

The role of drought- and disturbance-mediated competition in shaping community responses to varied environments

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Abstract By altering the strength of intra- and inter-specific competition, droughts may reshape plant communities. Furthermore, species may respond differently to drought when other influences, such as herbivory, are considered. To explore this relationship, we conducted a greenhouse experiment measuring responses to inter- and intraspecific competition for two grasses, *Schedonorus arundinaceus* and *Paspalum dilatatum*, while varying water availability and simulating herbivory via clipping. We then parameterized population growth models to examine the long-term outcome of competition under these conditions. Under drought, *S. arundinaceus* was less water stressed than *P. dilatatum*, which exhibited severe water stress; clipping alleviated this stress, increasing the competitive ability of *P. dilatatum* relative to *S. arundinaceus*. Although *P. dilatatum* competed weakly under drought, clipping reduced water stress in *P. dilatatum*, thereby enhancing its ability to compete with *S. arundinaceus* under drought. Supporting these observations, population growth models predicted that *P. dilatatum* would exclude *S. arundinaceus*

when clipped under drought, while *S. arundinaceus* would exclude *P. dilatatum* when unclipped under drought. When the modeled environment varied temporally, environmental variation promoted niche differences that, though insufficient to maintain stable coexistence, prevented unconditional competitive exclusion by promoting priority effects. Our results suggest that it is important to consider how species respond not just to stable, but also to variable, environments. When species differ in their responses to drought, competition, and simulated herbivory, stable environments may promote competitive exclusion, while fluctuating environments may promote coexistence. These interactions are critical to understanding how species will respond to global change.

Keywords Climate change · Coexistence · Herbivory · Plant community composition · Grassland

Introduction

Competition often structures plant communities experiencing water limitation (Fowler 1986; Goldberg and Novoplansky 1997; Bu et al. 2013). Due to the effects of climate change, both the duration and frequency of future droughts are predicted to increase for many areas around the world (Wetherald and Manabe 2002; Bedel et al. 2013). Severe drought may alter community composition directly via effects on survival and fecundity, as well as indirectly by influencing competitive interactions (Adler et al. 2012; López et al. 2013). Understanding the effects of water availability on competition between grasses may foretell future changes in community composition.

In order to compete under drought stress, grasses must efficiently acquire and use water (Schenk and Jackson

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2002; Flexas et al. 2004; Taylor et al. 2011). If water were consistently limiting, then drought-tolerant species could replace drought-intolerant competitors (Grime 1985). By contrast, when water is less limiting, competition may shift from belowground competition for water to aboveground competition for light (Tilman 1994; Angert et al. 2009; Huxman et al. 2013). Thus, fluctuating environmental conditions—including periods of high precipitation—will situationally favor species with different suites of traits (Adler et al. 2006), promoting coexistence (Chesson 2000).

Competition under drought stress can be an important determinant of plant community composition (Bu et al. 2013; Koyama and Tsuyuzaki 2013). For instance, increasing drought stress may shift interactions between plant species from facilitative to competitive (Bu et al. 2013). Drought stress may also decrease tolerance to competition, such that even reduced competition could have pronounced effects on community structure (Holt 1985). Yet species may be able to coexist under drought stress if they vary spatially or temporally in their resource use (Chesson and Huntly 1997; Chesson 2000; Angert et al. 2009). Furthermore, species may coexist if their responses to drought stress differ. This may occur because of physiological differences in drought tolerance or other environmental factors that alter water availability (Tilman 1990; Angert et al. 2009).

In grasslands, physiological responses to drought stress may be influenced by photosynthetic pathway (Taylor et al. 2011). Grasses use either the C3 or C4 photosynthetic pathway, which broadly shapes the distribution of grass species throughout the world (Taylor et al. 2010). The C4 pathway requires a greater initial energy investment, thereby minimizing energy and resource loss through photorespiration (Zhu et al. 2008). As a result, C4 species have higher water-use efficiency but lower maximal rates of photosynthesis than C3 species (Zhu et al. 2008; Wang et al. 2014). While C4 photosynthesis may have evolved as an adaptation to the open, arid habitats that C4 grasses currently dominate, recent studies have suggested that the physiological advantages conferred by the C4 pathway will not persist under predicted future drought conditions (Edwards and Still 2008; Taylor et al. 2011). During drought, photorespiration can promote quick recovery from drought stress in C3 plants, whereas photorespiration is limited in C4 plants (Ghannoum 2009). This may explain the greater susceptibility of C4 plants to drought stress despite superior water use efficiency (Ghannoum 2009). In part due to these differences, drought-induced declines in C4 photosynthetic performance relative to C3 performance may be a general trend (Taylor et al. 2011).

While each photosynthetic pathway will be favored under different moisture regimes (Taylor et al. 2011), these advantages could be mitigated by aboveground herbivory. Herbivores remove biomass, which can reduce evapotranspiration and increase water availability (Luo et al. 2012).

With more water available following herbivory, drought-intolerant species may coexist with drought-tolerant species under conditions where drought-intolerant species would otherwise be excluded.

To fully understand the long-term effects of variable environments on competition, an integrative approach combining unbiased empirical data with population growth models is desirable. Greenhouse experiments examining the effects of water availability and simulated herbivory on competition between plant species are often of limited duration, but can provide precise estimates of competition intensity (Gao et al. 2008; Carlyle et al. 2010). While observational studies highlight long-term community dynamics under current climatic conditions, they provide less precise estimates of competition-free growth, and intraspecific and interspecific competition in isolation. Furthermore, in field studies species traits are often more variable, obfuscating the relative importance of competition in explaining coexistence patterns (Gravel et al. 2011). Modeling random fluctuations in environmental factors between years further illustrates the potential cumulative effects of altered competition regimes in response to variable environments. Thus, combining short-term experiments with data-driven models may provide insight into mechanisms underlying the long-term outcome of competition.

Here we test whether drought and simulated herbivory can alter interspecific competition. We first measured the effects of drought and simulated herbivory on competition in the greenhouse between individuals of two dominant grasses of the southeastern USA that differ in photosynthetic pathway. To determine how drought and simulated herbivory would affect the long-term outcome of competition, we then parameterized population growth models for the two species in an environment in which drought and simulated herbivory fluctuated. We predicted that:

1. *Paspalum dilatatum* performance will be reduced more by drought than *Schedonorus arundinaceus* performance.
2. By alleviating drought stress, simulated herbivory will provide a relative advantage to *P. dilatatum* over *S. arundinaceus*.
3. If *P. dilatatum* and *S. arundinaceus* differ in their relative responses to drought and simulated herbivory, fluctuation in these two factors could promote coexistence.

Materials and methods

Study species

We examined the interactions between two co-occurring grass species that differ in physiology: *Paspalum dilatatum*

Poir. is a perennial C4 forage grass native to South America (Jacobó et al. 2009) and *Schedonorus arundinaceus* Schreb. is a perennial C3 grass native to Europe that has been planted widely throughout North America (Gibson and Newman 2001). These species often co-occur in herbaceous-dominated systems and, due to differences in photosynthetic pathway, these species may respond differently to future fluctuations in precipitation (Jacobó et al. 2009; Brion et al. 2011; Rúa et al. 2013; Elmore et al. 2013). Specifically, *S. arundinaceus* may be more tolerant of drought (Stuedemann and Hoveland 1988) than *P. dilatatum* (Jacobó et al. 2009).

Greenhouse experiment

We measured the individual-level responses of plants of each species experiencing either no competition, intraspecific competition, or interspecific competition to factorial manipulation of water availability and simulated herbivory. We collected seeds of *P. dilatatum* and *S. arundinaceus* (SCAR) from natural populations in Duke Forest (Orange County, NC) in 2013. We stratified the seeds in moist sand at 4 °C for 30 days and sowed them in flats of Fafard 3B potting medium (Sun Gro Horticulture, Agawam, MA) in the greenhouse at the University of North Carolina (Chapel Hill, NC), where the average temperature for the duration of the study was 23.5 °C. We watered the flats regularly to promote germination. At the two leaf stage (14 days after sowing), we transplanted equal-sized individuals of each species into 938-mL D60 Deepots (Stuewe and Sons, Tangent, OR) filled with Fafard 3B Mix either alone [*P. dilatatum* (PADI) alone (PADI_{single}), *S. arundinaceus* (SCAR) alone (SCAR_{single})], with one conspecific individual (PADI_{intra}, SCAR_{intra}), or with one heterospecific individual (PADI_{inter}, SCAR_{inter}) for a total of five competition treatments (both heterospecific competitors were measured in the same pots). Thus, our experiment comprised 120 pots (6 replicates × 5 competition treatments × 2 water treatments × 2 simulated herbivory treatments).

We allowed the plants to establish for 18 days after transplanting before assigning pots in each competition treatment to one of two watering treatments: drought and water-saturated. We calculated the water-saturated treatment (300 mL H₂O per watering) by slowly adding water until water began to drip from the pot. The drought treatment was 25 % of the high water treatment, mimicking typical drought-stressed conditions (75 mL H₂O per watering) (Emam et al. 2012). We watered all pots every other day for the duration of the experiment. We allowed the plants to acclimate to watering treatments for 15 days before simulating herbivory by clipping half of the pots at 5–6 cm

above the soil surface (clipped) while leaving the other half unmanipulated (unclipped) (Li et al. 2002, 2013).

We used these treatments to observe the effects of drought stress (water treatment) and simulated herbivory (hereafter, “clipping”) on *S. arundinaceus* and *P. dilatatum* in the absence of competition, and in inter- and intraspecific competition. We harvested all aboveground biomass 18 days after clipping for a total duration of 65 days. We dried all biomass harvested at the end of the experiment at 60 °C for a minimum of 48 h then weighed the samples to determine aboveground biomass. Despite the limited duration of this experiment, the roots of plants grown in competition could not be separated with certainty. This prevented us from estimating belowground biomass, a common occurrence among similarly designed studies (e.g., Carlyle et al. 2010; McGlone et al. 2012).

Relative competitive intensity

Following Carlyle et al. (2010), we used aboveground biomass to calculate the relative competitive intensity (RCI)—the effect of competition on the target individual from its neighbor—for each species in both intra- and interspecific competition for each of the four combinations of water and clipping treatments. RCI is the difference between the biomass of an individual grown alone (i.e., SCAR_{single}, PADI_{single}) and the mean biomass of conspecifics in either inter- or intraspecific competition with the same watering × clipping treatment, divided by the larger of the two values (Grace 1995; Brooker et al. 2005; Carlyle et al. 2010). High RCI denotes greater relative reduction in biomass and indicates increased competitive pressure on the target individual.

Foliar traits

In order to quantify the drought stress experienced by each plant, we calculated realized leaf water content (RLWC). At harvest we removed the youngest fully expanded leaf from each plant and weighed the leaf (wet mass). We then dried these leaves for 48 h at 60 °C and reweighed them (dry mass). We calculated RLWC as the percent foliar water content: the difference between wet mass and dry mass, divided by the wet mass.

Prior to our clipping treatment, we harvested the youngest fully emerged leaf from each individual to calculate leaf mass per area (LMA). While RLWC is an effective measure of short-term water stress, LMA may be a better indicator of long-term drought stress because there is a strong negative correlation between LMA and growth rates (Nielsen et al. 1996). We calculated LMA as the oven-dried

leaf mass divided by the leaf area (Winfolia, Regent Instruments, Canada) for each sample (Pérez-Harguindeguy et al. 2013).

Data analysis

We analyzed the effects of water availability (drought vs. water saturated), clipping (clipped vs. unclipped), and competition (competitor absent vs. intraspecific competitor vs. interspecific competitor) on biomass and RLWC for each species with a three-way ANOVA in Proc Mixed in SAS version 9.4 (SAS Institute, Cary, NC). Since LMA was measured prior to clipping treatment, we performed a two-way ANOVA on LMA with water availability and competition as predictors. We also ran a four-way ANOVA to determine the effect on RCI for each species with the added effect of species identity. In order to determine whether these species differed in their tolerance to clipping under different competitive regimes and water availabilities, we ran an additional four-way ANOVA focusing on the interactive effects of these treatments on biomass production. We compared the biomass responses to clipping under different conditions and across species in order to determine whether the slopes differed across species or environments (i.e., significant species \times clipping \times water \times competition interaction) (Hawkes and Sullivan 2001; Wise and Abrahamson 2005, 2007). Significant differences in responses (slopes) would indicate different tolerance to clipping (Wise and Abrahamson 2005, 2007). For the intraspecific competition pots, we averaged the biomass, RLWC, LMA, and RCI of the two individuals to maintain independence in design. As noted in previous experiments, our interspecific competition treatment lacks true independence between observations (i.e., SCAR_{inter} and PADI_{inter} were measured in the same pot) (Antonovics and Fowler 1985; Inouye 2001). Thus, results from this treatment are informative but should be viewed cautiously. Interspecific competition results were omitted from the four-way ANOVA examining tolerance to clipping. Spatial block did not contribute significantly to any of the models and was not included in any statistical analyses. When we detected a significant treatment effect in an ANOVA, we compared treatment means with Tukey's post hoc separation tests.

Discrete time population growth model

To project how changes in competitive effects due to drought and clipping may affect competition in grassland communities, we used a discrete time model based on the greenhouse experiment to examine how competitive reversals mediated by environmental conditions could alter the outcome of competition in the field. We emphasize that although the models are parameterized using our empirical

data and other data from the literature to match the biology of the focal species as closely as possible, we cannot expect to quantitatively predict the outcome of competition (Online Resource 1). Furthermore, the model does not explicitly make use of a seed bank due to the shorter duration of the study as well as a lack of relevant data for these two species. Instead, the model provides insight into the influence of drought and clipping on the outcome of competition for long-lived individuals in a biologically realistic setting. We modeled population growth for the two species as:

$$N_s(t+1)/N_s(t) = s_s + \lambda_s / (1 + \alpha_{ss} \times N_s(t) + \alpha_{sp} \times N_p(t))$$

$$N_p(t+1)/N_p(t) = s_p + \lambda_p / (1 + \alpha_{pp} \times N_p(t) + \alpha_{ps} \times N_s(t))$$

where $N_s(t)$ and $N_p(t)$ are the number of *S. arundinaceus* and *P. dilatatum* plants in year t , respectively. The rate of change in population size from 1 year to the next is equal to the fraction of individuals that survive the year, s , plus the newly germinated seedlings. The number of germinated seedlings is equal to the number of seeds per individual that germinate in the absence of competition, λ , decreased by the per capita effects of intra- (α_{ss} and α_{pp}), and interspecific (α_{sp} and α_{ps}), competition. This model begins tracking plants shortly after germination, rather than at the seed stage as in similar models (e.g., Levine and Rees 2004). The model assumes that dormant seeds do not contribute substantially to population growth. Simulations were conducted for a variable environment, constant average conditions, and each individual environment (Online Resource 1). Because our model incorporates germination into λ and tracks plants rather than seeds, it more closely resembles a lottery model (Dewi and Chesson 2003) than an annual plant seed bank model (e.g., Chesson 2000). For this reason, temporal fluctuations are unlikely to stabilize our model in a manner consistent with the storage effect (e.g., buffering through seed banks). Rather, our model examines variability in competition (and corresponding λ) between adult plants across environments, which can equalize niche differences and may also promote coexistence.

To determine if the model predicted stable coexistence for each set of parameters, we calculated growth rates when rare (GRWR) for both species. GRWR, also called invasion growth rates, measure the per capita rate of increase for a species introduced at low density when its competitor is at its single-species stochastic equilibrium. When GRWR of both species exceed 1, coexistence is stable; when only one species' GRWR exceeds 1, it competitively excludes the other species; when neither species' GRWR exceeds 1, priority effects occur with the outcome dependent on initial conditions (i.e., N_0 for each species). GRWR were calculated for all environments (Online Resource 1). Furthermore, to evaluate the effects of changes in our parameters

on the model outcome, we conducted a sensitivity analysis (Online Resource 1).

Results

Biomass

Clipping significantly reduced the biomass of *S. arundinaceus*, particularly when clipped plants also experienced drought ($P = 0.004$) or competition ($P < 0.001$; Table 1; Fig. 1a). *Schedonorus arundinaceus* individuals that experienced drought and competition also had less biomass than individuals that were exposed to drought but free of competition (Table 1; Fig. 1a). Unlike *S. arundinaceus*, competition did not significantly reduce the biomass of *P. dilatatum* in the water-saturated, unclipped treatment (Table 1; Fig. 1b). *Paspalum dilatatum* biomass was reduced by clipping ($P < 0.001$) and drought ($P < 0.001$; Table 1; Fig. 1b), confirming our prediction that drought would reduce *P. dilatatum* performance. Overall, drought and competition interacted to more strongly affect *S. arundinaceus* than *P. dilatatum*.

Realized leaf water content

Drought significantly reduced RLWC in *S. arundinaceus* ($P < 0.001$; Table 2; Fig. 1c). By contrast, under drought conditions, clipping increased RLWC of *S. arundinaceus* ($P < 0.001$; Table 3; Fig. 1c). Drought, clipped individuals free of competition exhibited significantly higher RLWC than the drought, clipped individuals in the interspecific competition treatment (Table 2; Fig. 1c). Under drought conditions, *S. arundinaceus* growing in interspecific competition had lower RLWC than when growing free of competition ($P = 0.01$; Table 2; Fig. 1c). Overall, drought and competition interacted to reduce RLWC most in *S. arundinaceus*.

Similarly, *P. dilatatum* had significantly lower RLWC under drought ($P < 0.001$), while clipping increased RLWC under drought ($P < 0.001$; Table 2; Fig. 1d), confirming our second prediction that clipping reduces drought stress in *P. dilatatum*. Furthermore, *P. dilatatum* experiencing competition in the drought, clipped group had lower RLWC than individuals free of competition ($P = 0.003$; Table 2; Fig. 1d). In *P. dilatatum*, unclipped pots experiencing drought had the lowest RLWC regardless of competition treatment (Fig. 1d). Overall, drought reduced RLWC most in *P. dilatatum*.

Leaf mass per area

LMA did not differ between treatments for *S. arundinaceus* (Table 3; Fig. 1e). For *P. dilatatum*, drought significantly

Table 1 Results of three-way ANOVAs for experimental treatment on aboveground biomass of *Schedonorus arundinaceus* and *Paspalum dilatatum*

Source of variation	df	<i>S. arundinaceus</i>		<i>P. dilatatum</i>	
		F	P-value	F	P-value
Drought	1	61.33	<0.001	13.96	<0.001
Clipping	1	122.33	<0.001	48.99	<0.001
Competition	2	56.58	<0.001	3.51	0.036
Drought × Clipping	1	9.18	0.004	10.24	0.002
Drought × Competition	2	4.05	0.022	0.27	0.76
Clipping × Competition	2	11.94	<0.001	1.91	0.16
Drought × Clipping × Competition	2	1.18	0.31	0.08	0.92

increased LMA regardless of competition treatment ($P < 0.001$; Table 3; Fig. 1f).

Competition

On average, *S. arundinaceus* had significantly higher RCI than *P. dilatatum* (Table 4; Fig. 2), indicating a larger relative effect of competition on *S. arundinaceus*. *Paspalum dilatatum* experienced higher intraspecific competition—with minimal interspecific competition indicated by negative RCI—in water-saturated, clipped pots (Table 4; Fig. 2). Across all species × competition combinations, only RCI for interspecific competition in *S. arundinaceus* was significant ($P < 0.001$). The species also differed significantly in their competitive responses to drought ($P = 0.007$). Overall, interspecific competition was greater on *S. arundinaceus* than any other competitive effect on either species.

Tolerance to clipping

These species differed significantly in their response to clipping under different water availability (Table 4). Overall, *S. arundinaceus* was more tolerant of clipping than *P. dilatatum*, especially in water-saturated pots. There, *P. dilatatum* was particularly intolerant of clipping as indicated by the large reduction in biomass of water-saturated *P. dilatatum* pots following clipping ($P = 0.025$; Fig. 3).

Population growth model

We simulated the population growth models with empirical parameter values for 5000 years (Table 5). First, we simulated the model under each of the four constant environment conditions. The outcome varied across the four scenarios. *P. dilatatum* stably coexisted with *S. arundinaceus* in the water-saturated, clipped environment, with GRWR of 1.063 and 1.012, respectively. *P. dilatatum* excluded *S.*

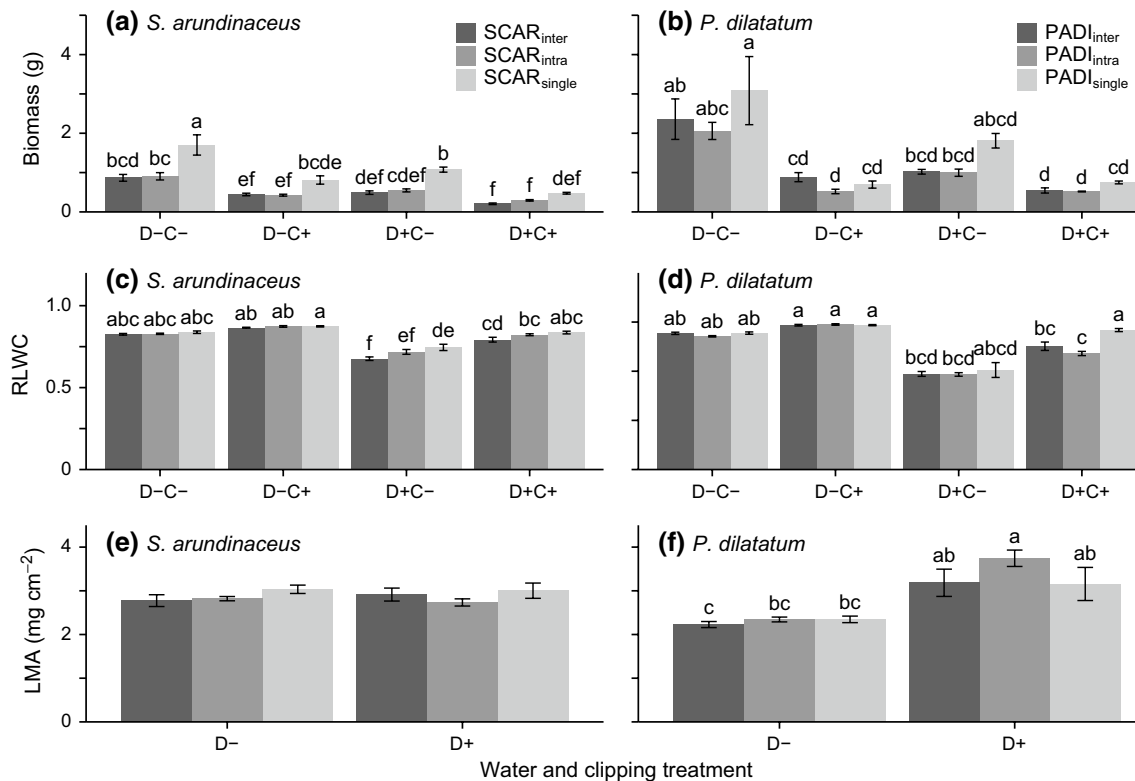


Fig. 1 Performance of *Schedonorus arundinaceus* and *Paspalum dilatatum* under three levels of competition {no competitors [*S. arundinaceus* (SCAR) alone (SCAR_{single}), *P. dilatatum* (PADI) alone (PADI_{single})], competition with conspecifics (SCAR_{intra}, PADI_{intra}), competition with heterospecifics (SCAR_{inter}, PADI_{inter})}, two levels of water availability [drought (D+), water saturated (D-)], and two clipping treatments [clipped (C+), unclipped (C-)]. Values are

mean \pm SE for **a** aboveground biomass of *S. arundinaceus*, **b** aboveground biomass of *P. dilatatum*, **c** mean relative leaf water content (RLWC) of *S. arundinaceus*, **d** mean RLWC of *P. dilatatum*, **e** mean leaf mass per area (LMA) of *S. arundinaceus*, **f** mean LMA of *P. dilatatum*. Shared letters denote no significant differences between treatments based on Tukey post hoc tests

Table 2 Results of three-way ANOVAs for experimental treatment on the realized leaf water content of *S. arundinaceus* and *P. dilatatum*

Source of variation	df	<i>S. arundinaceus</i>		<i>P. dilatatum</i>	
		F	P-value	F	P-value
Drought	1	202.97	<0.001	399.85	<0.001
Clipping	1	152.52	<0.001	186.34	<0.001
Competition	2	8.36	<0.001	10.61	<0.001
Drought \times Clipping	1	26.55	<0.001	50.65	<0.001
Drought \times Competition	2	4.84	0.010	7.43	0.001
Clipping \times Competition	2	0.28	0.76	2.67	0.075
Drought \times Clipping \times Competition	2	0.39	0.68	6.11	0.003

arundinaceus in the unclipped, water-saturated scenario (GRWR = 1.264 and 0.967, respectively). In the drought, clipped environment priority effects occurred, and *P. dilatatum* and *S. arundinaceus* had GRWR of 0.841 and 0.870, respectively. In drought, unclipped conditions *S. arundinaceus* excluded *P. dilatatum* with GRWR of 1.204 and 0.777, respectively.

Table 3 Results of two-way ANOVAs for experimental treatment on the leaf mass per area of *S. arundinaceus* and *P. dilatatum*

Source of variation	df	<i>S. arundinaceus</i>		<i>P. dilatatum</i>	
		F	P-value	F	P-value
Drought	1	0.039	0.84	49.62	<0.001
Competition	2	2.69	0.073	1.70	0.19
Drought \times Competition	2	0.59	0.56	1.14	0.32

In the temporally variable environment, the two species exhibited priority effects because both species had GRWR below 1 (GRWR of *S. arundinaceus* = 0.999, GRWR of *P. dilatatum* = 0.998); although *S. arundinaceus* excluded *P. dilatatum* in the simulation shown in Fig. 4a, the reverse occurs under different initial conditions. To illustrate priority effects, we used the same sequence of environmental conditions as in the GRWR simulations and simulated population dynamics from the initial conditions of 1 and 100 for each species, respectively. In each case, the species with the larger starting population won (Fig. 4b, c). However,

Table 4 Results of four-way ANOVA for treatment effects on relative competitive intensity (RCI) and biomass of *S. arundinaceus* and *P. dilatatum*

Source of variation	df	RCI		Biomass	
		F	P-value	F	P-value
Drought	1	11.63	0.001	27.60	<0.001
Clipping	1	12.25	<0.001	113.73	<0.001
Competition	1	2.06	0.15	33.55	<0.001
Species	1	39.76	<0.001	29.94	<0.001
Drought × Clipping	1	0.65	0.42	17.65	<0.001
Drought × Competition	1	7.38	0.008	1.11	0.30
Drought × Species	1	7.62	0.007	0.85	0.36
Clipping × Competition	1	1.66	0.20	10.42	0.002
Clipping × Species	1	7.23	0.009	16.93	<0.001
Competition × Species	1	9.33	0.003	0.08	0.78
Drought × Clipping × Competition	1	4.13	0.045	0.51	0.48
Drought × Clipping × Species	1	1.46	0.23	5.12	0.025
Drought × Competition × Species	1	1.23	0.27	0.41	0.52
Drought × Clipping × Competition × Species	1	0.69	0.41	0.39	0.53

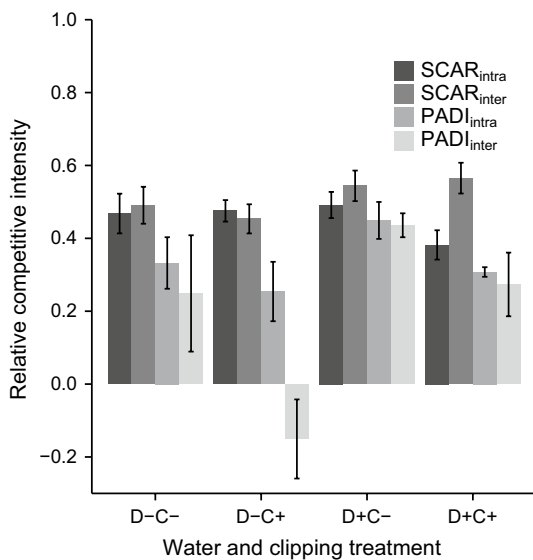


Fig. 2 Relative competitive intensity (RCI) for *S. arundinaceus* and *P. dilatatum* under two levels of competition [competition with conspecifics (SCAR_{intra}, PADI_{intra}), competition with heterospecifics (SCAR_{inter}, PADI_{inter})], two levels of water availability (D+, D-), and two clipping treatments (C+, C-). RCI indicates the competitive pressure exerted on the target individual by its neighbor and ranges from -1 to 1. Values represent mean ± SE (n = 120). For other abbreviations, see Fig. 1

the GRWR of both species were so close to 1 that the outcome of competition may depend on the exact sequence of environmental conditions, and could result in competitive exclusion or the demonstrated priority effects.

In the constant average-environment model, *S. arundinaceus* (GRWR = 1.001) excluded *P. dilatatum* (GRWR = 0.954; Fig. 4d), indicating that environmental

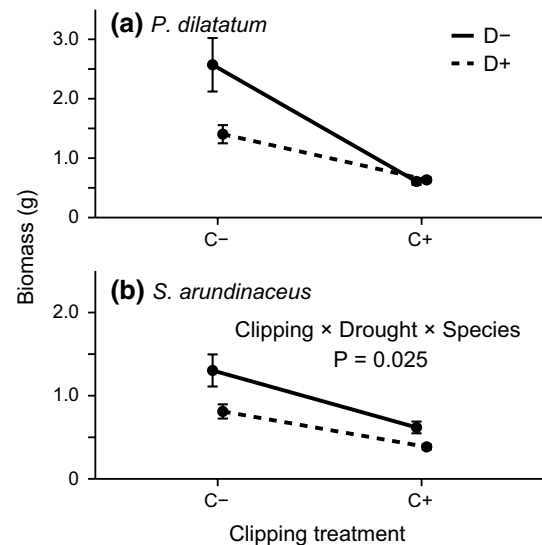


Fig. 3 Biomass response of **a** *P. dilatatum* and **b** *S. arundinaceus* to two levels of water availability (D+, D-), in relation to clipping treatments (C+, C-). Values represent mean ± SE (n = 120). For abbreviations, see Fig. 1

variation reduces species differences in fitness, and potentially also increases niche differences, but is insufficient to promote coexistence. This is likely due to the strongly destabilizing effect of interspecific competition exceeding intraspecific competition for *S. arundinaceus* in three out of four environment scenarios (Table 5).

The species exhibited a tradeoff between recruitment potential, which is likely due to higher germination rates for *S. arundinaceus*, and lower sensitivity to competition, particularly interspecific competition, for *P. dilatatum*

(Table 5; Clay 1987; Schrauf et al. 1995). A sensitivity analysis using 95 % confidence intervals demonstrated that the GRWR of the two species were far more sensitive to changes in competition parameters. This indicates that our model was more sensitive to parameters informed by our

experimental data (Online Resource Fig. S1). In summary, although fluctuations did reduce competitive differences between the two species, the models did not confirm our prediction of coexistence through varied responses to a fluctuating environment.

Table 5 Parameters used in the discrete time population growth model for each species and combination of drought and clipping treatments: drought ($D+$) or water saturated ($D-$), clipped ($C+$) or unclipped ($C-$)

Treatment	λ	Intraspecific α	Interspecific α
<i>S. arundinaceus</i> D– C–	29.9	0.88	0.96
<i>S. arundinaceus</i> D– C+	24.0	0.91	0.83
<i>S. arundinaceus</i> D+ C–	25.7	0.97	1.2
<i>S. arundinaceus</i> D+ C+	21.8	0.62	1.3
<i>P. dilatatum</i> D– C–	16.7	0.50	0.31
<i>P. dilatatum</i> D– C+	9.91	0.34	0.31
<i>P. dilatatum</i> D+ C–	13.1	0.82	0.77
<i>P. dilatatum</i> D+ C+	10.1	0.44	0.37

Survival probability was 0.44 and the initial population size was 1, 100, or resident density depending on the simulation being run

λ Number of germinated seeds produced per individual in the absence of competition, *Intraspecific* α per capita competitive effect of a species on itself, *Interspecific* α per capita competitive effect of the other species on the target species

Discussion

By quantifying the relative strengths of intraspecific and interspecific competition in variable environments, this study evaluates how drought stress and simulated herbivory could mediate plant–plant interactions under a range of future conditions. Specifically, clipping reduced interspecific competition on *P. dilatatum* without substantially altering intraspecific competition, while clipping actually increased interspecific competition on *S. arundinaceus*, especially under drought. Consequently, the model predicted that clipping would reverse the outcome of competition under drought; *P. dilatatum* was excluded under drought without clipping, whereas *S. arundinaceus* was excluded under drought with clipping. Furthermore, research suggests that intense grazing may promote germination in *P. dilatatum* (Cornaglia et al. 2009). Thus, our model may represent a conservative estimate of *P. dilatatum*'s advantage in this scenario. More broadly, the models

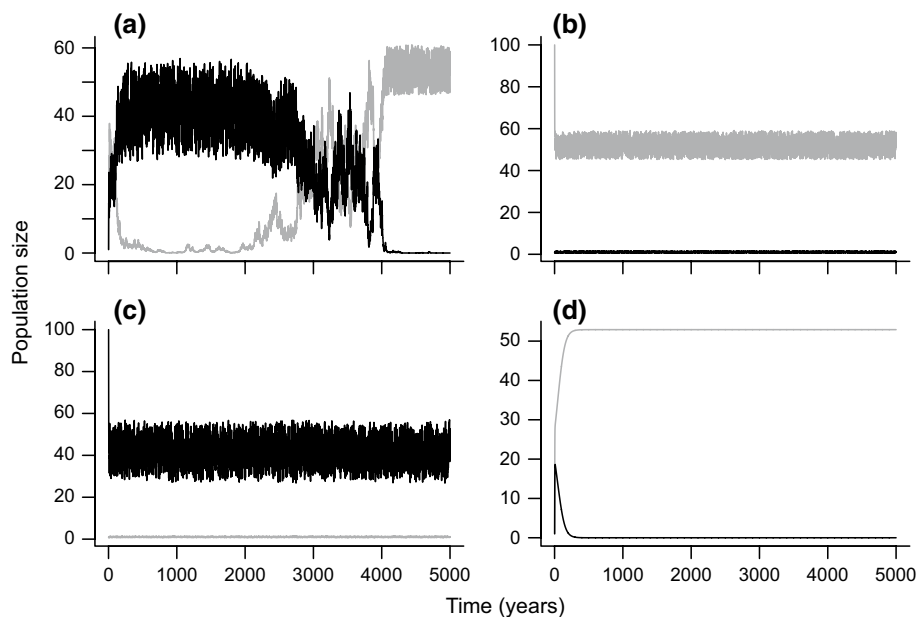


Fig. 4 Output from discrete time population growth model for *S. arundinaceus* (N_s ; grey line) and *P. dilatatum* (N_p ; black line) under different scenarios: **a** temporally variable environment simulation parameterized in each year with the parameter values for each species from a randomly selected set of environmental conditions (drought and clipping); in this scenario, priority effects determine the outcome. **b**, **c** Temporally variable environment simulations parameterized

as in **a** except **b** initial conditions [$N_s(0) = 100$, $N_p(0) = 1$], and **c** initial conditions [$N_s(0) = 1$, $N_p(0) = 100$] showing that neither species could invade when rare. **d** Constant model parameterized with the geometric mean of each parameter which simulated the temporal average of the four sets of environmental conditions. In this scenario, *S. arundinaceus* excludes *P. dilatatum*. For other abbreviations, see Fig. 1

confirmed that different sets of environmental conditions favored *S. arundinaceus* and *P. dilatatum*.

While certain environmental conditions may appear to promote coexistence, our model demonstrated that varying environmental combinations can result in outcomes that would otherwise be unexpected based on empirical evidence in isolation. We note that our goal in the model analysis was to explore how observed effects on biomass could scale to affect population dynamics, rather than to precisely identify the outcome of competition in the field, which will depend on additional factors. Regardless, these patterns largely support our predictions about the effects of drought and clipping; specifically, that species exhibit environment-specific responses that affect their ability to compete. Furthermore, the system was strongly destabilized because interspecific competitive effects on *S. arundinaceus* were greater than the intraspecific effects in three out of the four cases, in some cases leading to priority effects. When intraspecific and interspecific competition are of similar intensity, niche differences are small. Consequently, very small relative fitness differences between species can promote competitive exclusion (Chesson 2000; Carroll et al. 2011). On the other hand, when intraspecific competition is much greater than interspecific competition, niche differences are large. Thus, a much broader range of relative fitness differences between species can promote coexistence (Chesson 2000; Carroll et al. 2011). Environmental variation has the potential to eliminate the competitive exclusion predicted under constant average conditions by equalizing GRWR (i.e., reducing relative fitness differences). Contrary to our prediction, however, the system remained destabilized and priority effects occurred despite the stabilizing effect (i.e., increasing niche differences) also promoted by environmental variation.

Differential water stress across species can alter competitive outcomes in grasslands (Flexas and Medrano 2002). Analysis of foliar traits supports the importance of water stress in promoting differential responses to environmental conditions. Water stress, measured here as RLWC, can enhance or reduce niche differences when species respond differently to water availability (Chesson et al. 2004). *S. arundinaceus* exhibited little water stress in the drought, unclipped treatment, but *P. dilatatum* experienced markedly greater water stress in that treatment. These results concur with recent findings suggesting that C4 grasses lose their competitive advantage from higher water-use efficiency under drought conditions (Taylor et al. 2011).

By reducing transpiration, clipping can reduce water stress (Luo et al. 2012). In our experiment, increased RLWC indicates that clipping alleviated water stress in *P. dilatatum*; this suggests that differential water stress strongly influenced the differing model predictions of priority effects under constant drought and clipping, and the

exclusion of *P. dilatatum* under constant drought without clipping. By alleviating water stress, clipping effectively shifts competition to the next most limiting resource, which could facilitate coexistence or exclusion depending on resource supply and plant physiology (Olf and Ritchie 1998). In this experiment, since the water demands of both species were likely reduced by clipping, *P. dilatatum* may have benefited from both its own reduced water demands and reduced water consumption by *S. arundinaceus*. The outcome of competition under drought and clipping ultimately depended on initial conditions, as either species could potentially exclude the other.

Our model also predicted coexistence in clipped, water-saturated conditions, a result that appears strongly tied to differences in tolerance of clipping between *P. dilatatum* and *S. arundinaceus*. *Paspalum dilatatum* was less tolerant of clipping than *S. arundinaceus* in both water conditions, but the difference was particularly pronounced in water-saturated conditions. Because plants in this treatment had access to abundant light and nutrients, coexistence likely occurred because clipping prevented *P. dilatatum* from taking full advantage of high light availability in the greenhouse, conditions under which *P. dilatatum* would have otherwise excluded *S. arundinaceus*. These results are consistent with several studies, which have shown increasing tolerance to herbivory with decreasing resource availability (e.g., Hawkes and Sullivan 2001; Wise and Abrahamson 2005, 2007). Our model also emphasizes the importance of simulated herbivory in structuring grassland communities, in part due to indirect effects on plant competition (Huntly 1991; Olf and Ritchie 1998; Allan and Crawley 2011). While simulating herbivory via clipping is an effective way to control the amount of tissue removed from plants (e.g., Li et al. 2002, 2013), clipping is unable to induce the same chemical and physiological responses as true herbivory (Lehtila and Boalt 2004; Li et al. 2013). Despite this limitation, the effects of true herbivory and simulated herbivory, such as clipping, on biomass growth are often of similar magnitude (Lehtila and Boalt 2004). Therefore, incorporating biomass production in response to clipping into our model should reasonably mimic the effect of true herbivory on this plant–plant interaction.

Although RLWC is an effective measure of short-term water stress, it may provide less evidence of the long-term effects of drought stress on plant growth. LMA may effectively indicate long-term drought stress because it is negatively correlated with plant growth rate (Nielsen et al. 1996). Consequently, LMA tends to increase with increasing water stress (Damour et al. 2008). *Schedonorus arundinaceus* individuals varied little in RLWC or LMA across treatments, suggesting that short-term water stress was not severe enough to trigger long-term reduction in growth. By contrast, LMA in *P. dilatatum* increased due to drought.

Together, differences in LMA and RLWC suggest that *P. dilatatum* generally experiences both stronger growth limitation and more severe water stress under drought conditions than *S. arundinaceus*, especially in intraspecific competition.

Notably, *S. arundinaceus* might have demonstrated higher water-use efficiency due to an association with the endophyte *Neotyphodium coenophialum* which may confer drought resistance (Nagabhyru et al. 2013). Endophyte-infected *S. arundinaceus* show increased photosynthetic rate and stomatal conductance under water stress due to improved turgor maintenance compared to endophyte-free plants (Richardson et al. 1993). During droughts, species harboring endophytes may exhibit limited declines in performance, which could alter the outcome of competition (Arachevaleta et al. 1989). Endophyte prevalence was extremely high (>94 %) among *S. arundinaceus* in the field from which the seeds for this experiment were collected (Heckman et al., unpublished data). Since the endophyte is vertically transmitted (Nagabhyru et al. 2013), the vast majority of *S. arundinaceus* in the experiment likely harbored endophytes. Thus, endophyte-infection may explain some of the differences in the ability of *S. arundinaceus* and *P. dilatatum* to tolerate water stress.

The strength of competition in resource-poor environments has been the subject of much debate (Grime 1973; Tilman 1990; Goldberg and Novoplansky 1997; Rees 2013). When resource availability is pulsed, as water availability typically is, theory predicts minimal competition in resource-poor environments if resource availability is independent of vegetation (i.e., abiotic processes dominate), but that competition will be important in these environments when plants are able to deplete resources between pulses (Goldberg and Novoplansky 1997). Since both species in our experiment were able to deplete soil moisture between watering, our experiment may not reflect the dynamics of competition for water typical in arid environments with infrequent rain (Goldberg and Novoplansky 1997; Chesson et al. 2004; Carlyle et al. 2010). Rather, we found that competition was more intense under experimental drought that may more closely mimic possible future water stress scenarios where increases in precipitation will be strongly offset by increases in evaporation (Seager et al. 2009). Because competition for light and soil nutrients are often stronger in the field than under greenhouse conditions, the responses to drought, clipping, and competition might not translate directly into field responses. Field experiments that investigate functional responses to competition under natural conditions would expand the applicability of these results.

These results also support theoretical and experimental work suggesting that reducing biomass, here via clipping, may not lessen the importance of competition in

structuring communities (Chesson and Huntly 1997; Violle et al. 2010). We suggest that the combined indirect effects of drought and clipping on competition could structure and maintain diversity in plant communities across gradients of environmental stress and disturbance. Our results show that clipping reduced the importance of water availability under drought, promoting coexistence by increasing environmental heterogeneity. This suggests that life history tradeoffs, potentially combined with spatial and temporal environmental variation, could promote coexistence under the predicted climate change facing many grassland communities. By contrast, a more directional shift in future climate conditions could shift competitive dominance. The effects of global change that are mediated by competition can have an important but often overlooked influence on potential shifts in community composition. In fact, indirect effects even have the potential to reverse the direct effects of climate change (Adler et al. 2012).

In summary, our results reinforce the need to integrate indirect interactions into ecological forecasting of systems undergoing climate change (Adler et al. 2012). By modeling the long-term outcome of competition using empirical data, we further found that drought and simulated herbivory may indirectly alter plant–plant interactions in ways that would not have been easily detected with methods that do not incorporate environmental fluctuation. More broadly, this study shows that indirect impacts of global change, mediated by competition, may lead to unexpected effects on ecological communities.

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Author contribution statement J. D. N. and R. W. H. conceived, designed, and performed the greenhouse experiment. J. D. N. and R. W. H. analyzed the data. J. D. N. and E. A. M. developed and ran the modeling simulations. J. D. N., R. W. H., and E. A. M. wrote the manuscript.

Compliance with ethical standards This experiment complies with the current laws of the USA, where the experiment was performed.

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