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ORIGINAL ARTICLE

Kerstin Grant · Juergen Kreyling · Hermann Heilmeier
Carl Beierkuhnlein · Anke Jentsch

Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall

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Abstract Biotic interactions play an important role in ecosystem function and structure in the face of global climate change. We tested how plant–plant interactions, namely competition and facilitation among grassland species, respond to extreme drought and heavy rainfall events. We also examined how the functional composition (grasses, forbs, legumes) of grassland communities influenced the competition intensity for grass species when facing extreme events. We exposed experimental grassland communities of different functional compositions to either an extreme single drought event or to a prolonged heavy rainfall event. Relative neighbour effect, relative crowding and interaction strength were calculated for five widespread European grassland species to quantify competition. Single climatic extremes caused species specific shifts in plant–plant interactions from facilitation to competition or vice versa but the nature of the shifts varied depending on the community composition. Facilitation by neighbouring plants was observed for *Arrhenatherum elatius* when subjected to drought. Contrarily, the facilitative effect of neighbours on *Lotus corniculatus* was transformed into competition. Heavy rainfall increased the competitive effect of neighbours on *Holcus lanatus* and *Lotus corniculatus* in communities composed of three functional groups. Competitive pressure on *Geranium pratense* and *Plantago lanceolata* was not affected by extreme weather events. Neither heavy rainfall nor extreme drought altered the overall productivity of the grassland communities. The complementary responses in competition intensity experienced by grassland species under drought suggest biotic interactions as one stabilizing mechanism for overall community performance. Understanding competitive dynamics under fluctuating resources is important for assessing plant community shifts and degree of stability of ecosystem functions.

Keywords Plant–plant interactions · Climate change · Community composition · Competitive ability · Facilitation · Temperate grassland · Drought · Heavy rainfall

Introduction

Biotic interactions play a key role in the function and structure of ecosystems, influencing the provision of ecosystem services and patterns of biodiversity (Hillebrand et al. 2008; Cavieres and Badano 2009; Schweiger et al. 2010). Biotic interactions, such as competition and facilitation among plants, affect the abundance and distribution of species (Davis et al. 1998). All species within a plant community compete for the same resources, such as water, light, nutrients or space. Minor differences among species in environmental requirements promote species coexistence via niche differentiation (Whittaker 1965; Tilman 1982). Additionally, species can facilitate the invasion, coexistence, establishment or growth of other species by amelioration of their environment (Armas et al. 2008; Brooker et al. 2008; Gross et al. 2013; Schöb et al. 2013). For example, legumes can promote neighbouring plants due to their ability to fix additional atmospheric nitrogen which increases the nitrogen content in the soil (Arfin Khan et al. 2014). Further, plants of different growth forms can alter the canopy structure of plant communities (Tremmel and Bazzaz 1993) resulting in competitive hierarchies with effects on the plant performance due to the direc-

K. Grant (✉) · A. Jentsch
Disturbance Ecology, BayCEER, University of Bayreuth,
95440 Bayreuth, Germany
E-mail: Kerstin.Grant@uni-bayreuth.de

J. Kreyling · C. Beierkuhnlein
Biogeography, BayCEER, University of Bayreuth,
95440 Bayreuth, Germany

H. Heilmeier
Interdisciplinary Ecological Research Centre, TU Bergakademie
Freiberg, 09599 Freiberg, Germany

tional supply of light (Keddy and Shipley 1989; Anten and Hirose 1999; Hautier et al. 2009). Thus, plant communities exhibit a particular suite of dominant and minor species as a result of particular combinations of biotic interactions (Walker et al. 1999; Brooker 2006).

Due to climate change, extreme weather events, such as drought and heavy rainfall, are increasing in frequency and magnitude (IPCC 2012). Biotic interactions, such as competition and facilitation, are expected to mediate the effects of climate change, yet they are still not well understood (Jiang and Kulczycki 2004; Hulme 2005; Adler et al. 2006; Brooker 2006; Hillyer and Silman 2010; Lavergne et al. 2010). Thus, only few hypotheses exist on how extreme weather events will alter plant–plant interactions (Brooker 2006; Miranda et al. 2009; Levine et al. 2010; Soliveres et al. 2013). According to the 'stress-gradient hypothesis' introduced by Bertness and Callaway (1994), facilitation should be more common when plants are subject to high abiotic stress. This is supported by observations from environments with severe climatic or edaphic conditions which suggest that neighbouring plants are more facilitative and might increase community resistance under stressful conditions (Holmgren et al. 1997; Bertness and Ewanchuk 2002; Maestre et al. 2003; Brooker et al. 2008; He et al. 2013). In contrast, some studies have found that competition may increase with elevated stress regimes (Chen et al. 2009; Saccone et al. 2009). Under extremely severe environmental conditions, biotic interactions may become unimportant, relative to the effect of the abiotic stress, thus only the most stress-tolerant species can persist (Michalet et al. 2006; Maestre et al. 2009; Saccone et al. 2009). The balance between competition and facilitation can be further influenced by factors such as plant density and physiology, life stage, and invasion of species (Callaway and Walker 1997; Manea and Leishman 2011), which might also be altered by climate change.

Evidence suggests that facilitation is more likely and stronger under drought than under moist conditions (Callaway and Walker 1997; Holmgren et al. 1997; Kikvidze et al. 2006; Sthultz et al. 2007; Tylianakis et al. 2008). The majority of these studies stem from semi-arid or arid habitats, therefore it is unclear if drought events will also increase facilitative interactions in temperate grassland. Moreover, very little is known regarding the effects of heavy rainfall events on plant–plant interactions. Hypoxia in the rhizosphere, as a consequence of waterlogged soils after heavy rainfall events, could impair plant performance due to reduced photosynthetic activity and growth, or due to nutrient deficiency and toxicity (Steffens et al. 2005; Irving et al. 2007). Previous work simulating extreme rainfall has shown that the competitive balance of most species was unaffected by rainfall treatment, and only some grasses showed reduced competition intensity under heavy rainfall (White et al. 2001).

Understanding the role of plant–plant interactions under extreme weather events is important for modelling and projecting plant community dynamics and the stability of ecosystem functions under climate change. Therefore, we examined the effects of extreme weather events on plant–plant interactions by simulating extreme drought and heavy rainfall events. We investigated the response of five grassland species grown in three experimental communities differing in functional composition and quantified changes in the biotic interactions among these plants. We hypothesize that (1) extreme drought will decrease competition intensity among grassland species due to facilitation by neighbouring plants and that (2) extreme heavy rainfall will only reduce the competition intensity experienced by stress-tolerant species due to lower competition with their struggling neighbours. Further, we expect that (3) the presence of forbs or legumes in the grassland community will alter the biotic interactions of grass species under extreme weather events.

Materials and methods

Experimental design

Our study is part of the EVENT I experiment analysing the effects of extreme weather events and plant diversity on ecosystem functions (Jentsch et al. 2007). The experimental site is located in the Ecological Botanical Garden of the University of Bayreuth, Germany (49°55′19″N, 11°34′55″E, 365 m a.s.l.). The mean annual temperature for Bayreuth is 8.2 °C, and the mean annual precipitation is 724 mm (data: German Weather Service, 1971–2000). The experiment was carried out in a split-plot design, manipulating (1) precipitation (drought and heavy rainfall events) and (2) plant community composition. The three plant communities were blocked and randomly assigned within the two weather manipulations and control, with every combination having five replicates. Thus, the setup consisted of a total of 45 plots with a size of 2 × 2 m. In addition, one plant individual of each species was grown in isolation within each replicated treatment block using buried tubes (∅ 20 cm, h = 30 cm) next to the plots. The isolated plants ($n = 5$ per species and treatment) were exposed to the same weather manipulations. The species composition and plant isolation installed in 2005 has been maintained by periodic weeding. Before this study in 2007, the plant communities were already pre-exposed to manipulated extreme drought and rainfall events in 2005 and 2006, though community biomass had not changed in the weather treatments during these years (Kreyling et al. 2008; Mirzaei et al. 2008). Biomass of plant individuals which grew in isolation was also unaffected by weather treatments, except for *Lotus corniculatus* which decreased due to drought compared to control in 2005.

The texture of the previously homogenized soil consists of loamy sand (82 % sand, 13 % silt, 5 % clay) with pH = 4.5 in the upper (0– 20 cm), and pH = 6.2 in the lower, soil layer (measured in 1 M KCl). Drainage pipes at approximately 80 cm soil depth minimized lateral water flow. Data acquisition was only carried out in the central square meter of each plot in order to avoid edge effects.

Extreme weather events

The weather manipulations consisted of extreme drought and heavy rainfall. Ambient weather conditions were used in the control plots. Intensity of the treatments was based on the local 100-year extreme event in each category. Data from growing seasons (March to September) from 1961 to 2000 were used as the reference period (data: German Weather Service). The Gumbel I distribution (Gumbel 1958) was fitted to the annual extremes, and 100-year recurrence events were calculated. Drought was defined as the number of consecutive days with less than 1 mm of daily precipitation. Accordingly, a drought period of 32 days (May 21–June 21, 0 mm day^{-1}) and a rainfall extreme of 170 mm over 14 days (June 8–June 21, 12.1 mm day^{-1}) were applied in the experiment during the peak growing season in 2007 (Fig. 1). Drought was simulated using rain-out shelters, constructed with steel frames (Hochtunnel, E & R Stolte GmbH, Germany) and covered with transparent plastic sheets (material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany) that permitted nearly 90 % penetration of photosynthetically active radiation according to tests prior to set-up. Strong greenhouse effects were avoided by placing the roof 80 cm above ground level, allowing for near-surface air exchange. Heavy rainfall was simulated using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles. The total amount of added water was divided into two applications per day to ensure constantly high soil water content. If natural precipitation occurred, the amount of rain was deducted from the respective dose. Lateral surface flow was avoided through the application of small plastic sheet pilings around treated plots.

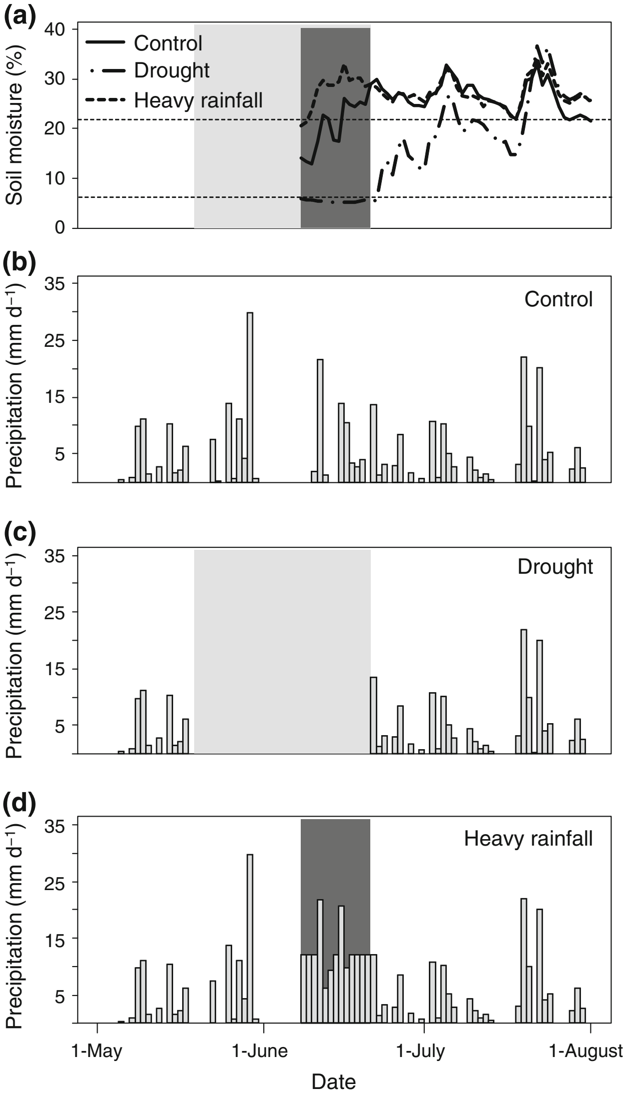

Fig. 1 Mean daily soil moisture (**a**) and daily sum of precipitation in the EVENT experiment during manipulation of drought (**c**) and heavy rain events (**d**) and following recovery. Soil moisture (vol. %) at 5–10 cm depth was recorded in all grassland plots with two functional groups using FD sensors (Echo.EC-5/k, Decagon). *Dashed lines* indicate permanent wilting point (6 vol. %) and field capacity (22 vol. %). Timing and duration of the weather manipulations are indicated by *grey shaded areas* (drought: *light grey*, heavy rainfall: *dark grey*). Soil moisture in weather manipulation is significant different form ambient conditions (**b**) within manipulation period (Linear mixed effect model F = 478 $p < 0.001$). Due to technical problems no soil moisture data was available before June 7th

Experimental plant communities

Five wide-spread plant species of the regional flora were chosen. Species were selected with respect to their lifespan (perennials), their overall importance in nearby and Central European grassland systems, and based on whether they naturally grow on substrate similar to that used in this experiment (Table 1). We have chosen grasses and forbs as the most dominant functional groups of grasslands (Bazzaz and Parrish 1982). Additionally, we added a legume species due to its ability to fix atmospheric nitrogen, which is seen to be facilitative for grasses under ambient conditions (Quinos et al. 1998). Plant individuals in defined quantitative composition were planted in a systematic hexagonal grid with 20 cm distance between individuals in early April 2005. Grassland plots were established in three combinations with an increasing number of plant functional types (Table 1). The experimental communities represent naturally occurring species combinations despite being reduced to two or four species for inevitable experimental simplification. Repetitions with other species

Table 1 Composition of the experimental grassland communities with three functional group combinations

Species combinations	Functional group number	Functional group types
Arrhenatherum elatius, Holcus lanatus	1	2 grasses
Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata, Geranium pratense	2	2 grasses, 2 forbs
Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata, Lotus corniculatus	3	2 grasses, 1 forb, 1 legume

combinations of the tested functional groups or monocultures of the grasses were not considered. The results, especially concerning the legume, could be caused by sampling effects of *Lotus corniculatus* as well as a legume effect.

Response parameter: biomass of plant individuals and community biomass

Our interest was the direct effect of the extreme weather events on the competitive balance among the grassland species. Thus, plant data were collected 10 days after the end of drought and heavy rainfall manipulations. At this date, we expected the largest manipulation effect on our response parameter for plant performance (aboveground biomass) on which the calculation of the competition indices is based. Aboveground biomass was quantified for all five grassland species by harvesting four individuals per plot separately (pseudo replicates) out of the central square meter on July 2nd. After harvesting the individuals, the remaining material of all plants in the inner square meter of each plot was harvested and sorted by species, which added to the harvested individuals forms the community biomass. Furthermore, plant individuals of each species, which were grown in isolation next to the plots, were harvested separately. All harvested biomass was dried at 75 °C to constant weight and weighed.

Calculation of competition indices

In this study, mathematical indices were used to quantify plant competition. This is a common and widespread method (Weigelt and Jolliffe 2003) but is also a topic of debate. The methodological challenges for tracking shifts in competitive balance with rapid changes in resources, and the usefulness of competition indices to quantify competition under changed environments is controversial (Freckleton and Watkinson 1997a, b; Markham 1997; Freckleton and Watkinson 1999; Peltzer 1999). Competition indices cannot distinguish between inter- and intraspecific competition when environmental conditions change, because they neglect the yield-density relationship (Freckleton and Watkinson 1997a). We used the Relative Neighbour Effect (RNE) introduced by Markham and Chanway (1996) in order to quantify shifts in competitive intensity. We interpret the general competitive variation under extreme weather events knowing that also individuals of the same species will probably contribute to this interaction. Thus, RNE, the effect of neighbours relative to the plant with the greatest performance, was calculated according to Eq. 1.

$$RNE = \frac{(y_{iso} - y_{mix})}{x} \tag{1}$$

with $x = y_{iso}$ if $y_{iso} > y_{mix}$ and $x = y_{mix}$ if $y_{mix} > y_{iso}$.

Where RNE (unitless) is Relative Neighbour Effect ($-1 \leq \text{RNE} \leq +1$), y_{iso} is the performance per plant, in this case biomass, for a plant individual growing alone and y_{mix} is the biomass per plant for a plant individual growing in a mixed community. Negative and positive values indicate respectively facilitation and competition by neighbours (Markham and Chanway 1996).

Furthermore, to track whether altered plant–plant interactions were due to crowding caused by altered environmental conditions or due to changed competition abilities of single species, the Relative Crowding (D_r') and the Interaction Strength (I) were calculated following the approach of Wilson (2007).

Relative Crowding (D_r') measures the relative degree of crowding by competitive neighbours whose growth might be altered by changes in habitat conditions, proportionally to the abundance of the neighbours present (Wilson 2007). It can be seen as a measure for competition related to the density or size of neighbour plants. High D_r' values indicate highly productive neighbours and therefore high crowding pressure on the target plant. D_r' is calculated as followed.

$$D_r' = \frac{z_{mix}}{\max(y_{iso}, y_{mix})} \tag{2}$$

where D_r' (unitless) is the generalized effect of Relative Crowding ($D_r' \geq 0$), z_{mix} is abundance of neighbour plants surrounding the target plant (g m^{-2}), y_{iso} is the biomass of a target plant growing in isolation and y_{mix} is the biomass of a target plant growing in a mixture. The abundance of neighbours surrounding the target plant (z_{mix}) was determined using the total plot biomass minus the weight of the target plant.

If there are plants which do not compete for shared limiting resources, the performance of a target plant will decrease less than a plant surrounded by neighbours with active or similar resource demands (Wilson 2007). In addition, suppression will occur throughout the range of actual neighbour abundance. Therefore, the Interaction

Strength I (unitless), a measure for the suppression of the target plant performance per neighbour biomass, is calculated as followed.

$$I = \frac{y_{iso} - y_{mix}}{z_{mix}} \tag{3}$$

Low I values show low suppression of the target plant performance by neighbouring plants and indicates the high competitive ability of the target plant in gaining the shared limiting resources.

Statistical analyses

We performed linear mixed effect models in combination with an ANOVA to test for significant effects of weather manipulation and community compositions, and their respective interactive effects on the response variables. The response variables were biomass, RNE, I and D_r'. We took the split plot design and pseudo replicates into consideration by adding 'repetition', 'plot' and 'individual number' as random factors. The model was simplified if no significant interaction was found by using weather manipulation or community composition as fixed factors. In order to validate the linear mixed effects models, residuals versus fitted plots and plots showing sample quantiles versus theoretical quantiles based on the model were checked for homogenous variance and normal distribution of residuals (Faraway 2006). If conditions of normality were not met or if data required an improved homogeneity of variance, data of biomass and Relative Crowding were transformed using $\log(y + 1)$. In all tests the level of significance was set to $p = 0.05$. All statistical analyses were performed using the statistical software R 2.4.1 (R Development Core Team 2006). For linear mixed effect models the software package "lme4" (Bates and Sarkar 2007) was used. Additionally, the package "multcomp" (Hothorn et al. 2007) was applied for multiple post hoc comparisons. The results of the post hoc comparison for specific treatment pairs are indicated by p-values without information on F-values and degrees of freedom.

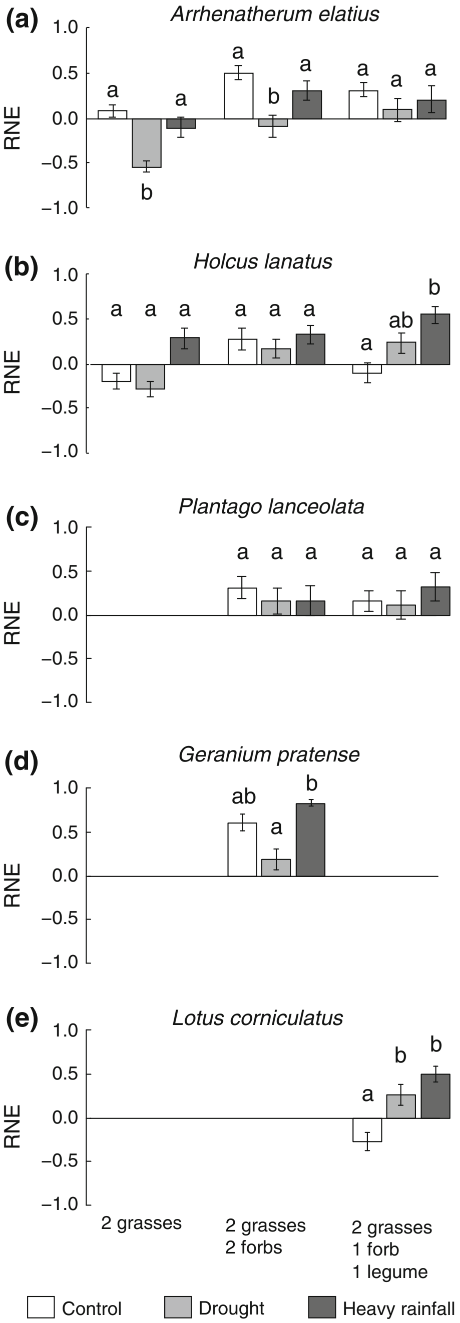

Fig. 2 Relative Neighbour Effect (RNE) on **a** *Arrhenatherum elatius,* **b** *Holcus lanatus,* **c** *Plantago lanceolata*, **d** *Geranium pratense*, and **e** *Lotus corniculatus* in three different community compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. *Small letters* indicate significant differences between weather treatments for a given community ($p < 0.05$)

Results

Drought effects on RNE on grassland species

We found mixed responses of Relative Neighbour Effect (RNE) to extreme drought, which varied across species. *Arrhenatherum elatius* was significantly facilitated by neighbouring plants under drought compared to controls in the communities where it was growing with one more grass species (Fig. 2a, $p = 0.006$) or with two grass and two forb species (Fig. 2a, $p = 0.049$). However, *Lotus corniculatus* RNE increased significantly under extreme drought compared to controls, (Fig. 2e, $p = 0.041$) representing a shift from facilitation to competition by neighbours. *Geranium pratense* and *Plantago lanceolata* had positive RNE values (Fig. 2c, d) both under ambient conditions and when exposed to extreme drought. However, RNE on *G. pratense* was marginally lower in the drought treatment than under ambient conditions ($p = 0.093$), indicating competitive release. Competition intensity experienced by *Holcus lanatus* was not affected by drought (Fig. 2b).

Heavy rainfall effects on RNE on grassland species

Heavy rainfall caused alterations of plant neighbour effects on two of the five studied grassland species. RNE on *L. corniculatus* and *H. lanatus* increased significantly under heavy rainfall compared to controls (Fig. 2, $p = 0.002$ and $p = 0.012$) representing a shift from facilitation to competition by neighbours. However, the higher competitive pressure of neighbouring species on *H. lanatus* individuals after heavy rainfall was found only in communities composed of three functional groups. Heavy rainfall did not alter the neighbour effects on *A. elatius, P. lanceolata* and *G. pratense* compared to ambient weather conditions (Fig. 2a, c, d). However, in communities composed of two functional groups, the competitive pressure on *G. pratense* was significantly higher than on all other species when subjected to heavy rainfall (interaction weather treatment × species: $F_6 = 2.47$ $p = 0.025$). Furthermore, RNE on *A. elatius* was significantly higher compared to RNE on *L. corniculatus* under ambient weather conditions in communities composed of three functional groups. This difference disappeared in the heavy rainfall treatment.

None of the five species were significantly facilitated by neighbouring plants under heavy rainfall compared to ambient weather conditions.

Grass species interactions in communities with altered functional composition

The grass species *A. elatius* and *H. lanatus* increased in the degree of crowding with increasing number of functional groups (Fig. 3, $F_2 = 34.6$ $p < 0.001$ and $F_2 = 72.8$ $p < 0.001$). The Relative Crowding on *A. elatius* was significantly higher in the heavy rainfall treatment (Fig. 3a) compared to control and drought treatment. Relative Crowding on *H. lanatus* was not affected by weather treatments (Fig. 3b, $F_2 = 0.6$, $p = 0.561$). Under extreme drought, Interaction Strength of *A. elatius* was significantly decreased compared to controls with the exception of communities with three functional groups (Fig. 4a). The Interaction Strength of *H. lanatus* per unit neighbour mass increased with heavy rainfall in presence of three functional groups (Fig. 4b, $p = 0.047$). In general, the competitive effect of neighbouring plants on *A. elatius* rose with increasing number of functional groups ($F_2 = 5.3$, $p = 0.006$). However, RNE on *H. lanatus* changed with altered community composition (Fig. 2b, $F_2 = 3.3$ $p = 0.040$) without clear direction.

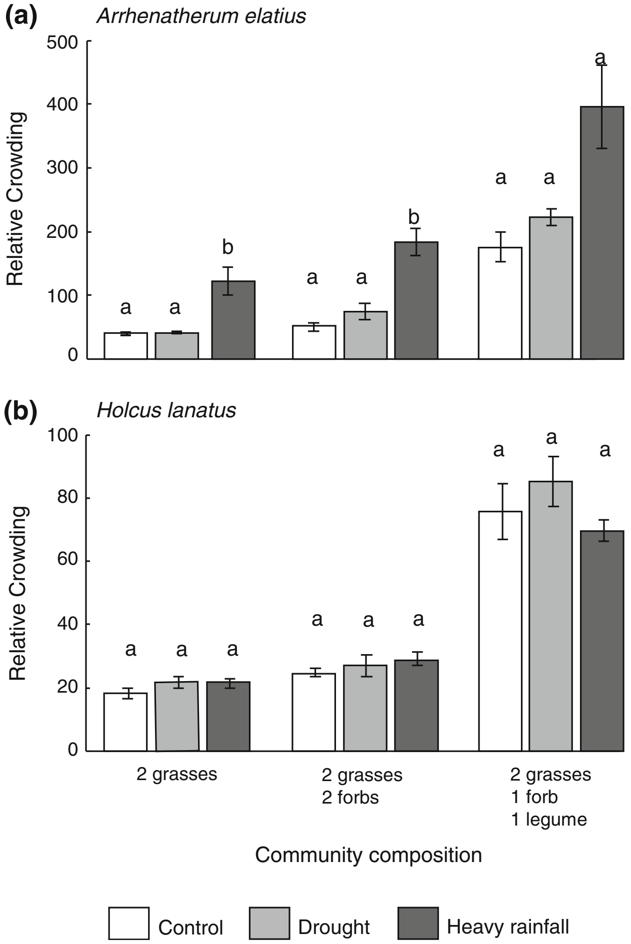

Fig. 3 Relative Crowding on **a** *Arrhenatherum elatius* and **b** *Holcus lanatus* in three different community compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. *Small letters* indicate significant differences between weather treatments for a given community ($p < 0.05$)

Aboveground biomass of species individuals and grassland communities

Aboveground biomass of isolated individuals of *A. elatius* decreased by drought ($p = 0.019$, Fig. 5a) and heavy rainfall ($p < 0.001$) compared to controls, whereas biomass of isolated *L. corniculatus* individuals increased by drought and heavy rainfall (both treatments $p < 0.001$; Fig. 5e). Biomass of individuals grown in mixtures responded only to extreme heavy rainfall (Fig. 5). Biomass of *L. corniculatus* grown in communities composed of three functional groups was lower in the heavy rainfall treatment than under ambient conditions ($p = 0.013$). *H. lanatus* and *A. elatius* showed reduced individual biomass only in communities composed of three functional groups ($p = 0.002$ and $p = 0.049$), though biomass of both species individuals in communities with two grass species was marginally lower in heavy rainfall compared to controls ($p = 0.092$ and $p = 0.058$).

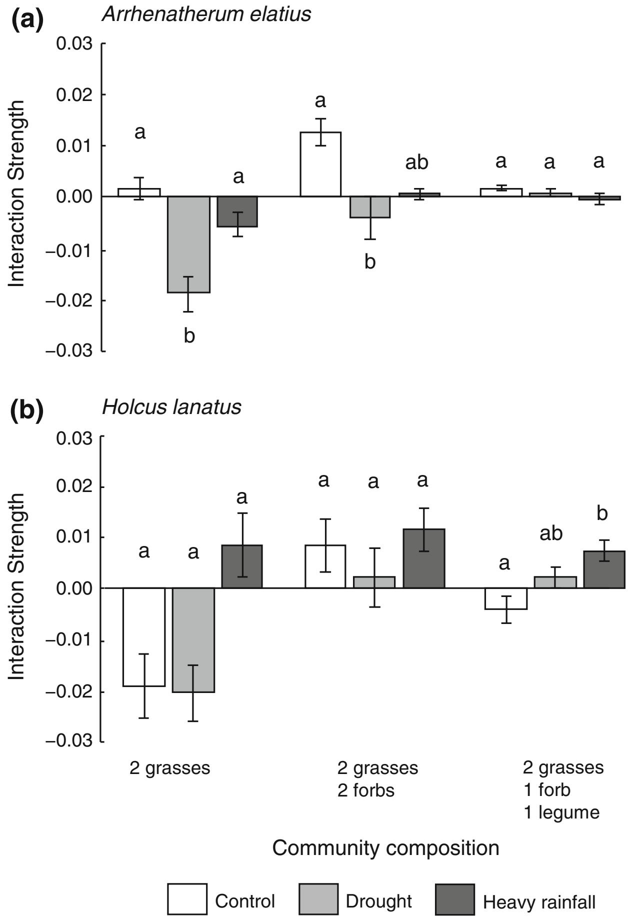

Fig. 4 Interaction Strength of (**a**) *Arrhenatherum elatius* and (**b**) *Holcus lanatus* in three different community compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. *Small letters* indicate significant differences between weather treatments for a given community ($p < 0.05$)

Total community biomass was not affected by extreme drought or heavy rainfall compared to ambient weather conditions ($F_2 = 0.4$, $p = 0.668$). Communities with most functional groups including the legume species *L. corniculatus* were always the most productive ($F_2 = 103.6$, $p < 0.001$).

Discussion

Plant-plant interactions in response to drought

We found indications of facilitation by neighbouring plants in the face of drought. *A. elatius* was facilitated by its neighbours when it grew in communities with the grass species *H. lanatus* and in communities with *H. lanatus, G. pratense and P. lanceolata*. Furthermore, *G. pratense* tended to be subjected to a lower competitive effect from neighbouring plants when exposed to drought. This could be indicative for release from competition with respect to growth under ambient conditions. Similar responses have been found in other field experiments, where facilitative effects were more evident in dry and hot years (Callaway and Walker 1997), and where positive effects became stronger as abiotic stress increased (Callaway 1997). There may be a nursing effect caused by neighbouring plants which cast shade and therefore lead to lower transpiration demands, increased soil water availability and improved conditions for root growth (Holmgren et al. 1997; Armas et al. 2008; Schöb et al. 2013). In addition, the anatomy of the neighbouring species *H. lanatus* and *G. pratense* regarding water and gas exchange is mesomorphic to hygromorphic (Ellenberg 1979) and we can assume that they might not be as effective as *A. elatius* in the use of the "additional" resources. *A. elatius* is expected to better exploit water from soils than other grasses due to its extensive root systems (Grime et al. 2007).

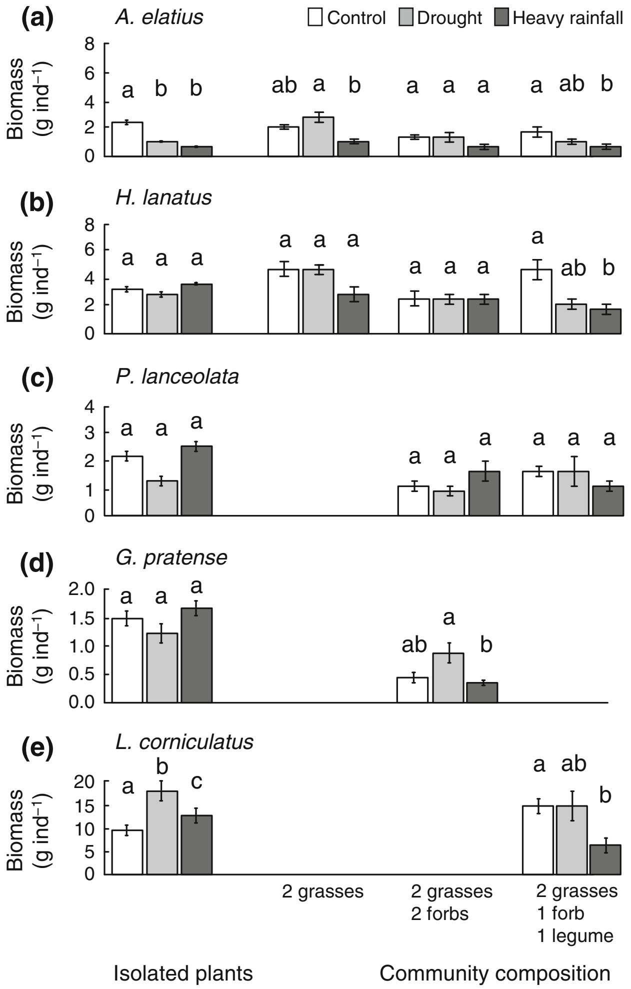

Fig. 5 Aboveground biomass of plant individuals of **a** *Arrhenatherum elatius*, **b** *Holcus lanatus*, **c** *Plantago lanceolata*, **d** *Geranium pratense*, and **e** *Lotus corniculatus* grown in isolation or in three different communities compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. *Small letters* indicate significant differences between weather treatments for a given community ($p < 0.05$)

The neighbourhood of the legume species *L. corniculatus* shifted from facilitative to competitive conditions under drought. Under ambient weather conditions, *L. corniculatus* had a competitive advantage most likely due to its ability to fix additional atmospheric nitrogen which led to bigger plant individuals compared to other species in this study. Drought very likely disrupted this competitive advantage. Abdelhamid et al. (2011) showed that the drying of the upper soil layer affected the root nodules and reduced the proportion of nitrogen derived from the atmosphere of *Vicia faba*. Furthermore, Arfin Khan et al. (2014) found that the presence of a legume species facilitated the community productivity of non-legume neighbour plants under ambient weather conditions but not under recurrent drought events. However, they saw reduced N-uptake rather than reduced N-fixation by the legume as an explanation for the missing facilitative legume effect under drought. Water is the major solvent and transport agent for nutrients and therefore it controls the nitrogen cycle (Akmal and Janssens 2004). The combination of water and nitrogen deficits limits plant productivity (Sadras 2005).

Hence, we can only confirm our first hypothesis—that under extreme drought competitive intensity will decrease—for one out of five studied species, as we also found inverse reactions within one of our study species. However, the facilitation of the competitor *A. elatius* in two plant communities and the increased competitive effect on the stress-tolerant-CSR-strategist *L. corniculatus* (Grime et al. 2007) support the idea that competitors are more facilitated than the stress-tolerators (Michalet et al. 2006).

Plant-plant interactions in response to heavy rainfall

Neighbouring plants imposed significantly more competitive pressure upon *L. corniculatus* and *H. lanatus* in communities composed of three functional groups when facing a heavy rainfall event. This contrasts with the findings of White et al. (2001) who found no effects on competitive intensity for grasses under extreme rainfall. However, several studies from arid or semi-arid systems observed competition rather than facilitation under a ‘less dry situation’ (Holmgren et al. 1997). The higher competition experienced by *L. corniculatus* and *H. lanatus* suggest that this tendency toward competition exists also under very wet conditions—such as water-logging due to heavy rainfall—and also applies for a mesic grassland system. Furthermore, with increased soil moisture other factors, such as light, might become more important and limiting (Holmgren et al. 1997; Novoplansky and Goldberg 2001; Holmgren et al. 2012). Thus, the canopy of neighbouring plants and its shading function might have increased the constraint for the target plants. This is indicated by highest Relative Crowding in the community including legumes and by the reduced biomass of *L. corniculatus* grown in mixture, compared to the increased biomass of isolated individuals due to heavy rainfall. Furthermore, the decrease in individual biomass of three of the target species in the mixture and in isolated biomass of *A. elatius* plants in response to heavy rainfall indicates that photosynthesis and transpiration were reduced as a consequence of decreased soil oxygen due to water-logging (compare Striker et al. 2005).

Reduced soil oxygen due to water-logging during the heavy rainfall event may limit the symbiosis between the legume *L. corniculatus* and nitrogen-fixing bacteria as a result of reduced oxygen transport in submerged nodules (James and Crawford 1998). This phenomenon may explain the reduced competitive advantage of *L. corniculatus* observed and the increased competitive effects of neighbouring plants on *L. corniculatus*.

The results for *H. lanatus* and *L. corniculatus* imply higher competition as opposed to facilitation for plants subjected to heavy rainfall. Facilitation by neighbouring plants for these grassland species was not visible when subjected to heavy rainfall. Thus, we have to reject our second hypothesis because we did not find species that were facilitated by the suppression of other species which struggle under heavy rainfall.

Grass species interactions in communities with altered functional composition

The importance of community composition for plant–plant interactions was indicated by alterations in competitive pressure of neighbouring plants on our target species *A. elatius* and *H. lanatus*. It is not surprising that with increasing number of species and functional groups the competition by density and size of neighbours (Relative Crowding) and the general competitive pressure (RNE) increased. Zhang et al. (2008) mentioned that species response to the stress imposed by changed environments can be modified or amplified by the presence of coexisting species. The facilitative effect of neighbouring plants on *A. elatius* was found in two of the three communities. Given that Relative Crowding was not affected by drought, this reduced competitive effect was mostly caused by higher competitive ability and a lower decrease in performance of *A. elatius* in the communities composed of one or two functional groups, as indicated by the decreased Interaction Strength. With the addition of another functional group—the legume *L. corniculatus*—into the community, neighbour effects on *A. elatius* were competitive in all treatments, caused by lower competitive ability of *A. elatius* (I) and the higher competition by neighbour abundance (D_r’).

The increase of competition induced by heavy rainfall experienced by *H. lanatus* was most pronounced in the presence of *L. corniculatus,* since the competitive ability of *H. lanatus* to gain the shared limiting resources decreased. There are controversial studies on the benefit for grasses grown in mixture with legumes (Quinos et al. 1998; Zhang et al. 2008). Ledgard and Steele (1992) noted that factors favouring legume performance decreased the performance of associated grasses and also that stress on legumes enhanced the competitiveness of grasses. The shift from facilitation to competition for *L. corniculatus* under drought and heavy rain and the modified responses of the tested grasses in the communities which included the legume indicate that a legume might play a key role in plant–plant interactions under climate change. However, we did not repeat our test with community compositions of other species, so that our findings might be a sampling effect of *L. corniculatus*. Further experiments are required with other species combinations to confirm the generality of our results. Nevertheless, these results provide evidence of climate extremes and induced alterations in competitive intensity including facilitation and competition among species, depending on the complexity of community composition.

Shifting directions of plant–plant interactions—one important mechanism for stability in aboveground biomass?

We found that aboveground biomass of the grassland communities was not altered by extreme drought or heavy rainfall events, although soil moisture was significantly reduced and increased, respectively, implying high plant water stress. Plant water stress was demonstrated during the same drought event in the same plots and year (Otieno et al. 2012), this was expressed as a decline of leaf water potential and less negative delta ^{13}C for *A. elatius*. Other studies have confirmed that plant communities facing extreme weather events are more stable than previously thought (Jentsch et al. 2011; Miranda et al. 2011; Lloret et al. 2012). There are several possible factors influencing the stability of plant community functioning in multi-species communities, such as complementary resource use, resilience of dominant or keystone species, or redundancy of species roles (Hooper et al. 2005). Species rich communities are hypothesized to insure ecosystem performance because they likely contain plant species which can compensate if other species suffer or die due to fluctuating environments (Yachi and Loreau 1999). Accordingly, plant species that are of minor importance today can become more relevant if previously dominant or more competitive species decline or fail in the face of climate change (Walker et al. 1999).

Neighbour effects can easily shift from competition to facilitation and vice versa, because what is facilitative for one plant might be negative for another plant (Holmgren et al. 1997). Thus, shifts in competitive intensity among species may prove to be a key mechanism contributing to the stability of plant community productivity under extreme weather events. In this study, the grassland species showed species specific responses in competition intensity to the extreme events. This species specific response is in accordance with other studies and can result from species specific optima and stress-tolerance as well as from possible modifications or amplifications induced by other species (Zhang et al. 2008). However, especially for drought, the event led to opposite species interactions. Facilitation strongly countered the direct effect of drought on *A. elatius* as isolated individuals were smaller than individuals grown in mixtures and probably helped to stabilize the biomass of the communities without the legume. Greater competition under drought prevented *L. corniculatus* from increasing the community biomass, although drought led to increases of this species when grown in isolation.

Conclusion

Our snapshot on the plant–plant interactions at the peak of abiotic plant stress due to extreme drought and heavy rainfall events in artificial grassland communities indicates that the competitive behaviour of grassland species can be species specific and reciprocal under the influence of extreme weather events. Single climatic extremes caused shifts in plant–plant interactions from facilitation to competition or vice versa for *A. elatius, H. lanatus* and *L. corniculatus*, but the nature of the shifts varied depending on the community composition. The presence of a legume in the plant communities appeared to have a key role in the response of competition intensity experienced by grasses to climate change. Furthermore, our results for plant–plant interactions suggest that a change in competitive balance among grassland plants might be one of the mechanisms for stable community productivity in the face of drought. Therefore, contrasting biotic interactions between grassland species should be acknowledged when modelling plant–plant interactions and predicting plant community shifts due to climate change.

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