whole pot belowground to aboveground biomass as co-variate.

Block was included as random effect (Venables and Ripley 2002) in all analyses. Maximal models were simplified using stepwise backward model selection by eliminating non-significant terms for which likelihood ratio tests produced  $P > 0.05$  to find minimal adequate models. Normal distribution of model residuals was verified by model checking plots (Crawley 2007). Significance of treatment and trait effects was confirmed when respective test statistics produced  $P < 0.05$  (Crawley 2007). Goodness of model fit was calculated as

described in Nakagawa and Schielzeth (2013) and Johnson (2014), distinguishing marginal  $R^2$  (the proportion of variance explained by the fixed factor(s) alone) and conditional  $R^2$  (the proportion of variance explained by both the fixed and random factors).

## RESULTS

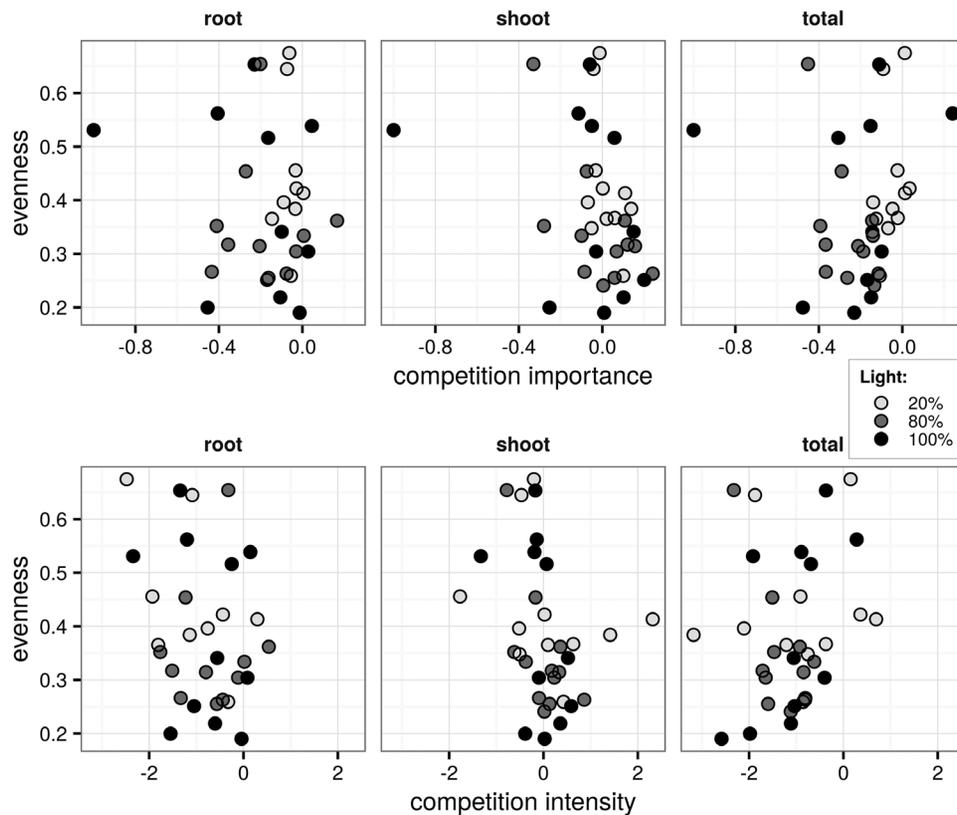
### Intensity and importance of plant interactions

For both phytometer species, there was a high degree of positive correlation between the intensity and the importance of root (*Dianthus*: 0.78, *Festuca*: 0.65), shoot (*Dianthus*: 0.83, *Festuca*: 0.64) and total (*Dianthus*: 0.76, *Festuca*: 0.50) competition (for all  $P < 0.01$ ). Facilitative effects were very common, especially by neighbouring shoots and occurred more often in communities with *Dianthus* than with *Festuca* phytometer plants (facilitative effects in *Dianthus*: 70%, *Festuca*: 52% of communities) (see Figs 1 and 2). When phytometer plants experienced root competition, irrespective of the aboveground interaction, competitive effects prevailed (root competition: *Dianthus*: 60%, *Festuca*: 84%; total competition: *Dianthus*: 73%, *Festuca*: 87% of communities).

In *Festuca* communities, intensity and importance of interactions were not significantly driven by environmental conditions, i.e. neither by abiotic factors nor by productivity, i.e. community biomass (Table 2). The only exception was total competition importance that was significantly influenced by light ( $\chi^2(2) = 6.5$ ,  $P < 0.05$ ), with weaker importance in low light conditions.

In contrast, in *Dianthus* communities, both the intensity and importance of interactions were largely influenced by the environment (see Table 3). Root competition intensity and importance increased, i.e. competition became weaker, with increasing root biomass of neighbour plants at high levels of aboveground resource supply (light) and decreased, i.e. competition got stronger, if light was strongly reduced. At high levels of belowground resources (water), only the intensity of root competition increased with increasing root biomass of neighbour plants and decreased at both lower water levels. Interestingly, shoot competition intensity was unaffected by aboveground resource supply, but showed the same response to water as root competition, i.e. it increased with shoot biomass of all neighbour plants at the highest water level, but decreased for the other. In contrast, shoot competition importance was affected by aboveground resources only. With increasing shoot biomass of neighbour plants shoot competition importance decreases, i.e. competition gets stronger, but for slightly reduced light. In *Dianthus* communities, only the total competition intensity was unaffected by environmental conditions (Table 3).

Though TCR was generally lower than  $TCR_{\text{predicted}}$  for both species over all scenarios, we found no evidence for root-shoot competition interactions, as TCR and  $TCR_{\text{predicted}}$  did not vary significantly for neither scenario in both species. Only in slightly light reduced communities with *Festuca* phytometer plants, the difference between TCR and  $TCR_{\text{predicted}}$  was marginally significant ( $W = 35$ ,  $P < 0.1$ ).



**Figure 1:** evenness of *Festuca brevipila* communities in relation to total, shoot and root competition intensity (lower panels) and importance (upper panels) for the different light levels. Negative values of competition intensity and importance indicate competition, while positive values indicate facilitation. Results of the statistical models are presented in Table 4.

### Effects of plant interactions on community evenness

Evenness of *F. brevipila* communities decreased with increasing shoot competition intensity and importance (Fig. 1, Table 4) and increasing total community biomass ( $P < 0.001$ , parameter estimate  $-0.09$ , intercept 0.5). Neither root nor total competition intensity and importance had a significant impact. Unlike in *Festuca* communities, evenness of communities with *D. carthusianorum* phytometer plants was best explained if root competition intensity and importance (Fig. 2, Table 5) together with total community biomass ( $P < 0.001$ , parameter estimate  $-0.13$ , intercept 0.5) and the relationship between total below-/aboveground community biomass were considered ( $P < 0.05$ , parameter estimate 0.11, intercept 0.5). Increasing root competition intensity and importance as well as increasing biomass reduced evenness. Neither shoot nor total competition intensity and importance significantly affected evenness in these communities.

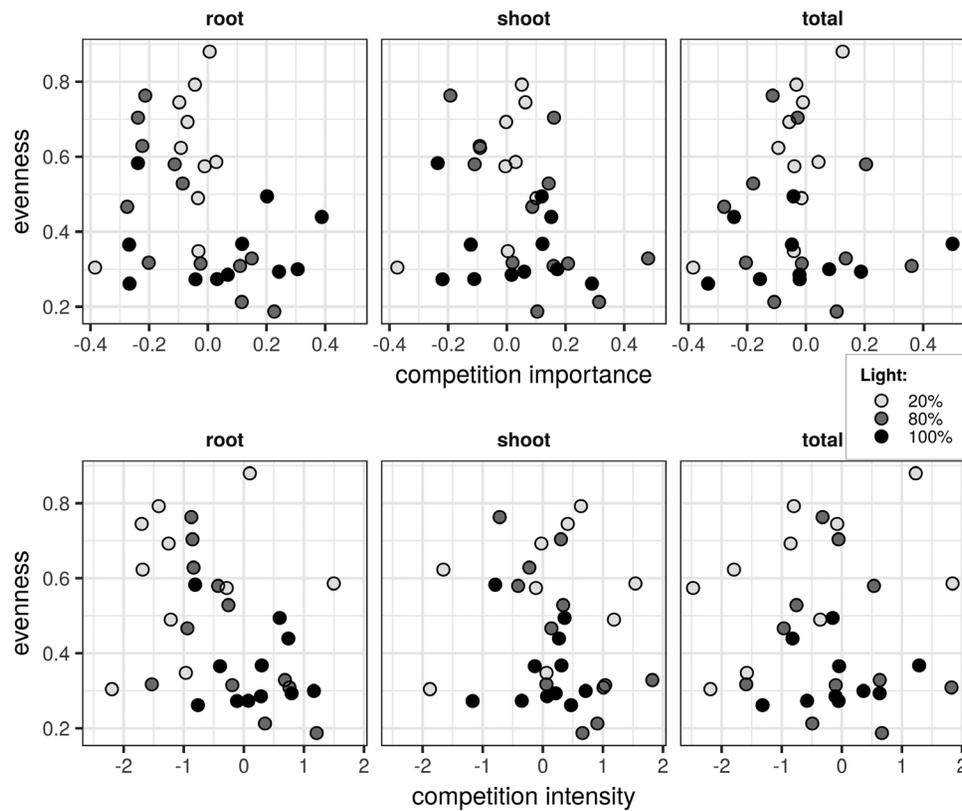
## DISCUSSION

In this study, we used a phytometer approach to assess both the intensity, i.e. the change in performance of a target plant due to neighbours, and the importance, i.e. the change in

performance due to neighbours compared with the effect of other environmental conditions. Specifically, we looked at root and shoot competitive interactions relative to above- and belowground resource availability. We aimed at explicitly exploring whether shoot and/or root competition or their interaction may influence community structure, measured as evenness. Using two different phytometer species, we found the variation in plant–plant interactions across the environments to be highly species specific, as has been shown in a growing number of studies (Gaucherand et al. 2006; Maestre et al. 2009; Michalet 2007; Song et al. 2012). There were also species-specific effects of plant–plant interactions on community structure. While shoot competition intensity and importance explained variation of evenness in communities with *Festuca* phytometer plants, root competition intensity and importance best explained variation of evenness in communities with *Dianthus* phytometer plants.

### Variations in the intensity and importance of plant–plant interactions

Across environmental conditions, phytometer responses to prevailing competition within the communities differed remarkably between both phytometer species. The grass *Festuca* has proven to be very insensitive, while *Dianthus*



**Figure 2:** evenness of *Dianthus carthusianorum* communities in relation to total, shoot and root competition intensity (lower panels) and importance (upper panels) for the different light levels. Negative values of competition intensity and importance indicate competition, while positive values indicate facilitation. Results of the statistical models are presented in Table 5.

was highly responsive. The only finding in common was that irrespective of competition intensity root, shoot and total competition was unimportant under severe light limitation (Figs 1 and 2). This result is in line with previous studies reporting a collapse of biotic interactions under

extreme conditions of stress or disturbance (Maalouf *et al.* 2012; Malkinson and Tielbörger 2010; Michalet *et al.* 2006; Mitchell *et al.* 2009). The effects of neighbours should vanish with their decreasing performance and size, as originally proposed by Grime (1973, 1974).

**Table 2:** results of likelihood ratio tests for all explanatory parameters on root (RCR), shoot (SCR) and total (TCR) competitive intensity and root (RI<sub>Imp</sub>), shoot (SI<sub>Imp</sub>) and total interaction (TI<sub>Imp</sub>) importance in *Festuca brevipila* communities

Fixed effects	RCR		SCR		TCR		RI <sub>Imp</sub>		SI <sub>Imp</sub>		TI <sub>Imp</sub>	
	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Light	(2) 0.3	0.847	(2) 0.8	0.665	(2) 0.5	0.782	(2) 3.3	0.192	(2) 3.1	0.211	<b>(2) 6.5</b>	<b>0.039</b>
Water	(2) 0.1	0.957	(2) 2.2	0.333	(2) 5.0	0.081	(2) 2.2	0.329	(2) 1.1	0.581	(2) 0.9	0.649
ln (Whole neighbour biomass)	0.2	0.658	0.2	0.690	0.8	0.375	0.4	0.515	1.6	0.210	0.4	0.503
ln (Whole neighbour biomass) × Light	(2) 2.1	0.351	(2) 1.2	0.545	(2) 4.0	0.132	(2) 2.3	0.310	(2) 1.1	0.575	(2) 2.4	0.296
ln (Whole neighbour biomass) × Water	(2) 3.1	0.212	(2) 2.2	0.337	(2) 0.2	0.890	(2) 0.6	0.753	(2) 1.0	0.615	(2) 3.1	0.209
Random effect variance	3.2E-05		1.2E-05		0.27		4.5E-06		2.1E-06		1.1E-06	
<i>R</i> <sup>2</sup> <sub>marginal</sub>	0.00		0.00		0.00		0.00		0.00		0.32	
<i>R</i> <sup>2</sup> <sub>conditional</sub>	1.7E-09		2.7E-10		0.10		4.4E-10		9.3E-11		0.32	

Significant predictors (*P* < 0.05) are in bold. Whole neighbour biomass relates to root, shoot or total biomass depending on the respective level of observation. Random effect variances and *R*<sup>2</sup> refer to the minimal adequate models. Block was set as random effect. *N* = 31.

**Table 3:** results of likelihood ratio tests for all explanatory parameters on root (RCR), shoot (SCR) and total (TCR) competitive intensity and root (RI<sub>Imp</sub>), shoot (SI<sub>Imp</sub>) and total interaction (TI<sub>Imp</sub>) importance in *Dianthus carthusianorum* communities

Fixed effects	RCR		SCR		TCR		RI <sub>Imp</sub>		SI <sub>Imp</sub>		TI <sub>Imp</sub>	
	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Light	a	—	(2) 2.5	0.288	(2) 4.2	0.123	a	—	a	—	<b>(2) 6.5</b>	<b>0.039</b>
Water	a	—	a	—	(2) 1.6	0.439	(2) 0.9	0.650	(2) 0.5	0.771	<b>(2) 6.4</b>	<b>0.042</b>
ln (Whole neighbour biomass)	a	—	a	—	0.8	0.360	a	—	a	—	<b>6.1</b>	<b>0.014</b>
ln (Whole neighbour biomass) × Light	<b>(2) 10.5</b>	<b>0.005</b>	(2) 4.7	0.095	(2) 0.5	0.776	<b>(2) 7.0</b>	<b>0.031</b>	<b>(2) 7.4</b>	<b>0.025</b>	(2) 1.8	0.407
ln (Whole neighbour biomass) × Water	<b>(2) 9.7</b>	<b>0.008</b>	<b>(2) 10.2</b>	<b>0.006</b>	(2) 1.5	0.468	(2) 0.7	0.680	(2) 4.2	0.121	(2) 0.8	0.683
Random effect variance	1.2E-04		4.1E-05		0.39		0.057		2.4E-06		1.1E-06	
$R^2_{\text{marginal}}$	0.67		0.33		0.00		0.37		0.33		0.32	
$R^2_{\text{conditional}}$	0.67		0.33		0.14		0.47		0.33		0.32	

Significant predictors ( $P < 0.05$ ) are in bold.

Abbreviations: a = parameters are part of a significant interaction and not tested independently as this would be an arbitrary imposition on the model (Venables and Ripley 2002). Whole neighbour biomass relates to root, shoot or total biomass depending on the respective level of observation. Random effect variances and  $R^2$  refer to the minimal adequate models. Block was set as random effect.  $N = 31$ .

**Table 4:** parameter estimates and results of likelihood ratio tests for the effects of competition intensity and importance on community evenness in *Festuca brevipila* communities

Fixed effects	Estimate	$\chi^2$	df	<i>P</i> value	Random effect variance	$R^2_{\text{marginal}} = R^2_{\text{conditional}}$
SCR	-0.06	5.1	1	0.024	2.3E-06	0.41
SI <sub>Imp</sub>	-0.21	5.3	1	0.021	1.5E-06	0.42
RCR	-0.03	1.1	1	0.291	2.3E-06	0.30
RI <sub>Imp</sub>	-0.14	1.9	1	0.168	2.3E-06	0.30
TCR	0.03	1.1	1	0.285	2.3E-06	0.30
TI <sub>Imp</sub>	-0.03	0.1	1	0.739	2.3E-06	0.30

Maximal models were set up for each of the competition indices separately and contained also ln (total community biomass), ln (belowground/aboveground total community biomass) as co-variate and block as random effect.  $N = 31$ . Random effect variances and  $R^2$  refer to the minimal adequate models.

Neither whole neighbour community biomass nor water supply affected plant interactions in the communities with the grass *Festuca* used as a phytometer. Similarly, water addition has been found to have only few effects on the intensity of root competition (Lamb et al. 2007 and studies therein), suggesting that root competition intensity is invariant along soil moisture gradients. This result is explained by the limited ability of plants to actively compete for water (Lamb et al. 2007). On the contrary, in *Dianthus* communities, root (and also shoot) competition intensity was highly dependent on the water treatment and in interaction with whole neighbour community biomass. With increasing root biomass of all neighbours, root competition became stronger with decreasing water availability. This is in line with theoretical predictions that the addition of a limiting resource will reduce the intensity of competition for that resource (Casper and Jackson 1997) and the general finding of Schenk (2006) that

root competition was more intense under resource-poor conditions. Moreover, additional (but unfortunately insufficient) measurements of leaf midday water potential indicated relevant water stress under low water supply in *Dianthus* but not in *Festuca* phytometer plants under root competition (K Geissler (personal observation)). This difference supports also the view of Wang et al. (2010) that the competitive response ability is not a species trait per se, but instead a set of options plants have for tolerating low levels of different resources.

The importance of root (and shoot) competition was, contrary to competition intensity, unaffected by water treatment in communities where *Dianthus* has been used as phytometer. It suggests that plant growth was always equally water- and neighbour limited. Drought stress suppressed the importance of competition, independent of its increasing intensity. Weak variations in competition importance along a water supply gradient in a grassland have been reported before (Bennett

**Table 5:** parameter estimates and results of likelihood ratio tests for the effects of competition intensity and importance on community evenness in *Dianthus carthusianorum* communities

Fixed effects	Estimate	$\chi^2$	df	P value	Random effect variance	$R^2_{\text{marginal}} = R^2_{\text{conditional}}$
RCR	-0.05	5.0	1	0.025	2.6E-06	0.58
RI <sub>imp</sub>	-0.27	4.8	1	0.028	2.2E-06	0.57
SCR	-0.00	0.0	1	0.998	2.4E-06	0.50
SI <sub>imp</sub>	-0.03	0.1	1	0.808	2.4E-06	0.50
TCR	-0.01	0.02	1	0.690	2.4E-06	0.50
TI <sub>imp</sub>	-0.23	2.9	1	0.090	2.4E-06	0.50

Maximal models were set up for each of the competition indices separately and contained also ln (total community biomass), ln (belowground/aboveground total community biomass) as co-variate and block as random effect.  $N = 31$ . Random effect variances and  $R^2$  refer to the minimal adequate models.

and Cahill 2012). In contrast, in subalpine grasslands of the French Pyrenees, Le Bagousse-Pinguet *et al.* (2014) found the importance of plant–plant interactions to be highly dependent on soil moisture. However, the length of their gradient was far beyond the water supply gradient we used in our study. Thus, we support the view that longer environmental gradients should be used in assessing patterns of plant interactions.

Interestingly, in *Dianthus* communities, phytometer plants benefitted from neighbouring roots under benign above- and belowground abiotic conditions (sufficient water and light). This might seem counterintuitive, as facilitative effects have been shown to play a role in plant communities under severe conditions (Brooker *et al.* 2008). It might be explained by the ability of *Dianthus* phytometer plants to reallocate resources to shoots under competition. The optimal allocation theory predicts that plants try to maximize their growth by allocating biomass between the shoot and the roots so that the uptake of the most limiting resource is increased (Aikio and Markkola 2002; Tilman 1988). The latter, therefore, proposed that any competition should increase allocation to shoots because inferiority in asymmetric competition for light would lead to a greater disadvantage in future resource uptake than inferiority in size-symmetric belowground competition for nutrients (Aikio and Markkola 2002). In our study, root competition enhanced shoot growth of *Dianthus* phytometer plants to such a level that negative effects of root competition on root growth are even counterbalanced under full light conditions (see online supplementary Figs S1 and S2). This seems to be a plausible explanation for our observation that facilitative effects by neighbouring shoots were very common. Bertness and Hacker (1994) interpreted such facilitative effects from shoots as increased humidity and reduced evaporation. In our study, they may have mitigated the negative effects of shading.

### Effects of plant–plant interactions on community evenness

Total competition intensity and importance had no explanatory power for the variation of community evenness in neither phytometer species. Instead, root competition intensity and

importance best explained variation of evenness in communities with *Dianthus* phytometer plants, and shoot competition intensity and importance affected evenness in communities with *Festuca* phytometer plants. In both cases, increasing community evenness was related to increased competition. This is a rather surprising result and in contradiction to previous field studies which found no effect of plant–plant interactions on diversity (Lamb and Cahill 2008; Mitchell *et al.* 2009) or an increase in diversity with increasing importance of facilitation (Le Bagousse-Pinguet *et al.* 2014). However, an increase in evenness related to increasing importance of competition has been reported (though not discussed) in an experimental setup similar to ours (Lamb *et al.* 2009). It might be a phenomenon characteristic for early stages of plant community development.

It is generally assumed that primarily shoot competition is the driving force for plant–plant interactions to structure communities (DeMalach *et al.* 2016; Hautier *et al.* 2009; Lamb *et al.* 2009) due to its asymmetric nature (Schwinning and Weiner 1998). However, it has been shown that interactions between root and shoot competition are an indirect mechanism through which root competition may structure communities (Lamb *et al.* 2009; Li *et al.* 2011; Mariotte *et al.* 2012). If root competition is more intense than shoot competition, root–shoot interactions should increase the overall size asymmetry of competition, and hence, this should increase the potential for competitive interactions to influence plant community structure (Lamb *et al.* 2009). We found an effect of shoot competition on community structure to be confirmed for *Festuca* communities. However, there was only weak evidence for the potential of root–shoot competition interactions to be an active driver. Though we found root competition to be more intense than shoot competition in all treatments, shoot competition itself was not very strong. It has been argued that root–shoot interactions should not be expected without significant shoot competition (Cahill 1999). Accordingly, we found no significant interactions of root and shoot competition in our *Dianthus* communities. However, the fact that shoot competition intensity was highly dependent on the belowground resources indicates a possible feedback.

Other than in our *Dianthus* communities, root competition is assumed to be unimportant in directly structuring communities because of the size symmetry of belowground competition and the lack of feedback mechanisms leading to competitive exclusion (Lamb and Cahill 2008; Mariotte *et al.* 2012). Moreover, this unimportance of root competition is explained by a lack of consistent relationships between root biomass and root competition intensity (Belcher *et al.* 1995; Cahill 2003; Lamb and Cahill 2008; Lamb *et al.* 2009). Contrary to this expectation and although we cannot make predictions about long-term effects of root biomass with our short-term experiment, we did find a significant relationship between community root biomass and root competition intensity and importance in *Dianthus* communities. This relationship was, however, dependent on environmental conditions (see above). Together with the changed allocation pattern towards shoot biomass production and an increase in plant height in *Dianthus* phytometer plants, this may explain why root competition intensity and importance in these communities were able to effect community structure. Here, root competition might have increased the size asymmetry of competition and by this the potential of root competition to influence community structure (Cahill 1999; Lamb *et al.* 2009).

### Methodological considerations

Root competition has been argued to potentially impact plant community structure under non-equilibrium conditions, e.g. following human disturbances (Rajaniemi *et al.* 2003), conditions that might apply to our experiment. However, this could not explain the differences between both phytometer species. Moreover, it is argued that the limitation of rooting space in experimental conditions might result in an overestimation of the influence of belowground competition (Bartelheimer *et al.* 2006; McConnaughay and Bazzaz 1992) and indeed our experiment allowed roots to deepen no further than 10 cm. However, root biomass in central European grasslands has been shown to concentrate in the upper soil layer (Prechsl *et al.* 2015), and we have no information to suppose that our phytometer species would have been differentially affected by the rooting depth in our experiment. It is clear that the species specificity of our results makes it difficult to draw general conclusions. The choice of the phytometer species can affect the results of empirical studies (Cahill *et al.* 2008; Gaucherand *et al.* 2006), and the role of competition for a single phytometer may not reflect the role of competition at the community level. Community-wide knowledge on belowground interaction intensities and their importance for community structure might be gained with the upcoming knowledge of belowground plant traits and the help of new techniques in belowground vegetation research (Faget *et al.* 2013; Wilson 2014). Furthermore, approaches integrating experimental results with individual- and trait-based community modelling (Pfeistorf *et al.* 2016) might be promising to the understanding of community-level consequences of (belowground) plant–plant interactions.

## CONCLUSION

Given the validity of our experiment being limited to early stages of plant community development, our results demonstrate the potential of belowground plant–plant interactions to affect community structure. In the light of the importance of biotic interactions at local scales in the prediction of communities' responses to global environmental changes (Grassein *et al.* 2014), our results show that root competition might not always be as symmetric as it is commonly assumed and belowground interactions require more attention and explicitness.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

## FUNDING

This study was supported by the Leibniz Centre of Agricultural Landscape Research (ZALF e.V.) and by the BMBF in the framework of the BIBS project (01LC1501B).

## ACKNOWLEDGEMENTS

We thank Christine Lange and Gaby Wende for support in the experiment, and Michael Ristow, Johannes Metz, Hans Pfeistorf and Robert Hering for valuable comments on the study. We further thank two anonymous reviewers for their comments, which substantially improved the manuscript.

*Conflict of interest statement.* None declared.

## REFERENCES

- Aikio S, Markkola AM (2002) Optimality and phenotypic plasticity of shoot-to-root ratio under variable light and nutrient availabilities. *Evol Ecol* **16**:67–76.
- Bartelheimer M, Gowing D, Silvertown J (2010). Explaining hydrological niches: the decisive role of below-ground competition in two closely related *Senecio* species. *J Ecol* **98**:126–36.
- Bartelheimer M, Steinlein T, Beyschlag W (2006) Aggregative root placement: a feature during interspecific competition in inland sand-dune habitats. *Plant Soil* **280**:101–14.
- Belcher JW, Keddy PA, Twolan-Strutt L (1995) Root and shoot competition intensity along a soil depth gradient. *J Ecol* **83**:673–82.
- Bennett JA, Cahill JF Jr (2012) Evaluating the relationship between competition and productivity within a native grassland. *PLOS ONE* **7**:e43703.
- Bennett JA, Lamb EG, Hall JC, *et al.* (2013) Increased competition does not lead to increased phylogenetic overdispersion in a native grassland. *Ecol Lett* **16**:1168–76.
- Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. *Am Nat* **144**:363–72.
- Brooker RW, Fernando T, Maestre Ragan M, *et al.* (2008) Facilitation in plant communities: the past, the present and the future. *J Ecol* **96**:18–24.

- Brooker RW, Kikvidze Z, Pugnaire FI, *et al.* (2005) The importance of importance. *Oikos* **109**: 63–70.
- Cahill JF Jr (1999) Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology* **80**:466–80.
- Cahill JF Jr (2002) Interactions between root and shoot competition vary among species. *Oikos* **99**:101–12.
- Cahill JF Jr (2003) Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. *J Ecol* **91**:532–40.
- Cahill JF Jr, Casper BB (2000) Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. *Oikos* **90**:311–20.
- Cahill JF Jr, Kembel SW, Lamb EG, *et al.* (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspect Plant Ecol* **10**:41–50.
- Casper BB, Jackson RB (1997) Plant competition underground. *Annu Rev Ecol Syst* **28**:545–70.
- Crawley MJ (2007) *The R Book*. Chichester: John Wiley & Sons Ltd.
- DeMalach N, Zaady E, Weiner J, *et al.* (2016) Size asymmetry of resource competition and the structure of plant communities. *J Ecol* **104**:899–910.
- Faget M, Nagel KA, Walter A, *et al.* (2013) Root-root interactions: extending our perspective to be more inclusive of the range of theories in ecology and agriculture using *in-vivo* analyses. *Ann Bot* **112**:253–66.
- Gaucherand S, Liancourt P, Lavorel S (2006) Importance and intensity of competition along a fertility gradient and across species. *J Veg Sci* **17**:455–64.
- Grassein F, Lavorel S, Till-Bottraud I (2014) The importance of biotic interactions and local adaptation for plant response to environmental changes: field evidence along an elevational gradient. *Glob Change Biol* **20**:1452–60.
- Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature* **242**:344–7.
- Grime JP (1974) Vegetation classification by reference to strategies. *Nature* **250**:26–31.
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* **324**:636–8.
- Johnson PC (2014) Extension of Nakagawa & Schielzeth's  $R^2_{GLMM}$  to random slopes models. *Methods Ecol Evol* **5**:944–6.
- Keddy PA (1989) *Competition*. Population and community biology series. London: Chapman and Hall.
- Kiær LP, Weisbach AN, Weiner J (2013) Root and shoot competition: a meta-analysis. *J Ecol* **101**:1298–312.
- Kunstler G, Albert CH, Courbaud B, *et al.* (2011) Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *J Ecol* **99**:300–12.
- Lamb EG, Cahill JF Jr (2008) When competition does not matter: grassland diversity and community composition. *Am Nat* **171**:777–87.
- Lamb EG, Kembel SW, Cahill JF Jr (2009) Shoot, but not root, competition reduces community diversity in experimental mesocosms. *J Ecol* **97**:155–63.
- Lamb EG, Shore BH, Cahill JF Jr (2007) Water and nitrogen addition differentially impact plant competition in a native rough fescue grassland. *Plant Ecol* **192**:21–33.
- Le Bagousse-Pinguet Y, Maalouf JP, Touzard B, *et al.* (2014) Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. *Oikos* **123**:777–85.
- Li W, Wen S, Hu W, *et al.* (2011) Root–shoot competition interactions cause diversity loss after fertilization: a field experiment in an alpine meadow on the Tibetan Plateau. *J Plant Ecol* **4**:138–46.
- Liancourt P, Callaway RM, Michalet R (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* **86**:1611–8.
- Maalouf JP, Le Bagousse-Pinguet Y, Marchand L, *et al.* (2012) The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. *Ann Bot* **110**:821–8.
- Maestre FT, Callaway RM, Valladares F, *et al.* (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol* **97**:199–205.
- Malkinson D, Tielbörger K (2010) What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos* **119**:1546–52.
- Mariotte P, Buttler A, Johnson D, *et al.* (2012) Exclusion of root competition increases competitive abilities of subordinate plant species through root–shoot interactions. *J Veg Sci* **23**:1148–58.
- McConnaughay KDM, Bazzaz FA (1992) The occupation and fragmentation of space: consequences of neighbouring shoots. *Funct Ecol* **6**:711–8.
- McPhee CS, Aarssen LW (2001) The separation of above- and below-ground competition in plants—A review and critique of methodology. *Plant Ecol* **152**:119–36.
- Michalet R (2007) Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytol* **173**:3–6.
- Michalet R, Brooker RW, Caviries LA, *et al.* (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol Lett* **9**:767–73.
- Mitchell MG, Cahill JF Jr, Hik DS (2009) Plant interactions are unimportant in a subarctic-alpine plant community. *Ecology* **90**:2360–7.
- Moeslund JE, Arge L, Bøcher K, *et al.* (2013) Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodivers Conserv* **22**:2151–66.
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* **4**:133–42.
- Pfendorfer H, Körner K, Sonnemann I, *et al.* (2016) Coupling experimental data with individual-based modelling reveals differential effects of root herbivory on grassland plant co-existence along a resource gradient. *J Veg Sci* **27**:269–82.
- Prechtl UE, Burri S, Gilgen AK, *et al.* (2015) No shift to a deeper water uptake depth in response to summer drought of two lowland and sub-alpine  $C_3$ -grasslands in Switzerland. *Oecologia* **177**:97–111.
- Rajaniemi TK, Allison VJ, Goldberg DE (2003) Root competition can cause a decline in diversity with increased productivity. *J Ecol* **91**:407–16.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Schenk HJ (2006) Root competition: beyond resource depletion. *J Ecol* **94**: 725–39.

- Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* **113**:447–55.
- Seifan M, Seifan T, Ariza C, *et al.* (2010) Facilitating an importance index. *J Ecol* **98**:356–61.
- Soliveres S, Smit C, Maestre FT (2015) Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biol Rev Camb Philos Soc* **90**:297–313.
- Song M, Hu Q, Tian Y, *et al.* (2012) Seasonal patterns of root and shoot interactions in an alpine meadow on the Tibetan Plateau. *J Plant Ecol* **5**:182–90.
- Song M, Tian Y, Xu X, *et al.* (2006) Interactions between root and shoot competition among four plant species in an alpine meadow on the Tibetan Plateau. *Acta Oecol* **29**:214–20.
- Tilman D (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities* (No. 26). Princeton, NJ: Princeton University Press.
- Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*, 4th edn. New York, NY: Springer.
- Wang P, Stieglitz T, Zhou DW, *et al.* (2010) Are competitive effect and response two sides of the same coin, or fundamentally different? *Funct Ecol* **24**:196–207.
- Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Q Rev Biol* **61**:23–44.
- Wilson SD (2014) Below-ground opportunities in vegetation science. *J Veg Sci* **25**:1117–25.