

# Contrasting trait responses in plant communities to experimental and geographic variation in precipitation

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## Summary

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- Patterns of precipitation are likely to change significantly in the coming century, with important but poorly understood consequences for plant communities. Experimental and correlative studies may provide insight into expected changes, but little research has addressed the degree of concordance between these approaches.
- We synthesized results from four experimental water addition studies with a correlative analysis of community changes across a large natural precipitation gradient in the United States. We investigated whether community composition, summarized with plant functional traits, responded similarly to increasing precipitation among studies and sites.
- In field experiments, increased precipitation favored species with small seed size, short leaf life span and high leaf nitrogen (N) concentration. However, with increasing precipitation along the natural gradient, community composition shifted towards species with higher mean seed mass, longer leaf life span and lower leaf N concentrations.
- The differences in temporal and spatial scale of experimental manipulations and natural gradients may explain these contrasting results. Our results highlight the complexity of responses to climate change, and suggest that transient dynamics may not reflect long-term shifts in functional diversity and community composition. We propose a model of community change that incorporates these differences between short- and long-term responses to climate change.

## Introduction

There is a growing need to predict how plant communities will respond to changes in climate (Parmesan & Yohe, 2003; Hoegh-Guldberg *et al.*, 2008). Analyses based on plant strategies and functional traits may help to understand the responses of species, providing both a mechanistic explanation for changes and a means to apply predictions to other communities (Lavorel & Garnier, 2002; Fukami *et al.*, 2005; Suding *et al.*, 2008). Thus, there has been considerable interest in understanding the relationships among plant

functional traits (Westoby *et al.*, 2002; Wright *et al.*, 2004) and between these traits and the environment (Wright *et al.*, 2005; Cornwell & Ackerly, 2009). If functional traits prove to be generally predictive of responses to a particular climate change factor, couching climate change predictions in terms of shifts in community trait composition may be more useful and general than presenting them in species-specific terms (McGill *et al.*, 2006; Westoby & Wright, 2006; Violle *et al.*, 2007; Suding *et al.*, 2008).

Several methods have been used to describe trait composition at the community level, the most common being a

mass-ratio approach where the product of each species' mean trait and its relative abundance is summed across all species within a community (Garnier *et al.*, 2004; Diaz *et al.*, 2007a). Changes in trait composition at the community level can be caused by species turnover, shifts in species abundance and intraspecific trait variation resulting from plasticity and genetic differentiation. For example, drought might lead to a community with deeper average rooting depth if deep-rooted species invade the community, deep-rooted species increase their abundance within the community or individuals increase allocation to deep root production. In this study, we are concerned with changes in community composition with changes in climate, so we focus primarily on the first two causes of change.

Patterns of precipitation are likely to change over the next century, including both local increases and decreases in annual precipitation, as well as changes in the distribution of rainfall through the year (Meehl *et al.*, 2007). These changes are expected to have significant impacts on plant community composition (Weltzin *et al.*, 2003). Responses to changed water availability are likely to be species-specific, and may be predictable by the leaf, seed and growth characteristics of species. For example, drought tolerance is related to more conservative growth and resource use strategies (e.g. long leaf life span; Wright *et al.*, 2004; Angert *et al.*, 2007), water-conserving leaf traits (including high leaf N concentration; Wright *et al.*, 2001) and larger seed masses (Baker, 1972; Leishman & Westoby, 1994; Pakeman *et al.*, 2008). If these traits predict species' responses to precipitation, changes in community composition (including both relative abundance and species presence/absence) caused by altered precipitation should correspond with changes in community mean trait values.

Predictions of response to climate change may be derived from experimental and observational studies (Saleska *et al.*, 2002; Dunne *et al.*, 2004), both of which are amenable to a functional trait-based approach (Tautenhahn *et al.*, 2008). While both types of study are common, relatively few authors have asked whether they produce similar predictions (but see Dunne *et al.*, 2004). Experimental studies are typically limited in scope, both spatially and temporally (Rustad, 2006). Observational studies can often achieve broader spatial and temporal scales, but suffer from a lack of control over covariates. To minimize the weaknesses of each approach, it has been suggested that more research should explicitly unite observational and experimental work, perhaps by nesting experiments at multiple sites within a larger observational context (Saleska *et al.*, 2002; Dunne *et al.*, 2004; Hewitt *et al.*, 2007; Wiedermann *et al.*, 2009).

In this paper, we take such a nested approach. We synthesize the findings of four experimental precipitation addition studies with an analysis of community changes along the natural gradient of precipitation across the continental

United States. We use a trait-based approach, summarizing community changes as shifts in community mean values of growth, leaf and seed traits. We ask three main questions: which traits predict a species' response to experimental water addition; do community mean trait values shift in the same manner after experimental water additions as along a natural precipitation gradient; how does the duration of the experimental treatment influence the direction and magnitude of trait shifts?

## Materials and Methods

### Experimental data

We compiled data from four experimental studies of water addition in grassland or mixed shrubland/grassland systems that ranged widely in their baseline precipitation (drawn from the dataset assembled by Cleland *et al.*, 2008). These studies were conducted at Konza Tallgrass Prairie, a Long Term Ecological Research (LTER) site in Kansas (Knapp *et al.*, 2001), the Shortgrass Steppe LTER in northern Colorado, the Sevilleta LTER in New Mexico (S Baez *et al.*, unpublished) and Jasper Ridge in California (Zavaleta *et al.*, 2003). The longest-running experiment is at Konza, which was initiated in 1991 and includes plant community composition data from 1991 to 2005. We also analyzed data for the first 4 yr of the watering study at Jasper Ridge (1999–2002), the first 3 yr at Sevilleta (2004–2006) and year 4 at the Shortgrass Steppe (2000). Experimental sites received between 280 and 1450 mm of ambient precipitation each year, which was augmented in treatment plots by 10–190% (mean 50%) with experimental water additions.

For each year of each study, we obtained the relative abundances of all species from replicated control and treatment plots. We determined the annual rainfall at each site in each year of the experiments by using publicly available weather data from stations close to the experimental sites or from the sites themselves, when available. We also determined the annual amounts of water added to each treatment site using experimental design information posted on associated LTER websites or described in Cleland *et al.* (2008).

### Natural gradient

We used the VegBank database (<http://www.vegbank.org>) to investigate changes in species composition and community mean trait values along the natural precipitation gradient in the continental United States. We downloaded data for all 21 566 plots that were available on 20 April 2008. These plots ranged in size from 9 to 50 000 m<sup>2</sup>, with a median size of 400 m<sup>2</sup>. Data for each plot included its location and the relative abundance of all plant species in the plot. We then obtained a 30 yr average (1971–2000) annual

precipitation value for each of our VegBank plots (Daly *et al.*, 2008, PRISM Group, Oregon State University, 2008).

### Traits

In total, there were 219 species in the experimental plots and 7813 in the VegBank plots. To obtain trait information for these species, we used several data sources. We used the USDA Plants database (USDA, NRCS, 2008) to determine the growth form and life span of each species. Growth form was separated into three categories: woody plant, forb and grass. Life span was similarly categorized into perennial, biennial and annual. Species that fit two life span categories (such as annual/perennial) were classified as having the longest applicable life span. We obtained seed size data by querying the Kew Gardens Seed Information Database (Liu *et al.*, 2008) for each species. For species with more than one record, we took the average of all available records. We obtained leaf trait data by searching the Glopnet dataset (Wright *et al.*, 2004) and two additional studies (Reich & Oleksyn, 2004; Tjoelker *et al.*, 2005). These traits included carbon assimilation and nitrogen per unit mass ( $A_{\text{mass}}$ ,  $N_{\text{mass}}$ ) and area ( $A_{\text{area}}$ ,  $N_{\text{area}}$ ), as well as specific leaf area (SLA) and leaf life span (LL). Finally, we used plant height data from Cleland *et al.* (2008), which were available only for species at the experimental sites. Here, height was a categorical variable, where species were described as typically reaching the lower, middle or upper third of the vegetation canopy. To meet the assumptions of normality, all quantitative trait variables were log-transformed before analysis.

For each natural or experimental plot, we calculated abundance-weighted and unweighted mean trait values for each continuous trait, based on the relative abundances and trait values across all species for which trait data were available (Garnier *et al.*, 2004; Ackerly & Cornwell, 2007; Violle *et al.*, 2007). Categorical traits were summarized at the plot level by simply summing the relative abundance of all species within each category. To improve normality, these proportions were then square root arcsine-transformed.

### Analysis – experimental responses

In order to determine which traits responded to experimental water addition, we performed a two-way ANOVA on plot-level abundance-weighted trait values for each trait, treating study site and treatment as fixed factors. In this portion of the study, we limited our analyses to single years of data from each study in order to resolve problems with highly unequal numbers of years used in each study. We took two approaches to this: first, using data from just the last year of each experiment to maximize our potential to detect treatment effects and, secondly, using data from just the third year (or fourth year, at the Shortgrass Steppe

LTER) of each study, to ensure that results among studies are as comparable as possible. These two approaches produced similar results, so we focus here on the last-year analysis (but see Supporting Information, Table S1, for results of the third-year analysis). For each analysis of a particular trait's response to experimental watering, we used only plots that had trait data for at least 50% of the cumulative abundance of species present.

We asked whether trait means continue to shift over time in long-running experiments using the fifteen years of data available for the Konza experiment. We performed a repeated-measures ANOVA (RM-ANOVA) on trait means at Konza, using treatment as a factor, with plots measured repeatedly across years. To avoid creating missing cases between years, we did not use the 50% coverage cutoff in this case.

We repeated the ANOVA and RM-ANOVA analyses, substituting unweighted plot trait means for abundance-weighted means. The use of unweighted means to describe community composition means that only changes in species presence and absence can cause plot mean trait values to change; any change in species abundances within the plot could not affect the plot mean trait value.

Finally, to examine rates of species turnover in experimental plots, we calculated species–time relationships (STRs) for each experimental plot. These curves represent the cumulative richness observed in plots after each successive year of sampling. We calculated the slope of the STR for each plot by regressing log(cumulative richness) against log(years). We then tested for a treatment effect on STR slope.

### Analysis – natural gradient

We divided the continental United States into a  $1 \times 1$  degree grid. For each  $1 \times 1$  degree cell, we calculated the average trait value across all plots in that cell, weighted by the coverage of that trait in each plot. We then calculated an average precipitation for each cell (PRISM Group, Oregon State University, 2008). Finally, we performed a simple linear regression of cell-aggregated trait values on mean precipitation.

Natural variation in precipitation in the years before sampling a plot may weaken the overall relationship between 30 yr mean precipitation and mean trait values. Specifically, plots sampled in unusually wet or dry years may produce unusually high or low mean trait values, relative to that expected given the 30 yr mean precipitation at the site. We addressed this possibility by obtaining, for each natural vegetation plot, the annual precipitation in the year that the plot was sampled (PRISM Group, Oregon State University, 2008). We then performed a linear regression of log(mean precipitation) and log(mean trait value) for each trait across all natural vegetation plots. We took the residuals from this

regression, aggregated them at the  $1 \times 1$  degree resolution, and regressed the precipitation anomaly (precipitation in the year of sampling – mean precipitation) against these aggregated residuals.

### Sensitivity

The VegBank database included a wider precipitation range than that encompassed by the experiments, and accordingly spanned a wider variety of vegetation. Most significantly, VegBank plots contained a higher abundance of woody species (mean woody cover = 53%). To ensure that our results were not driven simply by the inclusion of this other vegetation type in our analyses, we conducted separate analyses for the full VegBank dataset, and for a reduced dataset including only plots that exhibited < 50% cover by woody species. This reduced dataset showed a mean woody cover of 23% (range 0–50%). Experimental plots contained an average of 20% cover by woody species (range 0–100%).

Incomplete trait sampling can limit large-scale comparative analyses such as this one. We asked whether systematic variation in trait coverage with respect to water availability could explain our experimental and natural gradient results. In order to determine whether we had trait data for a larger portion of the community for watered or control plots, we used ANOVAs on the last year of data from each experiment (as described earlier), using percentage coverage for each trait as the response variables. Similarly, we tested for a correlation between percentage coverage and precipitation along the natural gradient for each trait.

Additionally, while we are primarily interested in using community mean traits as a means to summarize changes in community membership and abundance, we also sought to estimate the possible impact of trait plasticity in modulating the actual trait means in experimental plots. We asked how strong within-species trait variation would have to be to overturn our results. To examine the effect of intraspecific trait variation on experimental results, we assumed within-species trait–precipitation relationships were linear, with a fixed slope equal to a constant factor of the between-plot natural gradient slope. These factors were allowed to vary between –1 (within-species trait variation is qualitatively opposite to between-plot) and 2 (within-species trait variation is twice as extreme as between-plot variation). One study that measured these within-species slopes relative to between-plot slopes found that most species had within-species slopes for SLA of between *c.* 0.1 and 0.55 times the between-plot slope, and between 0.13 and 0.66 for individual leaf area (Cornwell & Ackerly, 2009; see also Ackerly & Cornwell, 2007).

Some species in the Glopnet database have trait measurements from more than one location (Wright *et al.*, 2004).

We used these species, and associated precipitation values from their sampling sites, to estimate the slope of within-species precipitation–trait relationships. For each species, we calculated the slope of the relationship between precipitation at its sampling locations and the trait values measured at those locations. These slopes were arctan-transformed (transformed to angles) to improve normality. We asked if all such slopes across species differ collectively from zero, using a one-sample *t*-test.

### Results

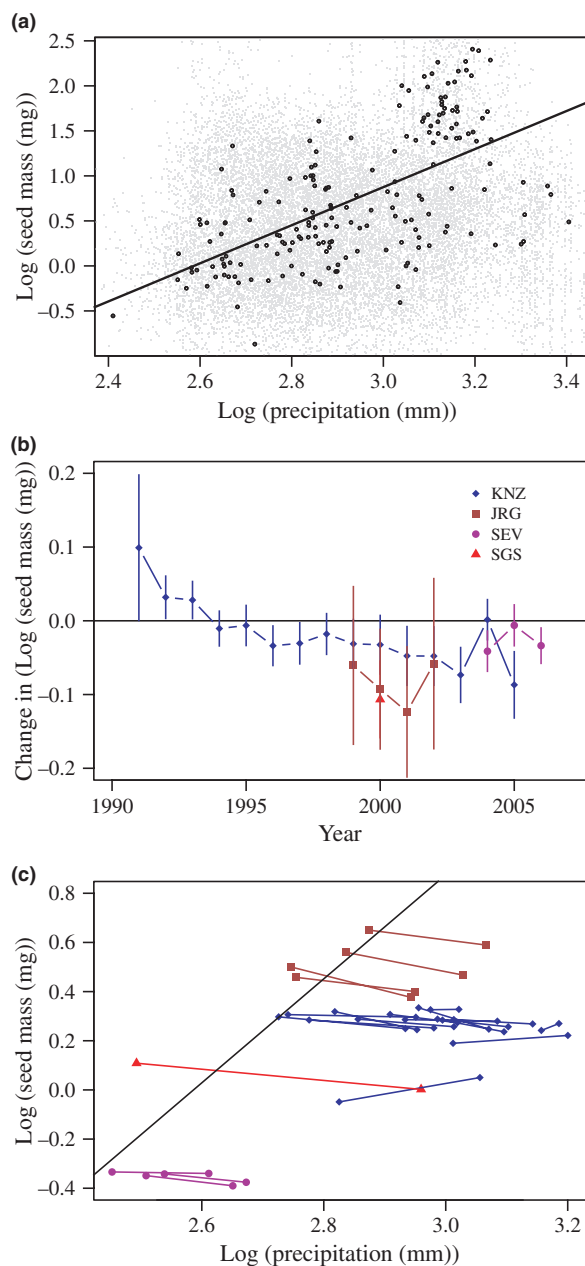
Community composition, summarized by abundance-weighted community mean trait values, changed along the natural precipitation gradient. Leaf life span and seed mass (Fig. 1a) increased, while  $N_{\text{mass}}$ ,  $N_{\text{area}}$  (Fig. 2a),  $A_{\text{mass}}$  and  $A_{\text{area}}$  decreased with increasing precipitation (Table 1). Naturally wetter plots showed lower cover of grass species, forb species and annual species (Table 1, Fig. S1), resulting in an increase in woody and perennial species.

Across experimental sites, communities showed consistent changes in composition following experimental water addition. Watering led to communities with greater cover by forbs ( $F_{1,561} = 6.842$ ,  $P = 0.0091$ ), and reduced cover of annual species ( $F_{1,561} = 60.67$ ,  $P < 0.0001$ ) and short species ( $F_{1,561} = 89.32$ ,  $P < 0.0001$ , Table 1). The abundance-weighted community mean values of quantitative traits also responded to watering in consistent ways. Mean leaf life span ( $F_{1,67} = 6.525$ ,  $P = 0.0129$ , Fig. S2) and seed mass ( $F_{1,560} = 7.294$ ,  $P = 0.0071$ , Fig. 1b) decreased with watering, while SLA ( $F_{1,89} = 4.882$ ,  $P = 0.0297$ ) and  $N_{\text{area}}$  ( $F_{1,89} = 13.73$ ,  $P = 0.0003$ , Fig. 2b) increased. Watering had no effect on the slopes of species–time relationships ( $F_{1,88} = 0.0166$ ,  $P = 0.898$ ).

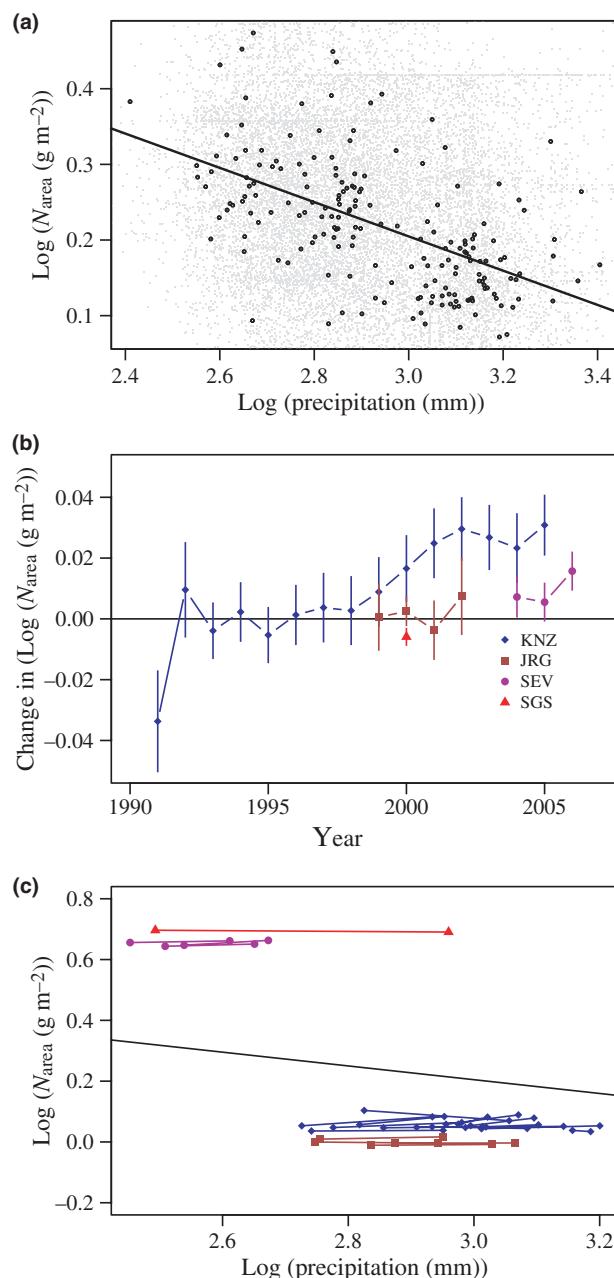
Overall, there was low concordance between the effects of naturally and experimentally increased precipitation on community composition (Table 1, Figs 1c, 2c, S3). Of the traits that showed significant shifts in the experimental and natural gradient studies, four out of five shifted in opposite directions in the two study types. These were leaf life span,  $N_{\text{area}}$ , seed mass and growth form (percentage cover of forbs). Only changes in the percentage cover of annuals were consistent between the experiments and natural gradient.

Focusing on changes over time in the Konza experiment, there was little indication that the directions of watering effects were approaching those of the natural gradient. For example, while seed mass did show a significant treatment  $\times$  yr interaction ( $F_{13,520} = 2.0435$ ,  $P = 0.0161$ , Fig. 1b), the effect of watering on seed mass at Konza generally became more, not less, strongly negative over time. Similarly, the watering effect on  $N_{\text{area}}$  became more positive over time ( $F_{13,520} = 5.3164$ ,  $P < 0.0001$ , Fig. 2b), while treatment effects on other traits showed little trend over time (Fig. S2).





**Fig. 1** Summary of the response of community mean seed size to natural (a) and experimental (b) variation in precipitation. Small gray points (a) represent individual sampling plots, while the large black circles are the aggregated 1 × 1 degree cells. In the experimental sites (b), we calculated a change in seed mass for each site and year as the mean treatment seed mass minus the mean control seed mass. In most cases, watering reduced plot mean seed mass relative to controls. Experimental and natural gradient results can be combined (c), by plotting the control plot precipitation vs control plot seed mass (left symbol on each line segment) and the equivalent values for the water addition plots (right symbol on each line segment) for each site and year. The black line represents the regression relationship determined from the natural gradient analysis. Control plots tended to lie close to this line, but water addition plots did not. The experimental sites are abbreviated KNZ (Konza Prairie), JRG (Jasper Ridge), SEV (Seville LTER) and SGS (Shortgrass Steppe LTER).



**Fig. 2** Responses of community mean  $N_{area}$  (leaf N concentration per unit area) to natural (a) and experimental (b) variation in precipitation. Details are as in Fig. 1. Community mean  $N_{area}$  tended to decline as natural precipitation increased, while experimental water addition produced an increase in  $N_{area}$ . The experimental sites are abbreviated KNZ (Konza Prairie), JRG (Jasper Ridge), SEV (Seville LTER) and SGS (Shortgrass Steppe LTER).

Analyses of trait shifts in the experimental studies were sensitive to the use of standard or abundance-weighted averaging. In some cases, abundance-weighting simply changed the perceived magnitude of the treatment effect, and generally made treatment effects more difficult to detect (Table S2). However, in eight of the 15 yr at Konza and

**Table 1** Summary of community changes, summarized by community trait composition, in response to experimental and natural variation in precipitation

Trait <sup>a</sup>	Experimental <sup>b</sup>			Natural gradient <sup>c</sup>			
	Treatment			All plots			
	Coverage (%)	Effect	<i>P</i>	Coverage (%)	Effect	<i>r</i> <sup>2</sup>	< 50% woody ( <i>r</i> <sup>2</sup> )
LL	30	–	<b>0.0129</b>	21	+	0.154	0.160
SLA	41	+	<b>0.0297</b>	34	ns	0.006	0.002
<i>N</i> <sub>mass</sub>	42	ns <sup>†</sup>	0.1601	43	–	0.158	0.121
<i>N</i> <sub>area</sub>	40	+	<b>0.0003</b>	32	–	0.309	0.164
<i>A</i> <sub>mass</sub>	38	Mixed <sup>†</sup>	<b>0.0189</b>	23	–	0.047	0.061
<i>A</i> <sub>area</sub>	40	ns <sup>†</sup>	0.3116	23	–	0.101	0.108
Seed	94	–	<b>0.0071</b>	80	+	0.362	0.061
Grass	100	ns <sup>†</sup>	0.0717	89	–	0.373	
Forb	100	+	<b>0.0091</b>	89	–	0.066	
Annual	98	–	<b>&lt; 0.00001</b>	90	–	0.122	
Short	100	– <sup>†</sup>	<b>&lt; 0.00001</b>				

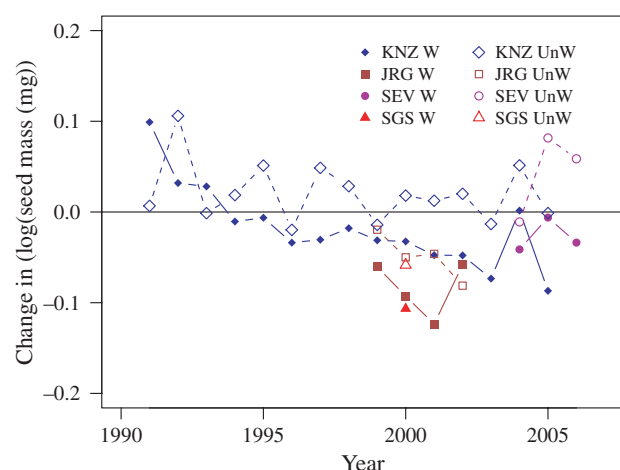
ns, not significant.

<sup>a</sup>Trait abbreviations are leaf life span (LL), specific leaf area (SLA), leaf N concentration per unit mass (*N*<sub>mass</sub>) and area (*N*<sub>area</sub>), carbon assimilation rates per unit mass (*A*<sub>mass</sub>) and area (*A*<sub>area</sub>) and seed mass (Seed). Grass, forb, annual and short refer to the summed relative abundance of all members of the named group within a plot.

<sup>b</sup>Summaries of ANOVAs on the last year of data for each trait. Coverage refers to the mean percentage of species for which trait data were available. When the main treatment effect was significant, the direction of the watering effect is indicated with a '+', '–', or 'Mixed', if there was no consensus among sites on the direction. †, indicates a significant treatment × site interaction. Significant *P* values (*P* < 0.05) are in bold.

<sup>c</sup>Summaries of linear regressions relating precipitation and aggregated natural vegetation plots (see text). For all traits, *N* = 189, except for leaf life span (*N* = 187). All regressions except SLA were significant (*P* < 0.0028 in all cases shown).

two of the 3 yr at Sevilleta, seed mass responded in opposite directions to watering, depending on whether abundance-weighted or unweighted means were used (Fig. 3). Several other traits showed similar sensitivity to abundance-weighting (*N*<sub>mass</sub>, *N*<sub>area</sub>, *A*<sub>area</sub>; Fig. S4).



**Fig. 3** Comparison of weighted and unweighted methods for calculating community mean traits, illustrated with seed mass. Treatment effects calculated from abundance-weighted (W) community means (as in Fig. 1b) differed from unweighted (UnW) means, and were qualitatively opposite in some cases. Study sites are Konza Prairie (KNZ), Jasper Ridge (JRG), Sevilleta LTER (SEV) and Shortgrass Steppes LTER (SGS). Standard error bars are omitted for clarity.

In several cases, the precipitation in the particular years that plots were sampled explained residual variation from the 30 yr mean precipitation–community mean trait regression (Table 2). In all such cases, the direction of the relationship between the precipitation anomaly and the trait–precipitation residuals was opposite to the overall relationship between precipitation and trait means. For example, wetter sites tended to have lower *A*<sub>mass</sub>, but in unusually wet years, plots had unusually high *A*<sub>mass</sub>.

### Sensitivity

Removing natural vegetation plots with > 50% cover by woody species did not change the direction or significance of any trait–precipitation relationships, although *r*<sup>2</sup> values were altered in several cases (Table 1).

At the experimental sites, for most traits, coverage did not vary between control and watering treatments. Only seed mass showed such an effect, and only weakly (1.3% increase with watering, *F*<sub>1,560</sub> = 4.435, *P* = 0.0357). In the natural gradient analysis, correlations between precipitation and trait coverage were weak (*r*<sup>2</sup> < 0.08) and nonsignificant in most cases.

There were 154 species in Glopnet with records from more than one site and associated precipitation values (mean = 2.32 records). For several traits (SLA, *N*<sub>mass</sub> and *N*<sub>area</sub>), > 100 of these species had more than one measurement of the trait, while for LL, *A*<sub>mass</sub> and *A*<sub>area</sub>, there were

**Table 2** Relationship of 1 yr precipitation anomaly with residuals of trait mean–precipitation regressions

Trait <sup>a</sup>	Main effect	Anomaly effect <sup>b</sup>
LL	+	–
SLA	ns	ns
$N_{\text{mass}}$	–	ns
$N_{\text{area}}$	–	ns
$A_{\text{mass}}$	–	+
$A_{\text{area}}$	–	+
Seed	+	ns
Grass	–	+
Forb	–	ns
Annual	–	ns

ns, not significant.

<sup>a</sup>Trait abbreviations are leaf life span (LL), specific leaf area (SLA), leaf N concentration per unit mass ( $N_{\text{mass}}$ ) and area ( $N_{\text{area}}$ ), carbon assimilation rates per unit mass ( $A_{\text{mass}}$ ) and area ( $A_{\text{area}}$ ) and seed mass (Seed). Grass, forb, annual and short refer to the summed relative abundance of all members of the named group within a plot.

<sup>b</sup>The relationships between the precipitation anomaly (precipitation in the year a plot was sampled minus that plot's 30 yr mean average) and the residuals of the 30-yr mean precipitation–plot trait mean regression. When there was a significant relationship between anomalies and residuals, the direction of that effect is indicated with a '+' or '–'.

only eight or nine such species. Hence, the power to detect intraspecific trait variation is fairly high for SLA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ , but not for the other three traits. However, none of the traits showed consistent precipitation–trait relationships among species ( $t$ -test,  $P > 0.48$  in all cases). Furthermore, if we incorporate the estimated degree of within-species trait responses to precipitation into our estimates of trait shifts in response to experimental watering, treatment effects usually become stronger (Fig. S5). Thus, while strong intraspecific trait variation that is also correlated with precipitation could potentially overturn or strengthen our experimental results, we found no evidence that empirical patterns are strong enough or sufficiently well correlated with climate to produce this result (Fig. S5).

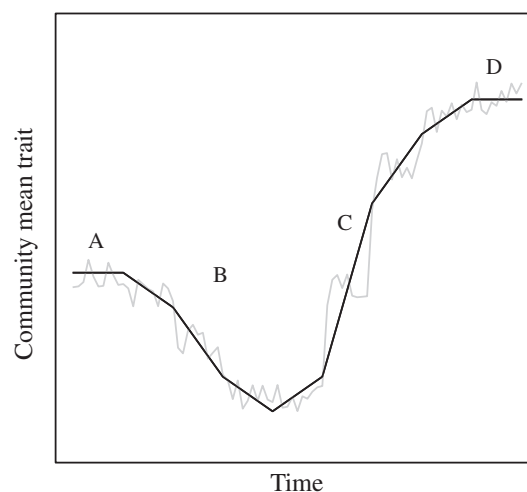
## Discussion

Community composition, as summarized by seed size, leaf traits and growth form, showed significant shifts both along the natural precipitation gradient and within experimental manipulations of water availability. Thus, in addition to being a useful common measure that allows synthesis of results from multiple studies, functional traits also appear to have predictive power with respect to responses to changing precipitation.

However, there were striking discrepancies in the direction of trait shifts between the experimental and observational components of this study. Our synthesis of results from four experimental studies suggests that in conditions of increased precipitation, species with smaller seeds, shorter leaf life

spans and higher  $N_{\text{area}}$  are favored. In contrast, the analysis of trait patterns along the natural precipitation gradient suggests precisely the opposite. We propose that a two-phased response to climate change may explain this discrepancy (Fig. 4). In the initial phase, shifts in abundances of species within the local species pool cause shifts in community mean traits. In the second phase, immigration and extirpation of species cause trait shifts over longer timescales (Adler & Levine, 2007; Smith *et al.*, 2009). Based on our results, we argue that trait shifts in these two phases may often be in opposite directions.

This model has close ties to similar ideas in ecosystem ecology. For example, Shaver *et al.* (2000) described multi-phase responses of net primary productivity to warming in several experimental warming studies, and showed that the directions of shifts can differ among phases. Similarly, the slope of the precipitation–productivity relationship is steeper among sites than it is among years at a particular site (Lauenroth & Sala, 1992), suggesting that local conditions, including community composition, constrain the response to short-term increases in resource availability. Prolonged exposure to increased resource availability (as experienced in areas with higher mean annual precipitation) produces stronger changes in productivity because community



**Fig. 4** Hypothetical two-phase process by which community mean trait values respond to a climate perturbation. The light gray line represents hypothetical yearly data, showing fluctuations around the smoothed curve (black line) resulting from interannual variability. Initially (A), a community shows stochastic fluctuation over time around some equilibrium trait value. A climate perturbation (B) causes shifts in the community, which are driven primarily by changes in abundance within the fixed local species pool. Over time (C), immigration into and extirpation from the species pool overwhelm trait shifts caused by changes in local abundance, causing initial, transient trait shifts to reverse. Rates of immigration eventually diminish, and the community settles at a new equilibrium (D). The timescale over which these transitions occur is largely unknown, but critical for the understanding of community responses to climate change.

turnover can occur. We propose that similar mechanisms drive changes in plant community trait composition with increasing precipitation.

We address two important questions regarding the proposed two-phase process. First, why would the changes in community composition (as summarized by trait composition) in the two phases be opposite? Secondly, what determines the timescales of the process? Answers to both of these questions will be critical as we seek to understand the impacts of climate change on plant communities.

### Short- vs long-term responses

Theoretical work on population dynamics has shown that a population perturbed from equilibrium may show complex transient dynamics before arriving at a new equilibrium (Hastings, 2004; Stott *et al.*, 2010). Although a particular change may increase the equilibrium population of a species, its initial response to it may be to decline. Such transient dynamics may occur in communities if changing biological interactions cause feedbacks that reverse the initial changes caused by the experimental treatment. For example, in an experimental study of water addition in northern California grasslands, species richness increased initially after water addition (Suttle *et al.*, 2007). This increase was caused, in part, by an increase in N fixer diversity, which enriched the soil and led eventually to dominance by a few annual grass species and a subsequent decrease in species richness.

In the experimental studies we examined, initial changes seem to represent a response to increased resource availability, while hypothetical long-term changes may reflect changes in vegetation type, biological interactions and shifts in the limiting resource. Our experimental results are consistent with expectations regarding which plant traits are likely to be advantageous when resources become more abundant. Species with leaves that produce rapid returns on investments (Wright *et al.*, 2004) should be better able to utilize pulses in resources. Species with slow returns on leaf investments should be expected to respond more slowly to an increase in resources. The shifts in traits we observed in experimental studies, including shorter leaf life span and higher SLA, are consistent with faster return on leaf investments in watered plots (Cunningham *et al.*, 1999). Reduced seed size in experimental plots is likely the result of a higher colonization probability of small seeded species, and a decreased importance of seed provisioning as seedling growth is facilitated by greater water availability (Leishman & Westoby, 1994).

Trait shifts over longer timescales and across the natural gradient are likely a result of fundamentally different mechanisms. Cover of woody species increased with increasing precipitation, which may cause light to become an increasingly important limiting resource. Under low-

light conditions large seeds are often favored (Bazzaz, 1979; Coomes & Grubb, 2003; Pakeman *et al.*, 2008). Similarly, high  $N_{\text{area}}$  may be an adaptation to low precipitation by allowing high water use efficiency in photosynthesis, but it is costly to maintain when water is not limiting (Reich *et al.*, 1999; Wright *et al.*, 2001, 2005). Thus, the mismatch between experimental and natural gradient results may be a result of long-term shifts in vegetation type and corresponding biological interactions, which were not observed on the timescale of our experiments. However, given sufficient time, continued application of precipitation might cause a change in the limiting resource, causing further shifts in functional traits, possibly reversing the earlier, transient, shifts (Fig. 4; Smith *et al.*, 2009). That short-statured species became less abundant over time in experimentally watered plots may be a subtle indication that this shift is beginning to occur in the experiments.

In several cases, traits shifted in one direction when calculated as an abundance-weighted mean, but in the opposite direction when calculated as an unweighted mean, reflecting changes in species presence and absence (Fig. S4). Thus, trait shifts resulting from changes in species presence and absence were opposed by trait shifts caused by changes in species abundance. This strongly supports the notion of a two-phase process, in which the directions of shifts in the two phases do not necessarily match (Fig. 4). Another piece of evidence for the proposed two-phase response is that natural plots sampled in unusually wet years tended to approach the trait composition of naturally drier plots (for the traits leaf life span,  $A_{\text{mass}}$ ,  $A_{\text{area}}$  and % grass). Thus, the short-term temporal response to naturally increased precipitation resembles the response of experimentally wetter communities, both of which share the property of having been exposed to higher precipitation for only a short time.

### Response timescales

Understanding the course of community changes over time will be a critical component of climate change predictions (Shaver *et al.*, 2000). Two lines of evidence suggest that changes observed in the experiments were primarily the result of abundance shifts (phase 1). First, abundance-weighted plot trait means revealed more significant treatment effects than did unweighted means, indicating that including information on abundance differences between control and treatment plots was crucial for understanding treatment responses. Secondly, were there significant species turnover in watered plots, we should expect them to show higher rates of species accumulation over time, or steeper species–time relationships (Adler & Lauenroth, 2003; Adler *et al.*, 2005). However, we detected no difference in the slopes of species–time relationships between control and treatment plots. The duration of the experiments examined here (3–15 yr) may have been insufficient to observe



significant changes in species composition. However, over perhaps a century, persistent changes in precipitation might allow the colonization of novel species and the extinction of other species from the regional pool.

Small spatial scales of the experimental studies may lead to slow turnover relative to what might be expected in naturally changing communities. Species may be lost only slowly from plots that are no longer suitable for them if their populations are maintained by immigration from a surrounding source habitat, particularly if plots are small relative to dispersal distances (Pulliam, 1988; Dias, 1996). Conversely, although an experimentally altered plot might be a suitable habitat for a certain species, if that plot is embedded in a matrix of unsuitable habitat, dispersal to the plot could be very rare. Both of these effects should reduce community turnover rates to the extent that experimental changes in abiotic conditions are imposed over a small area. Thus, small spatial scales may prevent even long-running experiments from demonstrating strong trait shifts as a result of changing species pools. Although we detected some trait shifts resulting only from changing species occurrences, the small spatial scale of the experiments may have limited these shifts.

### Intraspecific variation

This study addressed changes in the species composition of communities, as summarized by changes in community mean trait values. We have shown that mean trait values for species, available from the literature and databases, are a useful tool to predict how communities change with experimentally or naturally increased precipitation. However, we cannot predict from these data how the traits of species might change with precipitation resulting from plasticity or evolutionary changes. For example, individual plants might increase their rooting depth with drought, and after prolonged drought, populations might evolve to be deeper-rooted. Thus, the community trait mean value for a plot should not be interpreted literally, as the traits of individuals within a particular plot may not be similar to those found in databases. However, our analysis of the ability of intraspecific variation to reverse experimental results indicated that this was unlikely, assuming reasonable (and empirically derived) relationships of precipitation and within-species trait variation.

The two-phase model we propose could easily be extended to incorporate intraspecific trait shifts with climate change. This would align our model closely with the hierarchical-response framework of Smith *et al.* (2009). Under this framework, ecosystem responses to chronic resource alterations are dominated first by individual responses, then by changes in species abundance, and finally by immigration of new species. More work will be required to determine whether intraspecific trait shifts (including both plasticity and evolutionary responses) strengthen or dampen

the short-term responses of plant traits to changes in precipitation (Cornwell & Ackerly, 2009).

### Conclusion

In this manuscript we are primarily concerned with the manner in which the abiotic environment, such as precipitation and water availability, can act as a 'filter' by restricting community membership to plants with a limited set of traits (Cornwell & Ackerly, 2009). However, higher trophic levels, such as herbivores, can also act as strong filters in their own right (Diaz *et al.*, 2001). It will be valuable to explore how the intensity of these biotic filters will change with increasing precipitation in these systems, as these abiotic and biotic filters may have interactive effects on plant composition (Diaz *et al.*, 2007b).

We have proposed a two-phase process by which communities change in response to climate perturbations. In the first phase, community change is dominated by shifts in abundances of resident species. In the second phase, changes are dominated by the arrival of new species and the loss of resident species. Changing biological interactions, shifts in the limiting resource and new feedback mechanisms may cause the shifts in the second phase to differ in kind from those initially observed.

This model has important implications for predictions of climate change impacts on plant communities. First, the duration of these phases is largely unknown, and may differ substantially depending on community type and the severity and type of the climate change. We suggest that understanding the timescales of these changes should be a major objective of future research. Secondly, when making climate change predictions, we must use the data and tools appropriate to the timescale of interest, and extrapolate beyond that timescale only with extreme caution. Experiments can provide useful insight into the immediate, but possibly transient, responses of communities to a change. On the other hand, observational studies may reveal the expected long-term changes in a community type (over perhaps centuries), but offer little information regarding immediate responses in plant communities to climate change.

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## References

- Ackerly DD, Cornwell WK. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* 10: 135–145.
- Adler PB, Lauenroth WK. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecology Letters* 6: 749–756.
- Adler PB, Levine JM. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* 116: 221–232.
- Adler PB, White EP, Lauenroth WK, Kaufman DM, Rassweiler A, Rusak JA. 2005. Evidence for a general species-time-area relationship. *Ecology* 86: 2032–2039.
- Angert AL, Huxman TE, Barron-Gafford GA, Gerst KL, Venable DL. 2007. Linking growth strategies to long-term population dynamics in a guild of desert annuals. *Journal of Ecology* 95: 321–331.
- Baker HG. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.
- Bazzaz FA. 1979. The physiological ecology of plant succession. *Annual Review Ecology and Systematics* 10: 351–371.
- Cleland EE, Clark CM, Collins SL, Fargione JE, Gough L, Gross KL, Milchunas DG, Pennings SC, Bowman B, Burke IC *et al.* 2008. Species responses to nitrogen fertilization in herbaceous plant communities, and associated species traits (Data Publication). *Ecology* 89: 1175.
- Coomes DA, Grubb PJ. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology and Evolution* 18: 283–291.
- Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in the distribution of trait values across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.
- Cunningham SA, Summerhayes B, Westoby M. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecology* 69: 569–588.
- Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28: 2031–2064.
- Dias PC. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11: 326–330.
- Diaz S, Lavorel S, de Bello F, Quetier F, Grigulis K, Robson TM. 2007a. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences, USA* 104: 20684–20689.
- Diaz S, Lavorel S, McIntyre S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I *et al.* 2007b. Plant trait responses to grazing – a global synthesis. *Global Change Biology* 13: 313–341.
- Diaz S, Noy-Meir I, Cabido M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38: 497–508.
- Dunne JA, Saleska SR, Fischer ML, Harte J. 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology* 85: 904–916.
- Fukami T, Bezemer TM, Mortimer SR, van der Putten WH. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8: 1283–1290.
- Garnier E, Cortez J, Billes G, Navas M, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A *et al.* 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.
- Hastings A. 2004. Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution* 19: 39–45.
- Hewitt JE, Thrush SF, Dayton PK, Bonsdorff E. 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *The American Naturalist* 169: 398–408.
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD. 2008. Assisted colonization and rapid climate change. *Science* 321: 345–346.
- Knapp AK, Briggs JM, Koelliker JK. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* 4: 19–28.
- Lauenroth WK, Sala OE. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397–403.
- Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- Leishman MR, Westoby M. 1994. The role of seed size in seedling establishment in dry soil conditions – Experimental evidence from semi-arid species. *Journal of Ecology* 82: 249–258.
- Liu K, Eastwood RJ, Flynn S, Turner RM, Stuppy WH. 2008. *Seed information database* (release 7.1, May 2008) <http://www.kew.org/data/sid>
- McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21: 178–185.
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A *et al.* 2007. Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. *Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press, 747–845.
- Pakeman RJ, Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Freitas H, Golodets C *et al.* 2008. Impact of abundance weighting on the response of seed traits to climate and land use. *Journal of Ecology* 96: 355–366.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- PRISM Group, Oregon State University. 2008. <http://www.prismclimate.org>, created 29 May 2008.
- Pulliam HR. 1988. Sources, sinks, and population regulation. *The American Naturalist* 132: 652–661.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.

- Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences, USA* 101: 11001–11006.
- Rustad LE. 2006. From transient to steady-state response of ecosystems to atmospheric CO<sub>2</sub>-enrichment and global climate change: conceptual challenges and need for an integrative approach. *Plant Ecology* 182: 43–62.
- Saleska SR, Shaw MR, Fischer ML, Dunne JA, Still CJ, Holman ML, Harte J. 2002. Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. *Global Biogeochemical Cycles* 16: 1055.
- Shaver GR, Canadell J, Chapin FS, Gurevitch G, Harte J, Henry G, Ineson P, Melillo J, Pitelka L, Rustad L. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience* 50: 871–882.
- Smith MD, Knapp AK, Collins SL. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90: 3279–3289.
- Stott I, Franco M, Carslake D, Townley S, Hodgson D. 2010. Boom or bust? A comparative analysis of transient population dynamics in plants. *Journal of Ecology* 98: 302–311.
- Suding KN, Lavorel S, Chapin FS, Cornelissen JHC, Diaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas ML. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125–1140.
- Suttle KB, Thomsen MA, Power ME. 2007. Species interactions reverse grassland response to changing climate. *Science* 315: 640–642.
- Tautenhahn S, Heilmeyer H, Gotzenberger L, Klotz S, Wirth C, Kuhn I. 2008. On the biogeography of seed mass in Germany – distribution patterns and environmental correlates. *Ecography* 31: 457–468.
- Tjoelker MG, Craine JM, Wedin DA, Reich PB, Tilman DG. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* 167: 493–508.
- USDA, NRCS. 2008. *The PLANTS database*. <http://plants.usda.gov>. 29 May 2008.
- Violle C, Navas MM, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G *et al.* 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* 53: 941–952.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review Ecology, Evolution and Systematics* 33: 125–159.
- Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21: 261–268.
- Wiedermann MM, Gunnarsson U, Nilsson MB, Nordin A, Ericson L. 2009. Can small-scale experiments predict ecosystem responses? An example from peatlands. *Oikos* 118: 449–456.
- Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Groom PK, Hikosaka K, Lee W, Lusk CH, Niinemets U, Oleksyn J *et al.* 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.
- Wright IJ, Reich PB, Westoby M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* 15: 423–434.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, Field CB, Mooney HA. 2003. Grassland responses to three years of elevated temperature, CO<sub>2</sub>, precipitation, and N deposition. *Ecological Monographs* 73: 585–604.

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Changes in community composition along a natural precipitation gradient, summarized by shifts in community means of eight traits.

**Fig. S2** Changes in community composition with experimental water addition, summarized by shifts in community means of eight traits.

**Fig. S3** Combination of trait responses to experimental and natural variation in precipitation.

**Fig. S4** Comparison of abundance-weighted and unweighted means for all traits at the experimental sites.

**Fig. S5** Robustness of experimental results to simulated intraspecific trait variation.

**Table S1** Treatment effects assessed in the third year of the experiments

**Table S2** Treatment effects assessed using unweighted trait means from experimental plots

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