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Aridity modulates grassland biomass responses to combined drought and nutrient addition

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Abstract

Plant biomass tends to increase under nutrient addition and to decrease under drought. Biotic and abiotic factors influence responses to both, making the combined impact of nutrient addition and drought difficult to predict. Using a globally distributed network of manipulative field experiments, we assess grassland aboveground biomass response to both drought and increased nutrient availability at 26 sites across 9 countries. Overall, drought reduced biomass by 19% and nutrient addition increased it by 24%, resulting in no net impact under combined drought and nutrient addition. Among the plant functional groups, only graminoids responded positively to nutrients during drought. However, these general responses depended on local conditions, especially aridity. Nutrient effects were stronger in arid grasslands and weaker in humid regions and nitrogen-rich soils, although nutrient addition alleviated drought effects the most in sub-humid sites. Biomass responses were weaker with higher precipitation variability. Biomass increased more with increased nutrient availability and declined more with drought at high-diversity sites than at low-diversity sites. Our findings highlight the importance of local abiotic and biotic conditions in predicting grassland

responses to anthropogenic nutrient and climate changes.

Introduction

Nutrient inputs and extreme droughts are rising in terrestrial ecosystems worldwide due to global changes[1,2], even in already co-limited grasslands where plant growth is constrained by water and nutrients[3,4]. Resource supplies (e.g., nutrient availability or soil moisture) often affect grasslands, causing increases (e.g., nutrient addition) and reductions (e.g., drought) in the aboveground biomass[5,6,7,8]. Combined effects of drought and nutrient increases can yield a proportional impact, equivalent to the sum of their individual effects. However, non-proportional effects showing higher or lower responses than this sum can arise when one factor exacerbates (e.g., nutrient addition intensifies the impact of drought) or diminishes the effect of the other (e.g., drought reducing nutrient-use efficiency)[9]. Nutrients can also buffer drought impacts, especially in co-limited grasslands[10]. Variation in responses depends on soil water availability[11], plant community[12], and species-specific stoichiometric needs for water and nutrients[13]. Thus, nutrient addition can shift plant community interactions[14], affecting drought sensitivity[15] and drought can reduce productivity, diminishing nutrient sensitivity[16]. Understanding the underlying mechanisms behind is crucial for predicting responses to climate change-induced increases in drought frequency and nutrient availability.

Biotic factors such as plant richness, species abundance[17], along with abiotic factors like water availability, interannual precipitation variability, and soil texture, contribute to different responses to drought and nutrient addition[18]. Aridity critically modulates plant species responses to these factors[19]. In arid grasslands, water is the primary limiting factor, heightening drought sensitivity[20,6], while sub-humid grasslands are mainly co-limited by nutrient and water availability, and humid grasslands are typically limited by nutrients or light[2]. High plant diversity and different functional groups may enable compensatory responses[21,22]. Communities with high graminoid abundance may experience drought-induced declines[23], benefit from nutrient addition[24], or show no sensitivity[25]. This variability in graminoid responses may stem from differences in water and nutrient use, with faster-growing strategies and relatively shallower rooting systems compared to other resource-conservative plant functional groups[8,14,26]. However, community composition may shift under enhanced nutrient availability, driving to increased dominance of certain functional groups and altering biomass production [21].

The NPK-D Network (NPK-D Net; https://www.bayceer.uni-bayreuth.de/npkd/index.php?lang=en) was established as a global experiment using a standardized design to assess the effects of nutrient addition and drought in grasslands across different environments. We aimed to examine the short-term effects of nutrient increases (through nutrient addition) and water limitation (through drought manipulation) in grassland biomass across environmental gradients and evaluate the influence of biotic and abiotic factors, such as plant diversity and aridity[27]. We analyzed 1-year biomass response of grasslands and their main plant functional groups to drought and nutrient addition at 26 sites across 9 countries on 6 continents (Figure 1). We tested three hypotheses (Figure 2):

1) Arid grasslands are primarily limited by water and thus, sensitive to drought which reduces biomass. In contrast, humid grasslands are primarily nutrient-limited, so nutrient addition significantly increases biomass.

2) Grasslands co-limited by nutrients and water, mostly located in sub-humid regions, can experience proportional (Additive, equal to the sum of individual effects) or non-proportional effects of drought and nutrient addition, which may be positive

(>Additive) or negative (<Additive), depending on the influence of one factor over the other.

3) Graminoid species, due to having faster-growth strategies and relatively shallower roots, respond more to nutrient additions and are more affected by drought than plant species from resource-conservative groups.

Results

Across the 26 grasslands, drought reduced biomass by 19%, while nutrient addition increased biomass by 24%, though high inter-site variability in responses was observed (Figure 3; Figures SM1-2). We observed that the positive effects of nutrient addition and the negative effects of drought on biomass counteracted each other when treatments were applied together. This resulted in no significant difference compared to ambient conditions and produced non-proportional effects that were lower than the sum of the individual treatments (Figure 3). At the local-scale, individual site effects showed that nutrient addition significantly increased biomass in six sites (23%), drought significantly decreased biomass only in four sites (15%) while the rest of the sites lacked significant treatment effects (Table SM6; Figures 3-SM2). The driest site (urat.cn; arid grassland located in China Table 1 and SM1) experienced the greatest decline (80%) in biomass with drought (Figure 3; Table SM6). The combined treatments had significant effects in nine of 26 sites (35%). Of these, three sites showed higher values than the sum of individual effects, while most of them exhibited lower effects (Figure 2; Table SM6). In the remaining 17 sites, no significant differences of nutrient addition + drought were found compared to ambient conditions (Table SM6; Figure 3). In arid sites, drought significantly reduced biomass by 28%, while nutrient addition increased it by 34% (Figure 3). Biomass reduction under drought and increase with nutrient addition were higher at arid sites than at sub-humid and humid sites, indicating stronger water and nutrient limitations at the former (Figure 3; Table SM7). In sub-humid sites, biomass increased by 20% with nutrient addition, decreased by 14% under drought and increased by 12% under nutrient addition + drought. Only in this aridity category, the combined treatment had a higher effect than the sum of the individual effects and enhanced biomass where nutrients stimulated greater additional biomass under drought than ambient precipitation (Figure 3; Table SM7). Finally, biomass at the humid sites increased 13% in response to nutrient addition but was not significantly suppressed by drought (Figure 3; Table SM7). However, effects of the combined treatment were lower than expected at both extremes of the gradient (arid and humid).

The general response of our grassland sites to drought and nutrient addition was mostly driven by a response between graminoids, legumes and forbs (Figure 4; Table SM8). For graminoids, nutrient addition increased biomass by 30%, drought decreased it by 20% and nutrient addition + drought increased biomass of a similar magnitude (20%), suggesting a non-proportional effect (higher than the sum of the individual effects, >Additive) in which nutrients overcompensate the effects of drought in graminoids biomass. Within the other groups (though in low abundance), legumes biomass increased more strongly in response to nutrient addition under ambient precipitation than under drought (Figure 4), while woody biomass only showed a surprisingly significant increase of more than 40% after nutrient addition (Figure 4; Table SM8).

We found that certain biotic and abiotic factors influenced the LRR biomass more strongly than others and interacted more with drought and nutrient addition effects individually rather than when both were applied jointly (Table SM5; Figure 5). Nutrient addition effects decreased with increases in mean annual precipitation and estimated soil N (Figure 5A, D). Interannual precipitation variability interacted with drought and with nutrient addition, resulting in a more negative impact on biomass sites with more variable precipitation (Table SM5; Figure 5B, E). The negative effects of drought and the positive effect of nutrient addition on biomass were amplified in more diverse sites (Table SM5; Figures 5C, F).

Discussion

Our globally coordinated, drought and nutrient addition multi-site experiment showed that, after one year, both factors independently affected biomass with nutrient addition increasing grassland biomass and drought reducing it. However, when combined, these factors, resulted in no overall impact. This general pattern is largely explained by the strong response of a few grasslands within the global gradient, while most grasslands showed little to no response to drought or nutrient addition after one year. The lack of response in biomass to drought and nutrient addition combined might be due to a stronger aboveground biomass response to nutrient addition, potentially also changing water use by redistributing resources[28]. These effects may vary based on pre-existing resource conditions and site-specific characteristics such as climate, plant species composition and their idiosyncratic responses or soil nutrient availability[28], highlighting the importance of considering aridity levels[29]. The combined effects of these factors specifically vary with aridity. In sub-humid grasslands, they were significantly higher than the additive individual effects (i.e., more than proportional to the sum of the individual effects). Here, nutrient addition mitigated drought-induced biomass reduction more effectively, resulting in higher biomass relative to ambient levels. On the other hand, the combined effects were lower than proportional to the sum of the individual effects (though, not significantly) in arid and humid grasslands. These general responses in different aridity levels exhibited high inter-site variability, with many sites lacking significant treatment effects and a few showing strong responses that may influence the overall outcome. Notwithstanding, this study offers a global perspective on short-term patterns, while acknowledging site-specific factors that can contribute to local variability. Focusing on a single year enhances the relevance of the study by capturing global geographical variability and emphasizing the need to analyze grasslands locally, considering factors like aridity and water limitations that influence species composition and drought sensitivity[6,14]. This approach allows evaluation of short-term responses, which can differ greatly from long-term outcomes. Key processes, such as soil nutrient availability, plant growth, and resource allocation, are highly sensitive in short time scales (e.g., one year), often trigger resource changes at individual and community levels that may lead to longer-term ecosystem shifts[30,31]. Further multi-year studies with an expanded number of sites are needed to fully analyze longer-term responses.

Grasslands often experience co-limitation from water and nutrients, affecting vegetation responses, where one factor may reduce the efficiency of the other or lessen its negative impact[31,2]. Many of the studied grasslands fall within the co-limitation zone (Figure 2), since water and nutrients influenced plant biomass[3,4]. Unlike ecosystems with extreme water (e.g., hyper-arid environments) or nutrient (e.g., tropical rainforests) limitations, our grasslands do not encompass extremely severe deficiencies in either of each resource. Arid and sub-humid sites exhibited significant increases in aboveground biomass in response to nutrient addition, primarily driven by the pronounced responses of a few sites within each aridity level. However, some of these sites also showed negative effects from drought. While sub-humid grasslands experienced some water limitations, it was less severe than in arid regions, where water is most strongly limiting for biomass accumulation[2,20,6]. However, sub-humid sites exhibited significant nutrient constraints, as shown by the high increases in aboveground biomass in response to nutrient addition, which also mitigated the negative impact of drought and compensated for drought-induced biomass reduction.

Previous studies found that drought negatively and nutrient addition positively affected grasslands, but no overall positive or negative effects emerged after one year [32,15,31]. In our studied arid sites, the negative impact of drought was the highest among all the grasslands analyzed. However, the response to nutrient addition was greater than expected, as a higher sensitivity to drought rather than to nutrients had been anticipated[20,4]. Thus, the combined treatment was expected to exacerbate water scarcity, cause nutrient immobilization[33] and reduce nutrient use efficiency[16]. Our results suggest that although nutrients may provide a buffering effect on biomass, drought simultaneously diminishes the ability of plants to utilize these nutrients[9]. In humid sites, where growth is mainly limited by nutrient-poor soils or light availability (when nutrients are highly available) and fast-growing species are more abundant, a lower sensitivity to droughts was expected[20,4]. However, they showed no strong responses to nutrient addition or drought and non-significant difference to ambient under combined treatments. This suggests that biomass regulation is likely driven by factors such as light availability in humid grasslands, which can be highly limited in grazing-excluded areas, surpassing the effects of nutrient addition or drought on plant competition[24,33,34].

Graminoids increased biomass with additional nutrients but decreased under drought conditions, in line with previous studies[9,15]. Graminoids typically benefited more from nutrient addition (in nutrient-poor soils) than other plant functional groups. Nonetheless, in the studied grasslands, graminoids showed sensitivity to both: nutrient addition and drought, with considerable biomass increases and decreases, particularly in certain arid and sub-humid grasslands. This response may be associated with the capacity of certain species of exploiting resource pulses with a fast-growing strategy or the promotion of annual graminoids[35] and the associated concentration of roots in the upper soil horizons (unlike woody or other conservative-strategy species)[23]. Nutrient addition mitigated drought-induced biomass reductions in graminoids, which may be explained by an increase in the photosynthetic rates, leaf area and root density allowing increased water-use efficiency[36]. Another possible explanation is that drought may indirectly reduce light limitation in humid grasslands, where light is most limiting, allowing graminoids to use nutrients more efficiently for growth[24]. Legumes, though scarce, were highly sensitive to drought and their biomass was reduced under combined treatments, likely due to decreased N-fixing activity and drought stress[37]. In contrast, woody plants and forbs may have shown greater drought resistance, as species in these functional groups typically have more conservative growth strategies, often linked to long-lived perennials[36,38]. Woody biomass, though very low in abundance, unexpectedly increased with nutrients, possibly due to pre-existence in nutrient-poor soils combined with above-average precipitation. The variability in drought and nutrient addition responses across all plant functional groups, with two out of four showing no significant effects, aligns with previous studies. These studies suggest that other factors, such as belowground traits (e.g., extensive vs. non-extensive rooting systems) or species origin (native vs. exotic), may also play a crucial role in influencing resistance to changes in resource availability and should be considered in further studies[35,8]. The observed one-year biomass responses to nutrient addition and drought indicate that if they persist or intensify over time, could alter the structure and composition of grasslands across various aridity levels, potentially affecting biodiversity and forage quality for livestock, which is mainly based in graminoid species[20]. Additional multi-year studies can complementarily assess how plant functional group responses may change over longer time scales.

Biomass responses to drought and nutrient addition were mediated by interannual precipitation variability, plant species richness, water availability and soil N. Drought and nutrient effects were strongly influenced by interannual precipitation variability, with more variable sites experiencing greater negative impacts. This aligns with studies emphasizing that sites with greater precipitation variability, typically the most arid, share similar responses to climatic extremes due to their influence on plant community structure and growth strategies[39,40,41]. Plant species that typically dominate in these conditions, lack the capacity to quickly acquire and utilize resource pulses but may persist during unfavorable periods[42.43]. However, large biomass reductions in arid ecosystems with high interannual precipitation variability may result from severe droughts, because extreme water reductions may exceed the ability of plants to tolerate the conditions[44]. Unexpectedly, high levels of species richness modulated treatment responses, amplifying both negative drought effects and positive nutrient ones. Plant richness impact on drought effects could be linked to its relationship with resilience rather than resistance[45], higher evapotranspiration rates[46], and intensified root competition[47]. The positive nutrient response with higher richness may be due to niche complementarity, reduced competition and nutrient depletion[48]. Negative relationships were observed between biomass response to nutrient addition and increases in water availability and soil N content, along with unexpected positive biomass increases at some arid sites, suggesting that nutrients, rather than water, may be the limiting factor in arid grasslands with low soil N[33,4,2,49].

This study addresses a critical gap in understanding how nutrient addition, drought, and their combined effects impact worldwide grassland biomass production through experimental manipulations focusing in the short-term. After one year, drought and nutrient addition showed mostly independent effects on biomass. However, in sub-humid regions, greater effects than the sum of the individual effects were found under combined treatments. Our findings suggest that many grasslands are generally co-limited by water and nutrients, especially in sub-humid environments. In the short term, biomass increases with nutrient addition and decreases under drought, which is mainly explained by graminoid responses. Notably, graminoids can withstand drought when nutrient availability is high. Additionally, since factors beyond water availability, such as interannual precipitation variability, plant species richness and soil N content, influence responses to drought and nutrient addition, considering the local context is essential to address the variability of these environmental factors. Further research should explore the mechanisms underlying the co-occurrence of nutrient addition and drought, as well as their effects over longer time scales, focusing on vegetation responses mediated by plant diversity, species composition, functional traits, or provenance. This knowledge, as generated in the present work, is essential for preserving grasslands and their valuable contributions to society in the context of global change.

Methods

Site selection

The NPK-Drought Network (NPKD Net; https://www.bayceer.uni-bayreuth.de/npkd/index.php?lang=en) is a collaborative, globally distributed experimental network of researchers committed to understand how terrestrial ecosystems respond to the combined effects of drought and nutrient addition. The network is composed of 26 sites located in grasslands across 9 countries on 6 continents, encompassing a wide range of environmental conditions (Figure 1; Tables 1-SM1). Sites follow standardized protocols for their experimental treatment and sampling regimes[50,6,34]. This study used data from the first year of the experiments.

Experimental treatments

All sites implemented four identical treatments: ambient (natural condition with total annual rainfall), drought (rainfall reduced to an amount that simulates a 1 in 100-year drought year based on local site condition, Table 1; https://droughtnet.weebly.com/; [6]), nutrient addition of nitrogen (N), phosphorus (P) and potassium (K) applied at 10 g m^{-2} yr^{-1} by elemental mass (with exception of two sites that fertilized only with P) and nutrient addition + drought. Nutrients were added as slow-release urea for N, calcium superphosphate (P_2O_5) for P, and potassium sulfate (K_2SO_4) for K. In addition, micronutrients (100 g m^{-2} yr^{-1} of a mixture composed of 6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo, and 1% Zn) were applied once at the start of the experiment to avoid toxic levels from over-application[50]. Drought was achieved by installing rainout shelters based on previous designs which passively remove a percentage of ambient rainfall[50,6]. Nutrient addition + drought was a joint rainfall reduction (drought) and nutrient addition treatment. There were between three and six replicate plots per site for each treatment, laid out in a randomized block design.

Data collection and analysis

Abiotic factors

Climate data were sourced from the MSWEP database, a gauge calibrated satellite estimate product which considers the period from 1979 to present (https://www.gloh2o.org/mswep/). MSWEP provides daily rainfall estimates, which were used to calculate the total rainfall over the 365 days preceding biomass harvest at each site. Additionally, these estimates were used to determine the mean annual precipitation (MAP, in mm yr^{-1}) based on data spanning from 1979 to the treatment year at each site. The interannual precipitation variability was quantified as the coefficient of variation (CV) of MAP, calculated as the ratio of the standard deviation to the MAP. Then, the WorldClim database (https://www.worldclim.org/data/worldclim21.html), which encompasses a time series from 1970-2000, was used to obtain mean annual temperature (MAT) at site level and MAP data for comparison purposes to the MSWEP database. Aridity index (AI) and the potential evapotranspiration (PET) for each site was obtained from gridded datasets of the *Global Aridity Index and Potential Evapotranspiration Climate Database v3* (https://csidotinfo.wordpress.com/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v3/) which implements the FAO-56 Penman-Monteith reference evapotranspiration equation and the ratio of precipitation and PET to estimate AI. The AI was classified according to the corresponding categories following Le Houérou (1996)[51] defined as Arid and Semi-arid (AI < 0.45; denominated to simplify here and afterwards as “Arid”), Dry sub-humid and Sub-humid (0.45 < AI < 0.75; denominated to simplify here and afterwards as “Sub-humid”), and Humid (AI > 0.75; denominated to simplify here as “Humid”, including in this category temperate grasslands). To estimate total soil N (%) at each site for depth (0-30 cm), we utilized models developed by Poggio et al., 2021[52]. The obtained modelled data was selected over actual site data as it ensures consistency in the applied metric, uniform calculation methodology, standardized analysis depth and the possibility to encompass all study sites data (Table 1).

Standing biomass and species richness

Total live aboveground biomass (i.e., current year’s growth) was measured in the first year of the experiment by clipping two quadrats of vegetation at peak biomass in each plot (quadrats ranged between 0.2-0.25 m^2). Clipped biomass from each plot was sorted by functional groups. The proportion of each dominant functional groups (i.e.

graminoids, legumes, non-legume forbs, woody-shrubs) in each plot, treatment, and site was calculated by dividing the biomass of each functional group by the total biomass (for details of each study site's data see Table SM2). The biomass was dried at 60 °C until a stable weight was achieved and then weighed to the nearest 0.01 g. Weights were expressed in grams per square meter. Species richness was quantified as the number of plant species in a permanent 1 m × 1 m subplot at peak biomass in each plot, when plant species cover data was assessed.

The log response ratio of aboveground live biomass (LRR Biomass) was calculated in each plot for each treatment, in each site, aridity category and functional group, according to the formula ln (Biomass $_{\text{Treatment}}$ / Biomass $_{\text{Ambient}}$). The corresponding confidence intervals (± 95%) were also calculated. To interpret the LRR outputs, the following criterium was applied: 0 represents a treatment effect identical to ambient, values greater than zero are positive treatment effects and values less than zero are negative effects[53]. To determine the significance of the effect of nutrient addition, drought and the combined effect of nutrient addition + drought on total biomass of each aridity level, site and plant functional groups biomass, the confidence intervals of each LRR coefficient were considered. The effect was deemed significant if the confidence intervals did not overlap with zero value. As well, further statistical analysis was conducted to evaluate how biotic and abiotic factors influence the impacts of treatments on biomass, using generalized linear mixed-effects models with the function *glmmTMB* using Template Model Builder (*TMB)*[54]. Treatments, biotic and abiotic factors were considered as principal effects, whereas site was included as a random effect with block and plot nested within it. For this final model, explanatory variables were selected from the previously described gathered data (Table 1), after evaluating their correlation and excluding the ones that presented high multicollinearity based on a Variance Inflation Factor (VIF), with a threshold of 3 (Tables SM 3-4). The set of variables included in the final model were MAP, richness, CV of MAP, the proportion of graminoids at each site, and % soil N, all of which were standardized and scaled following Z-score to ensure that the variables are on the same scale (mean 0 and standard deviation 1) before being entered into the model (Table SM5). Using the *DHARMa* package[55], a visual inspection of residuals, along with specific statistical tests (Kolmogorov-Smirnov and dispersion tests), confirmed that the model adequately meets the assumptions of normality and homoscedasticity. To visualize the model-predicted data, we also applied the R package *ggeffects*[56], which calculates the average marginal effects of the predictors from the mixed-effects model, and then we plotted them for the significant relationships obtained for the nutrient addition and drought treatments. All the statistical analysis was carried out on R software version 4.4.1.

Data availability

All data, including the measured biomass in the studied grasslands, as well as the applied biotic and abiotic data used for analysis, are available in the *Figshare* repository (https://figshare.com/s/ea1a00b5be946f2093f3).

Code availability

The R code used for analysis, are available in the *Figshare* repository (https://figshare.com/s/ea1a00b5be946f2093f3).

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Author contribution

YH and QY developed and framed the research question. YH, AJ, QY, LY, ETB, EWS and MDS coordinated the NPK-D Network collaboration. VFB and CX lead the writing of the manuscript. VFB, GRO, HDD analyzed data. CX, PW, JA, MCar, AK, SAP, TO and LB contributed to data analysis. PW, LY, QY, ETB, AJ, EWS, JA, GRO, HDD, MCar, AK, SAP, NE, FI, HAug, MCha, ACC, PD, TF, ACG, SEK, TO, PP, AP, DS, MT, AV, EV, GMW, CWer and GW contributed to writing the paper. VFB, CX, AJ, JA, MCar, AK, SAP, NE, FI, HAug, MCha, ACC, PD, TF, ACG, SEK, PP, AP, DS, MT, AV, EV, GMW, CWer, GW, HAn, HD, JG, LH, YGK, JL, YM, DTia, DTis, SW, CWei, KW, HW, AY, FZ, BZ, JZ, NZ and XZ contributed in data collection and as site level coordinators. Further details of each author's contribution can be found in the Supplementary Material (Table SM 11).

Competing Interests Statement

The authors declare no competing interests.

Tables and Figure captions

Table 1: Site characteristics including details on elevation (in meters above sea level), climate (mean annual precipitation in mm per year -MAP-, mean annual temperature in °C -MAT-, the aridity index (AI), interannual precipitation variability (CV of MAP, estimated as the coefficient of variation, calculated as the ratio of the standard deviation of precipitation to MAP); Soil % N (estimated based on Poggio et al. 2021[52] model); and the percentage of precipitation reduction used to simulate drought. Data from climatic variables are estimated through MSWEP database (https://www.gloh2o.org/mswep/) and assessed comparison for accuracy with WorldClim data base (https://www.worldclim.org/data/worldclim21.html). The corresponding categories following Le Houérou (1996)[51] defined as Arid and Semi-arid (AI < 0.45; denominated to simplify here and afterwards as "Arid"), Dry sub-humid and Sub-humid (0.45 < AI < 0.75; denominated to simplify here and afterwards as "Sub-humid"), and Humid (AI > 0.75; denominated to simplify here as "Humid").

Sites	Elevation	MAP	MAT	Aridity Category	AI	CV of MAP	Soil % N	% Reduction for Drought treatment
ayora.es	1050	446	12.6	Sub-Humid	0.49	0.26	0.20	40
baddrt.de	120	562	9.3	Sub-Humid	0.67	0.20	0.29	55
bange.cn	4590	497	-0.3	Arid	0.45	0.24	0.16	40
bayrdrt.de	365	817	8.5	Humid	0.84	0.16	0.24	40
cedarsav.us	280	761	6.3	Humid	0.84	0.17	0.33	43
cdptdrt.us	965	471	9.6	Arid	0.40	0.22	0.13	30
chilcasdrt.ar	15	920	15.2	Sub-Humid	0.73	0.23	0.21	50
dang.cn	4333	526	2.8	Arid	0.40	0.19	0.27	50

freiburg.de	238	974	11	Humid	1.03	0.16	0.26	30
haibei.cn	3196	564	-1.9	Sub-Humid	0.66	0.12	0.31	50
hong.cn	3500	788	2.0	Humid	0.86	0.14	0.69	50
hulun.cn	675	411	-2.2	Sub-Humid	0.51	0.25	0.29	50
llara.au	249	641	18.9	Arid	0.42	0.28	0.13	46
marcdrt.ar	7	879	14.3	Humid	0.75	0.19	0.33	50
naqu.cn	4602	532	-1.6	Sub-Humid	0.57	0.25	0.30	50
nor.cn	145	479	6.1	Sub-Humid	0.49	0.25	0.19	41
passogavia.it	2681	647	-2.8	Humid	3.76	0.16	0.33	43
paike.ar	150	321	6.6	Arid	0.29	0.36	0.15	54
rhijn.nl	8	792	9.7	Humid	1.16	0.15	0.24	51
sand.us	121	1180	16.2	Humid	0.90	0.15	0.12	30
ukulingadrt.za	838	868	17.7	Sub-Humid	0.64	0.18	0.16	50
urat.cn	1658	177	4.7	Arid	0.16	0.39	0.10	50
xilin.cn	1263	375	0.7	Sub-Humid	0.46	0.39	0.19	50
yanchi.cn	1523	371	8.2	Arid	0.32	0.23	0.08	50
yarradrt.au	24	863	17.3	Sub-Humid	0.66	0.27	0.20	65
youyu.cn	1348	443	4.6	Sub-Humid	0.46	0.22	0.12	50

Figure 1 - Spatial distribution of NPK-D Net sites (n = 26) with corresponding site codes, overlaid on a map displaying Mean Annual Precipitation (MAP; 1981–2022). Alongside the global map, example photos provided by co-authors illustrate the experimental design at selected sites. Precipitation data were obtained from TerraClimate[57], and shapefiles were sourced from naturalearthdata.com.

Figure 2: Predicted effects of Nutrient addition, Drought and the combined effects (Nutrient addition + Drought) on biomass along water and nutrient availability gradients. The hypothetical responses are shown by the log response ratio of biomass (LRR Biomass ± CI), where positive values indicate increased biomass and negative values indicate biomass reduction. At the left extreme, where water is the primary limiting factor, drought severely impacts biomass (red circles). At the right extreme, where nutrients are highly limiting, their addition significantly boosts biomass (blue circles). The combined treatment effects (violet circles) align with drought on the left and nutrient addition on the right, as one factor dominates at each extreme. The central portion (green ellipse) represents co-limited sites, where the combined effects are counteractive. Here, the response of biomass can be proportionally additive to both factors but in opposite directions, or non-proportionally additive with a positive effect (>Additive ~ greater than the sum of individual effects) or a negative effect (<Additive ~ less than the sum) if one factor influences the other (light violet empty and full triangles, respectively).

Figure 3 - (A) General, (B) aridity categories and (C) site responses in mean log response ratio of biomass (ln (Biomass $_{\text{Treatment}}$ / Biomass $_{\text{Ambient conditions}}$); LRR Biomass; *n* = 26) of Drought (red circles, D), Nutrient addition (blue circles, N), and the combined effect of both factors (Nutrient addition + Drought; violet circles, ND). Error bars represent 95% confidence intervals. Significant effects are indicated when the error bars do not overlap zero and (C) with full circles when sites exhibited significancy. The aridity category is defined according to the aridity index (AI) estimated as the mean annual precipitation divided by the potential evapotranspiration.

Figure 4 - (A) The mean log response ratio (ln (Biomass $_{\text{Treatment}}$ / Biomass $_{\text{Ambient conditions}}$); LRR; *n* = 26) of Nutrient addition (N), Drought (D) and their interaction (ND) of each functional group (Graminoids

with full squares, Legumes with full triangles, Woody with inverted full triangles and Forbs with full circles). Error bars represent 95% confidence intervals. Significant effects are indicated when the error bars do not overlap zero. (B) Biomass production for each plant functional groups (Mean ± SE for all study sites in g m^{-2}) for each treatment (Ambient conditions in black dots, “A”; Nutrient addition in blue, “N”; Drought in red, “D” and Nutrient addition + Drought in violet, “ND”).

Figure 5 - Relationships between the average predictive values with the corresponding 95% confidence intervals (lines and shady area, respectively) of the linear mixed-model of the log response ratio of biomass (ln (Biomass $_{\text{Treatment}}$ / Biomass $_{\text{Ambient conditions}}$); LRR Biomass) versus: (A) mean annual precipitation in mm yr^{-1}, (B, F) interannual variability of mean annual precipitation (CV of MAP, estimated as the coefficient of variation), (C, E) plant richness (number of species characteristic of each site) and (D) estimated proportion of the nitrogen in soil (% of N) for Nutrient addition treatment (blue color = With nutrient addition) and for Drought treatment (red color = With drought).

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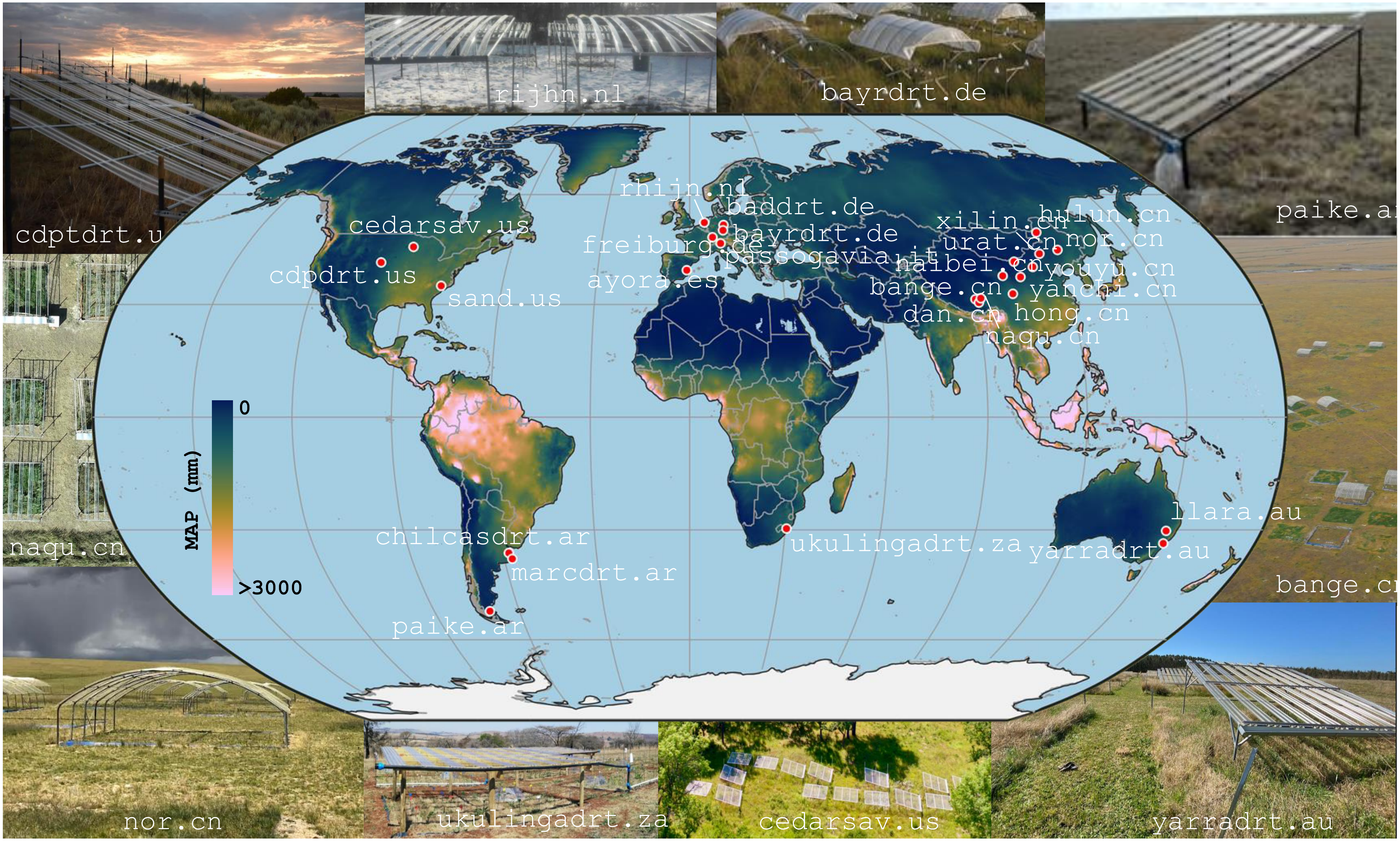
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0
MAP (mm)
>3000
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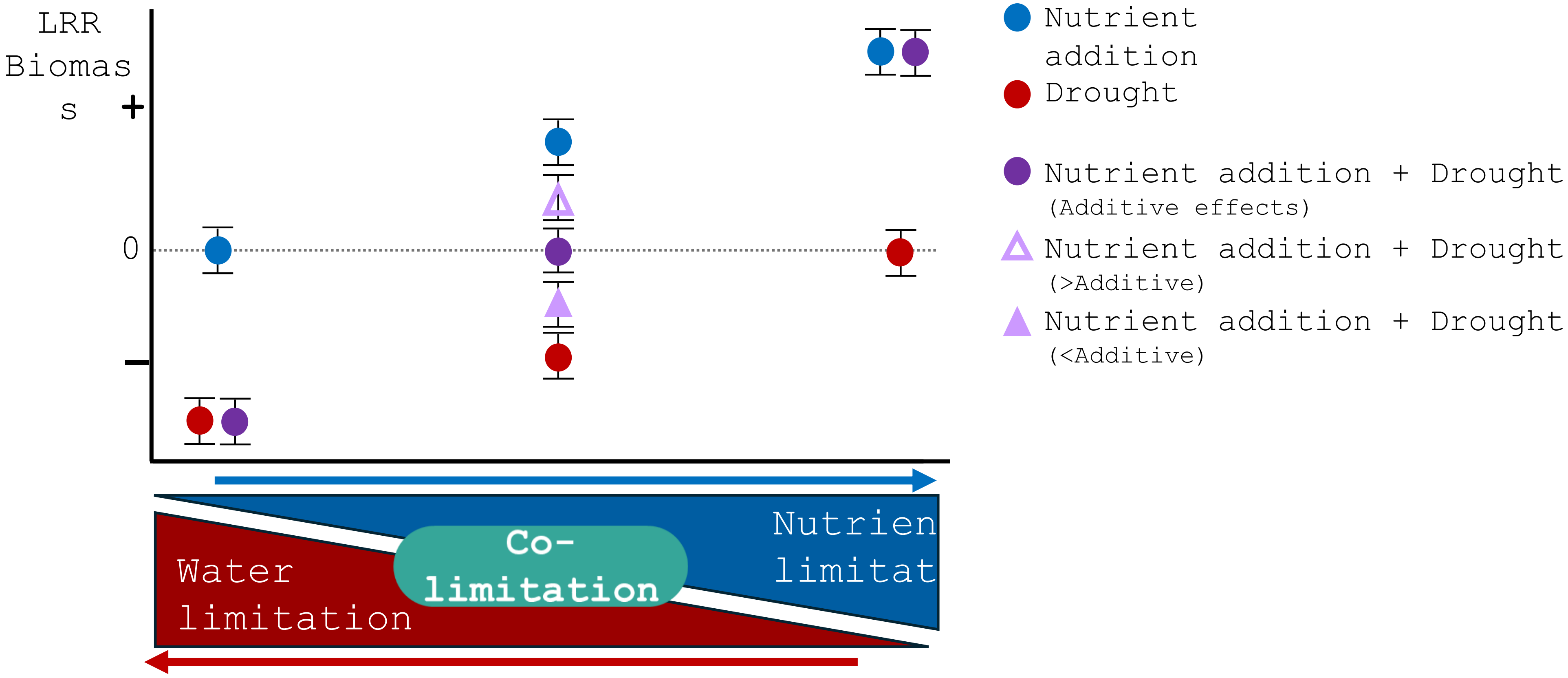
LRR
Biomas
s
+
0
−
Nutrient addition
Drought
Nutrient addition + Drought
(Additive effects)
Nutrient addition + Drought
(>Additive)
Nutrient addition + Drought
(<Additive)
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limitat
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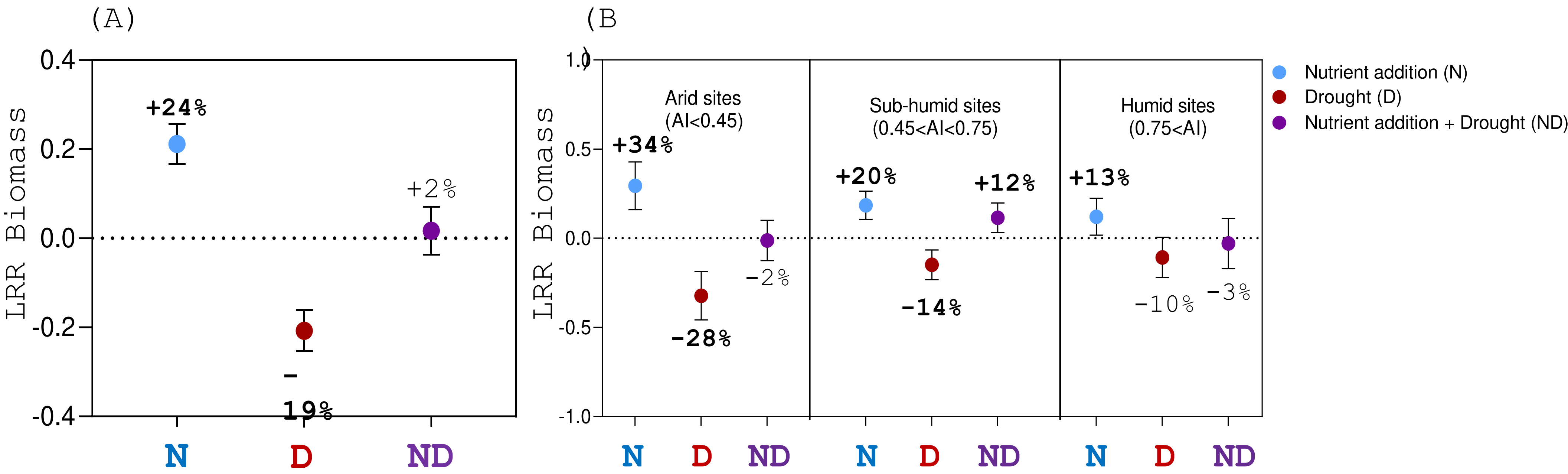
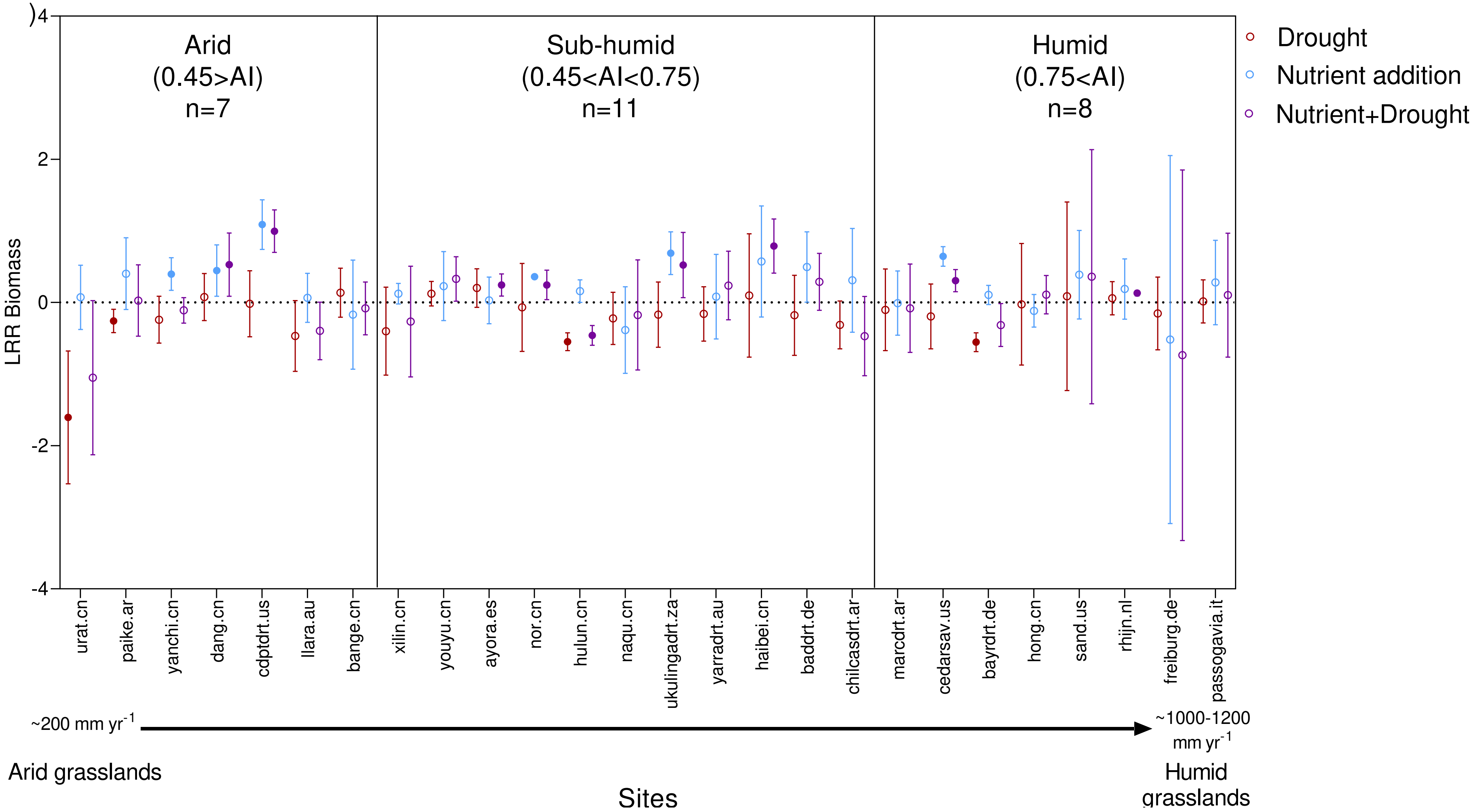
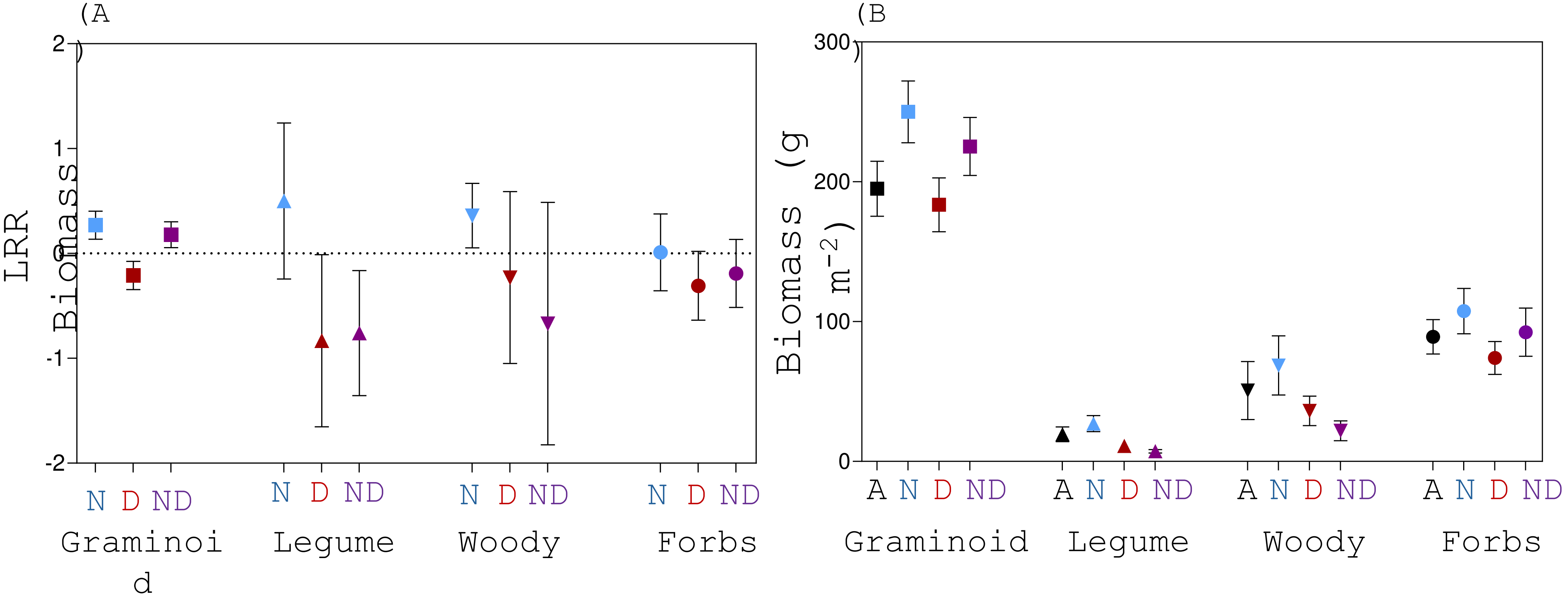
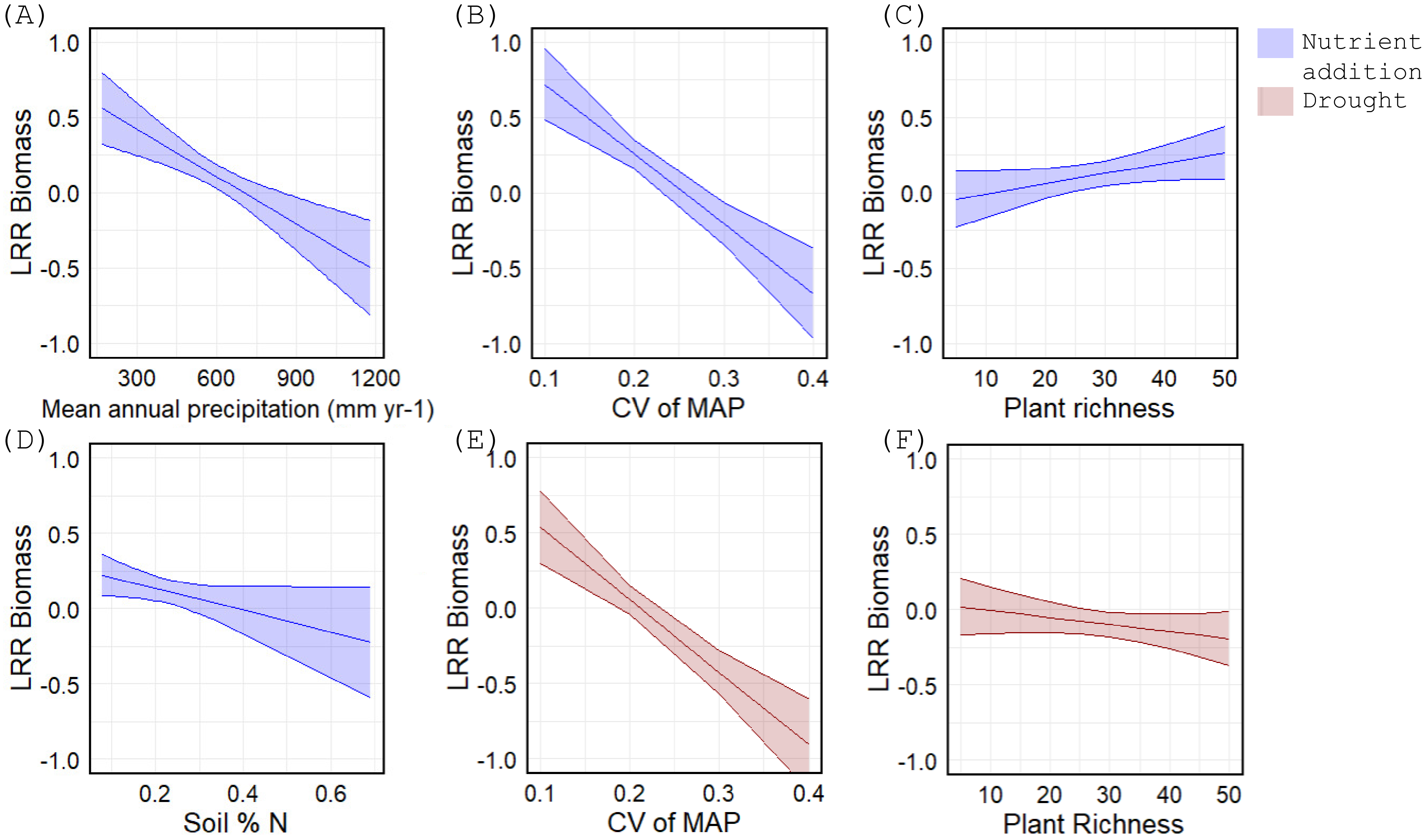

(A)
(B)
LRR Biomass
0.4
0.2
0.0
-0.2
-0.4
+24%
-19%
+2%
N
D
ND
1.0
0.5
0.0
-0.5
-1.0
Arid sites (AI<0.45)
Sub-humid sites (0.45<AI<0.75)
Humid sites (0.75<AI)
+34%
-28%
-2%
+20%
-14%
+12%
+13%
-10%
-3%
Nutrient addition (N)
Drought (D)
Nutrient addition + Drought (ND)

(C)


Arid
(0.45>AI)
n=7
Sub-humid
(0.45<AI<0.75)
n=11
Humid
(0.75<AI)
n=8
○ Drought
○ Nutrient addition
○ Nutrient+Drought
LRR Biomass
4
2
0
-2
-4
urat.cn
paike.ar
yanchi.cn
dang.cn
cdptdrt.us
llara.au
bange.cn
xilin.cn
youyu.cn
ayora.es
nor.cn
hulun.cn
naqu.cn
ukulingadrt.za
yarradrt.au
haibei.cn
baddrt.de
chilcasdrt.ar
marcdrt.ar
cedarsav.us
bayrdrt.de
hong.cn
sand.us
rhijn.nl
freiburg.de
passogavia.it
~200 mm yr-1
~1000-1200 mm yr-1
Arid grasslands
Sites
Humid grasslands


(A)
LRR Biomass
2
1
0
-1
-2
N D ND
N D ND
N D ND
N D ND
Graminoid
Legume
Woody
Forbs
(B)
Biomass (g m^{-2})
300
200
100
0
A N D ND
A N D ND
A N D ND
A N D ND
Graminoid
Legume
Woody
Forbs


(A)
1.0
0.5
0.0
-0.5
-1.0
LRR Biomass
300
600
900
1200
Mean annual precipitation (mm yr-1)
(B)
1.0
0.5
0.0
-0.5
-1.0
LRR Biomass
0.1
0.2
0.3
0.4
CV of MAP
(C)
1.0
0.5
0.0
-0.5
-1.0
LRR Biomass
10
20
30
40
50
Plant richness
Nutrient addition
Drought
(D)
1.0
0.5
0.0
-0.5
-1.0
LRR Biomass
0.2
0.4
0.6
Soil % N
(E)
1.0
0.5
0.0
-0.5
-1.0
LRR Biomass
0.1
0.2
0.3
0.4
CV of MAP
(F)
1.0
0.5
0.0
-0.5
-1.0
LRR Biomass
10
20
30
40
50
Plant Richness