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Inter-annual precipitation fluctuations alter the responses of above- and belowground biomass to water and N enrichment

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Abstract

Water availability has profound effects on plant growth and productivity in temperate and semi-arid grasslands. However, it remains unclear how variation of inter-annual precipitation by extreme rainfall events will alter the aboveground and belowground responses of plants, and how these responses may be contingent on N availability. In this study, we examined the interactive effects of inter-annual precipitation variation and N addition on aboveground and live fine root biomass of a semi-arid grassland in northern China for two consecutive years (2007 and 2008). Inter-annual variation in precipitation resulting mainly from the occurrence of extreme rainfall events in 2008 significantly affected above- and belowground plant biomass responses to water addition. In addition, variation of inter-annual precipitation by this extreme rainfall event suppressed plant responses to nitrogen addition and reduced the interaction effects between water and nitrogen addition. These effects of inter-annual precipitation fluctuation could be attributed to the negative influence of the extreme rainfall event on soil N and water availability, ultimately reducing plant rainfall use efficiency and nitrogen use efficiency. In conclusion, our results suggest ecosystem responses to water and N enrichment could be altered by inter-annual variation of precipitation regime caused by the naturally occurring extreme rainfall events.

1 Introduction

Plant growth and productivity in semi-arid grasslands are highly sensitive to changes in water availability (Knapp and Smith, 2001; Bai et al., 2004; Huxman et al., 2004a; Kong et al., 2010; Wu et al., 2011; Hus et al., 2012). With increasing water availability, plant growth may shift from water- to nutrient-limited (Xiao et al., 2007; Xia and Wan, 2008). Hence, under higher levels of precipitation, plant growth and productivity may be less responsive to water addition while being more responsive to nitrogen (N) addition (Hooper and Johnson, 1999; Xia and Wan, 2008). These response patterns

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have been widely demonstrated in semi-arid grasslands, but may vary considerably across geographic regions, as for example has been shown for the percentage change in plant biomass and productivity under water or N enrichment (e.g., Hooper and Johnson, 1999; Chen and Wang, 2000; LeBauer and Treseder, 2008; Xia and Wan, 2008; 5 Robinson et al., 2013). Uncovering mechanisms underlying variation in plant responses can provide new insights into how ecosystems respond to concurrent changes of multiple global environmental changes (Dukes et al., 2005; Bradford et al., 2012; Kardol et al., 2012). Further, integration of this knowledge in ecological models can be used to reduce uncertainty in prediction of terrestrial ecosystem responses to global climate 10 changes (Wu et al., 2011; Hsu et al., 2012).

Variation of plant responses to water and N enrichment can result from differential precipitation regimes within and among sites. Precipitation regimes are characterized by the size of individual rainfall events and the total amount of precipitation, but also by the interval, timing and seasonal allocation of rainfall events (Maestre and Reynolds, 15 2007; Fay et al., 2008; Craine et al., 2012; Robinson et al., 2013). Changes in each of these components of the precipitation regime can differently affect soil moisture, soil nutrient dynamics, and microbial activity, and hence, can lead to different response patterns of plant growth and ecosystem processes (Weltzin et al., 2003; Huxman et al., 2004b; Fay et al., 2008). Importantly, climate models predict increasing frequency of 20 extreme rainfall events under future climate scenarios (Easterling et al., 2000; Knapp et al., 2002, 2008; Weltzin et al., 2003; Austin et al., 2004; Zhang et al., 2007). A single extreme rainfall event can increase ecosystem carbon flux rates (Huxman et al., 2004b; Chen et al., 2009), whereas increasing the interval between extreme rainfall events can reduce carbon flux rates and thereby reduce soil respiration and plant productivity (Knapp et al., 2002; Fay et al., 2008). Given the close links between carbon 25 and water cycling (Chapin et al., 2002; Huntington, 2006), changes in carbon cycling resulting from increased frequency of extreme rainfall events may in turn feed back to precipitation regime and plant growth. However, we know little about how the oc-

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urrence of extreme rainfalls affects plant growth and productivity under conditions of water and N enrichment.

An important consequence of extreme rainfall events is the potential of surface runoff or leaching (Chapin et al., 2002; Zhou et al., 2008), which can reduce rainfall use efficiency (RUE) as water input from extreme rainfalls may be lost from the system rather than be taken up by plants for biomass production. Reduced RUE can also result from decrease of soil nutrient availability because of nutrient loss via runoff or leaching. The negative effects of extreme rainfall events on soil available nutrients and hence on RUE can eventually reduce plant responses to water addition. So far, most studies on the impacts of extreme rainfall events on plant productivity have focused on soil water content or its variability (Knapp et al., 2002; Fay et al., 2008; Chen et al., 2009), while few studies have considered the role of changes in soil N availability. Runoff and leaching will reduce N use efficiency (NUE) if surplus water cannot be used for improving photosynthetic efficiency at a given N supply rate (Patterson et al., 1997; Zhang and Cao et al., 2009). Hence, plant growth responses to extreme rainfall events can be mediated through effects both on RUE and NUE. Importantly, shifts in RUE and NUE suggest that extreme rainfall can alter the interaction effects between water and N addition. For example, soil microbes which are responsible for soil N nitrification are most active under high soil moisture conditions (Chapin et al., 2002; Wang et al., 2006; Liu et al., 2009). In case of extreme rainfall, combined addition of water and N may result in the loss of added N as mobile NO_3 -N leach out. Taken together, extreme rainfall events can represent an important source of variation in plant responses to water and N enrichment.

Most studies on the effects of extreme rainfall events are conducted by empirically manipulating individual rainfall size (e.g., Knapp et al., 2002; Fay et al., 2008; Chen et al., 2009). However, few studies have concentrated on naturally occurring extreme rainfall events and evaluated their influences on plant responses to multiple environmental changes. In this study, we examined the response of aboveground and fine root biomass to water and N addition in two consecutive years (2007, 2008) with highly

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contrasting precipitation regimes. Annual precipitation was 50 % higher in 2008 than in 2007. However, the majority of the inter-annual variation in precipitation resulted from a single extreme rainfall event in 2008. We tested the following hypotheses. The emergence of extreme rainfall event could (1) reduce above- and belowground plant growth responses to water addition, (2) reduce plant responses to N addition, and (3) reduce interaction effects of water and N addition on plant growth responses.

2 Materials and methods

2.1 Study site

This study was conducted in a representative Eurasian steppe near the Inner Mongolia Grassland Ecosystem Research Station of the Chinese Academy of Sciences (116°42' E, 43°38' N). The site has been fenced to exclude grazing from large animals since 1999. The dominant plant species at this site are *Stipa grandis* P. Smirn., *Agropyron cristatum* (L.) Gaertn., *Achnatherum sibiricum* (Linn.) Keng and *Cleistogenes squarrosa* (Trin.) Keng. Long term mean annual precipitation is approximately 15 345 mm, most of which falls from June to August. Long term mean annual temperature is 0.3 °C and the lowest and highest mean monthly temperature occurs in January and July, respectively (Chen and Wang, 2000). The soil is classified as Calcis-orthic Arisol according to US Soil Taxonomy.

2.2 Experimental design

20 In May 2007, twenty 4 m × 4 m plots were established. Plots were separated by 1 m buffer rows. Four treatments (control, C; N addition, +N; water addition, +W; nitrogen and water addition, +NW) were applied in a randomized block design (N = 5). Nitrogen was applied as urea (in dry form) in both mid May and early July in 2007 and 2008, respectively. In total, N addition plots received 17.5 g N m⁻² per year. It has been reported 25 that N added at this rate can be used by plants with high efficiency (Kong et al., 2010).

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Water corresponding to 10 mm precipitation was added weekly from May to September in both 2007 and 2008. To reduce loss from evaporation, water treatments were always applied after 16:00 h. In total, water addition plots received 180 mm water per year.

2.3 Field sampling and measurements

In 2007 and 2008, shoot biomass was sampled on the 15th day each month from June to September (the growing season) by clipping all plants level to the soil surface in one 1 m × 1 m quadrat per plot. Aboveground biomass was oven-dried at 60 °C to a constant mass, and weighted. At the time of clipping, in each quadrat, two soil samples (6 cm diameter, 20 cm in depth) were collected. For each plot, the two soil samples were mixed and bulked. Fine roots (diameter < 2 mm) were carefully picked from the soil, and rinsed with tap water. Live fine roots were separated from dead roots based on root color and flexibility (Kong et al., 2010) and dead roots were discarded. We concentrated on live fine roots rather than total root biomass because live fine roots are most important for plant water and nutrient uptake and have been shown to be highly sensitive to environmental changes (e.g., Neatrour et al., 2005). The live fine roots were oven-dried at 60 °C to a constant mass, weighed, and then ground to fine powder using a ball mill (Retsch MM 400; Retsch, Haan, Germany). A subsample of ground roots was used to determine N concentration using a semi-autoanalyzer (Kjeltec 2300 Analyzer Unit, Foss Tecator, Sweden).

To measure soil moisture and soil inorganic N concentration (sum of NH_4^+ -N and NO_3^- -N), two additional soil samples (5 cm diameter, 10 cm depth) were collected close to where the soil samples for root analyses were collected. Again, for each plot, the two soil samples were mixed and bulked. Then, these soil samples were sieved through 1 mm mesh. The sieved soils were extracted with 2.0 M KCl solution and filtered to determine NH_4^+ -N and NO_3^- -N concentration using a continuous flow spectrophotometer (FIAstar 5000, Foss Tecator, Denmark). Soil moisture was determined by oven-drying the soil at 105 °C for 24 h.

2.4 Data analysis

We tested effects of N and water addition, and their interaction on shoot biomass, live fine root biomass and root N concentration using two-way repeated measures ANOVA. These analyses were run separately for 2007 and 2008. Block was used

5 as a random factor. Within months, treatment effects were analyzed using two-way ANOVAs with N and water addition as fixed factors. Main treatment effects for water addition were calculated as $100 \times (W - C + NW - N)/(C + N)$ and for nitrogen addition as $100 \times (N - C + NW - W)/(C + W)$, where C, N, W, NW refer to control, nitrogen addition, water addition, and nitrogen + water addition, respectively. To compare treatment effects between years, two-way repeated measures ANOVA were run with plant biomass averaged across the four sampling dates per year. Pearson's correlations were used to analyze relationships between plant biomass and soil water content and between plant biomass and soil inorganic N. All analyses were conducted using SPSS 12.0 (SPSS Inc., Chicago, USA). The significant level was set at 0.05.

15 In addition, we analyzed effects of "accumulated precipitation", i.e., the sum of water from both irrigation and rainfall events accumulated over the year up to the sampling date. To evaluate the influence of variation in inter-annual precipitation regime on plant responses, we compared the slopes of regressions of aboveground biomass and live fine root biomass with accumulated precipitation in each year. We used the slope of 20 the regression between aboveground plant biomass and accumulated precipitation as rainfall use efficiency (RUE). In addition, we also analyzed the relationship between live fine root N uptake and aboveground biomass. Live fine root N uptake was calculated as the product between live fine root biomass and root N concentration. There is a strong correlation between roots and shoots in both biomass and N concentration 25 (Kong et al., 2010; Yang et al., 2010); therefore, we used the slope of the regression between aboveground plant biomass and root N uptake as a proxy for plant N use efficiency (NUE). Between-year differences in slopes were analyzed by standardized major axis (SMA) using SMART version 2.0 (Falster et al., 2006). We tested the fit

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of both linear and polynomial regressions. For 2008, the relationship between above-ground biomass and accumulated precipitation, and the relationship between root N uptake and accumulated precipitation were better fitted by a quadratic polynomial than by a linear regression.

5 3 Results

3.1 Precipitation regime

Total precipitation during the growing season (mid May to mid September) was 168.5 mm and 290.1 mm in 2007 and 2008, respectively. The higher precipitation in 10 2008 relative to 2007 mainly fell between the sampling dates in July and August (Fig. 1a).

During this period 142.6 mm of precipitation fell in 2008 (including a single large rainfall event of 63 mm), compared to only 43.3 mm in 2007. During this period, the 15 precipitation frequency was similar for 2007 and 2008 (intervals about 2.5 days), but the average amount per precipitation event was much higher in 2008 than in 2007 (11.9 mm vs. 3.3 mm) (Fig. 1b, c).

3.2 Aboveground biomass

Aboveground biomass peaked in August of 2007 and 2008 (Fig. 2). In both years, aboveground biomass was significantly increased by water addition (Fig. 2; Table 1). Averaged across the four sampling dates, water addition stimulated biomass equally 20 in 2007 (+47.1 %) and 2008 (+48.2 %) (Fig. 2; Table S1). There was a significant interaction between water addition and sampling date in each year, with the strongest effects observed in August (2007) and July (2008) (Fig. 2). Nitrogen addition did not affect aboveground biomass in 2007 (Tables 1, 2). In contrast, in 2008 N addition significantly increased aboveground biomass production (+11.6 %, Table 1); however, the N effect depended on the water treatment and varied with the season, as indicated by the 25

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significant N \times water \times sampling date interaction (Table 1). A main effect of N addition on aboveground biomass was found in July (+21.0 %) 2008, while significant N \times water interaction effects were found in August and September in 2008 (Fig. 2; Table 2).

3.3 Fine root biomass

5 Live fine root biomass was also stimulated by water addition both in 2007 and in 2008 (Table 1). Averaged across the four sampling dates, effects of water addition on live fine root biomass were stronger in 2008 (+41.0 %) than in 2007 (+28.8 %) as indicated by the significant water \times year interaction (Table 1, Table S1; Fig. 3). In 2007, effects of water addition on live fine root biomass were strongest in August 2007 (+51.8 %), as indicated by the significant water \times sampling date interaction (Table 1). In 2008, effects of water addition on live fine root biomass gradually declined from June to September (Fig. 3). N addition had little effect on live fine root biomass; only in August 2007 there was a significant positive effect (+19.6 %) (Table 3; Fig. 3).

15 **3.4 Across-treatment correlations between plant biomass and soil nutrient and water content**

Except for June and July 2007, and August 2008, aboveground biomass was positively correlated with soil water content (Table 4). Aboveground biomass correlated positively with soil inorganic N concentrations for all sampling dates in 2008, but not in 2007 (Table 4). Live fine root biomass correlated positively with soil moisture only in August and September 2007, and in July 2008 (Table 4). Live fine root biomass correlated positively with soil inorganic N only in August and September 2008 (Table 4).

3.5 Rainfall and nitrogen use efficiency

25 In 2007, aboveground biomass increased linearly with accumulated precipitation (Fig. 4). In 2008, however, the relationship between aboveground biomass and accumulated precipitation was best described by a quadratic polynomial regression: the

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slope of the relationship start to decrease when accumulated precipitation was about 190 mm (Fig. 4). A similar pattern was found for the relationship between root N uptake and accumulated precipitation (Fig. S1). Both in 2007 and 2008, live fine root biomass increased linearly with accumulated precipitation, and the rate with which live fine root biomass increased did not differ between the two years ($P = 0.10$ in slope comparison by SMA) (Fig. 5). NUE, measured as the slope of the regression between root N uptake and aboveground biomass production, did not differ between 2007 and 2008 ($P = 0.66$ in slope comparison by SMA) (Fig. 6).

4 Discussion

We showed significant effects of water addition on aboveground and fine root biomass, consistent with the view that water availability is a predominant factor driving plant growth and productivity in semiarid grasslands (Hooper and Johnson, 1999; Maestre and Reynolds, 2007; Kardol et al., 2010). Although the overall stimulation of plant biomass by water addition was consistent between the two years of study, we showed contrasting seasonality. For the dry year (2007), effects of water addition on plant biomass peaked in August, whereas for the wet year (2008), effects of water addition strongly declined from July to August. The decline of the water addition effects concurred with the occurrence of a large rainfall event (Fig. 1), providing support for our first hypothesis that extreme rainfall events negatively affect plant responses to water addition.

The inter-annual variation in effects of water addition on plant biomass as observed in our study may be related to shifts in rainfall use efficiency (RUE) with increasing accumulated precipitation. In 2007, the RUE was constant, while there was a remarkable decline of the RUE in 2008 when accumulated precipitation exceeded the 2007 value (Fig. 4). This finding suggests a threshold of water supply for plant growth above which additional water can no longer be efficiently used. The threshold value observed in our study (including both ambient and added precipitation) is much lower than values pre-

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viously reported for temperate grasslands (e.g., Paruelo et al., 1999; Huxman et al., 2004a; Bai et al., 2008; Hsu et al., 2012). The seasonal decline of RUE in 2008 probably can be attributed to changes in precipitation regime other than the total amount of precipitation, i.e., the occurrence of a 63 mm rainfall event between the July and August sampling dates. Such extreme rainfall events can result in surface runoff or leaching (Elrashidi et al., 2005; Li et al., 2007; Zhou et al., 2008), as was observed in our study (D. L. Kong, personal observation, 2008). Water and nutrient loss through runoff or leaching can lead to a lower threshold value of water supply above which RUE will decline.

However, reduced RUE resulting from runoff after extreme rainfall cannot explain the decrease of plant biomass responses to our water addition treatment. A large portion of water input by extreme rainfall events is lost rather than used to attenuate water limitation and, hence, effects of water addition in this case should not be affected. Detailed analysis of our data indicated that the decline of effects of water addition during the 2008 growing season could be largely contributed to reduced stimulation of aboveground biomass by water addition when combined with N addition. To illustrate, aboveground biomass was 19.7 % higher in N + water treatments than in N only treatments (t test: $P > 0.05$), while aboveground biomass was 63.6 % higher in water only treatments (W) than in control treatments (C) (t test: $P < 0.01$). In N + water treatments, more than in N only treatments, soil inorganic N may have been available mainly as NO_3^- -N because of greater activity of nitrifying soil microbes under wet conditions (Wang et al., 2006; Liu et al., 2009). Therefore, soil available N in N + water plots could have been more negatively affected by the extreme rainfall event as mobile NO_3^- -N can easily be lost in runoff and leaching. As such, in a previous study, Lü et al. (2011) found a greater loss of soil NO_3^- -N in N + water treatments than in N only treatments. Additionally, the negative effects of extreme rainfall events on soil available N may result in plant growth being N-limited rather than water-limited, and hence, explain the significant correlations of both aboveground and fine root biomass with soil inorganic N but not for soil water content in August of 2008 (Table 4). Given that the rate of root

N uptake began to decline just after the occurrence of extreme rainfall event in 2008, negative effects of extreme rainfall events could also have resulted from shifts in root N uptake (Lü et al., 2011). Taken together, our results suggest that reduced plant biomass responses to water addition in 2008 resulted from negative effects of an extreme rainfall event on RUE through nutrient loss rather than through water loss.

Our results differ from previous studies stressing the importance of extreme rainfall events in altering soil moisture variability (Knapp et al., 2002) or soil water content (Huxman et al., 2004b; Chen et al., 2009), and hence, suppressing plant productivity. The discrepancies among studies may be related to the different consequences extreme rainfall event can have depending on external factors. For example, surface runoff occurs more likely and more strongly in ecosystems with low vegetation coverage (Bai et al., 2008; Knapp et al., 2008) and in systems with high mean annual precipitation (Knapp et al., 2001; Huxman et al., 2004a). Results of our study support the idea that negative effects of extreme rainfall events on soil N, but not water availability, and hence, on RUE can drive inter-annual and seasonal variation in plant biomass response to water addition. Considering the global increases in N deposition (Galloway et al., 2008) and projected greater precipitation variability under future climate scenarios, our study suggests that effects of N deposition on plant growth and ecosystem processes can be suppressed in the case of extreme rainfall event.

The inter-annual fluctuation in precipitation caused by an extreme rainfall event can also affect plant biomass response to N addition. In 2007, there was no response of aboveground biomass to N addition, while in 2008 plant biomass responded positively. The significant effect of N addition in 2008 was found for the sampling dates before the extreme rainfall event (July), but not thereafter. The neutral effect of N addition in August 2008 was due to suppressed stimulation of plant biomass in responses to N addition when combined with water addition (-5.9% , NW vs. W treatments; t test: $P > 0.05$) compared to N addition only ($+28.6\%$, N vs. C treatments; t test: $P < 0.05$) (Fig. 2). The findings thus support our second hypothesis that plant biomass responses to N addition can be reduced by the occurrence of extreme rainfall events, as well as

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our third hypothesis for negative effects of extreme rainfall on the interaction effects between water and N addition. As for fine root response to N addition, it is interesting to note that in August 2008 there was no stimulation of fine root biomass production in response to N addition alone ($P > 0.05$ in t test, Fig. 3), while aboveground biomass was positively affected by N addition at this sampling date ($P < 0.05$ in t test, Fig. 2). Given that after extreme rainfall NO_3^- -N easier leach from the soil than NH_4^+ -N, a possible explanation for the contrasting aboveground and belowground responses is that plants in N-only plots may depend mainly on NH_4^+ -N for aboveground biomass production. This could be achieved by increasing root surface area rather than root biomass (Norby et al., 2004); however, this idea requires further study.

Negative effects of extreme rainfall events on soil available N can result in a decrease of fertilizer use efficiency, i.e., the ratio of aboveground net primary production to the amount of added N (Hooper and Johnson, 1999). However, for each unit of absorbed N, we found similar plant NUE for the two years of study as indicated by the very similar slopes of the regression between root N uptake and aboveground biomass (Fig. 6). Plant NUE generally increases with increasing precipitation because of enhanced stomatal conductance and photosynthetic efficiency under conditions of higher water availability (Patterson et al., 1997; Zhang and Cao et al., 2009). We suggest that the lack of increase in NUE in the wet year 2008 relative to the dry year 2007 could have resulted from water being lost from the ecosystem after the extreme rainfall event instead of being absorbed by the plants to increase NUE.

In summary, our study shows that inter-annual precipitation fluctuations resulting from the emergence of extreme rainfall event could have the potential to modify plant response to water and N enrichment. These effects were achieved through the negative influence of extreme rainfall on soil N and water availability ultimately reducing ecosystem RUE and NUE. Climate models predict higher variation of inter-annual precipitation with more frequent extreme rainfall events under future climate conditions (Easterling et al., 2000; Weltzin et al., 2003; Zhang et al., 2007; Knapp et al., 2008; Min et al., 2012). The influence of shifts in precipitation regime can be particularly

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important in semiarid grasslands as water availability is the predominant factors impacting on a range of key ecosystem processes (Weltzin et al., 2003; Nippert et al., 2006; Knapp et al., 2008). Despite there was only one extreme rainfall events in our study, its negative effects on the added N through runoff or leaching may be general (Chapin et al., 2002; Zhou et al., 2008). The striking effects of extreme rainfall events on plant response to water and N enrichment as observed in our study suggest that integrating variation in precipitation regime in ecological models can enhance the predictive power for ecosystem responses under multiple global environmental changes (Dukes et al., 2005; Bradford et al., 2012; Kardol et al., 2012).

10 **Supplementary material related to this article is available online at:**

[http://www.biogeosciences-discuss.net/10/13427/2013/
bgd-10-13427-2013-supplement.pdf](http://www.biogeosciences-discuss.net/10/13427/2013/bgd-10-13427-2013-supplement.pdf).

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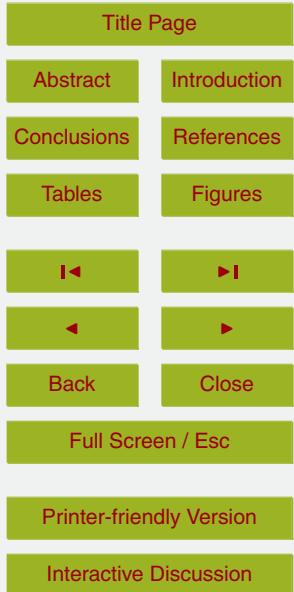
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Table 1. *P* values of repeated measures ANOVA testing for effects of nitrogen (N) and water addition (W), and sampling date (D) on aboveground biomass (AB), and live fine root biomass (LFRB) for 2007 and 2008. Significant effects (*P* < 0.05) are indicated in bold.

	AB		LFRB	
	2007	2008	2007	2008
N	0.22	< 0.01	0.15	0.62
W	< 0.001	< 0.001	< 0.001	< 0.001
N × W	0.65	< 0.01	0.96	0.62
D	< 0.001	< 0.001	< 0.001	< 0.001
D × N	0.35	0.24	0.07	0.89
D × W	< 0.001	0.01	0.001	0.68
D × N × W	0.82	< 0.01	0.17	0.79
Block	0.13	0.01	0.66	0.63



Sampling date	Effect	2007			2008		
		df	F	P	df	F	P
Jun	N	1	0.23	0.64	1	2.64	0.13
	W	1	18.38	< 0.001	1	13.08	< 0.01
	N × W	1	1.16	0.30	1	0.62	0.45
	Block	4	2.45	0.10	4	1.18	0.37
Jul	N	1	2.11	0.17	1	7.08	0.02
	W	1	24.33	< 0.001	1	48.06	< 0.001
	N × W	1	0.08	0.79	1	0.00	0.99
	Block	4	0.82	0.54	4	3.95	0.03
Aug	N	1	1.15	0.31	1	1.64	0.22
	W	1	93.29	< 0.001	1	36.42	< 0.001
	N × W	1	0.37	0.56	1	6.72	0.02
	Block	4	0.88	0.50	4	3.90	0.03
Sep	N	1	0.09	0.78	1	0.53	0.48
	W	1	86.21	< 0.001	1	90.14	< 0.001
	N × W	1	0.28	0.61	1	20.58	0.001
	Block	4	5.36	0.01	4	2.58	0.09

Table 3. Results from two-way ANOVA testing effects of nitrogen (N) and water addition (W) on live fine root biomass in 2007 and 2008. Significant effects ($P < 0.05$) are indicated in bold.

Sampling date	Effect	2007			2008		
		df	F	P	df	F	P
Jun	N	1	0.06	0.81	1	0.08	0.78
	W	1	0.53	0.48	1	14.71	< 0.01
	N × W	1	2.09	0.17	1	0.01	0.92
	Block	4	3.27	0.05	4	0.21	0.93
Jul	N	1	0.34	0.57	1	0.52	0.48
	W	1	25.81	< 0.001	1	20.41	0.001
	N × W	1	0.03	0.87	1	1.14	0.31
	Block	4	9.30	0.001	4	1.41	0.29
Aug	N	1	4.84	< 0.05	1	0.16	0.70
	W	1	25.72	< 0.001	1	12.73	< 0.01
	N × W	1	0.13	0.72	1	< 0.001	0.98
	Block	4	0.03	1.00	4	0.79	0.55
Sep	N	1	1.16	0.30	1	0.10	0.76
	W	1	19.38	0.001	1	10.65	< 0.01
	N × W	1	2.95	0.11	1	< 0.001	0.99
	Block	4	4.20	0.02	4	0.58	0.68

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Table 4. Correlation coefficients for plant biomass and soil water and nutrient content in 2007 and 2008. ^a, ^b and ^c indicate significant level at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively; ns is non-significant. Abbreviations: AB = aboveground biomass; LFRB = live fine root biomass; SWC = soil water content; SIN = soil inorganic N content.

Year	Sampling data	AB-SWC	AB-SIN	LFRB-SWC	LFRB-SIN
2007	Jun	0.28 ns	-0.05 ns	0.35 ns	-0.030 ns
	Jul	0.41 ns	0.20 ns	0.26 ns	-0.04 ns
	Aug	0.81 ^c	-0.002 ns	0.649 ^b	0.18 ns
	Sep	0.81 ^c	0.36 ns	0.59 ^b	0.43 ns
2008	Jun	0.58 ^b	0.52 ^a	0.39 ns	0.23 ns
	Jul	0.61 ^b	0.60 ^b	0.54 ^a	0.23 ns
	Aug	0.51 ns	0.55 ^a	0.10 ns	0.53 ^a
	Sep	0.76 ^c	0.77 ^c	0.41 ns	0.75 ^c

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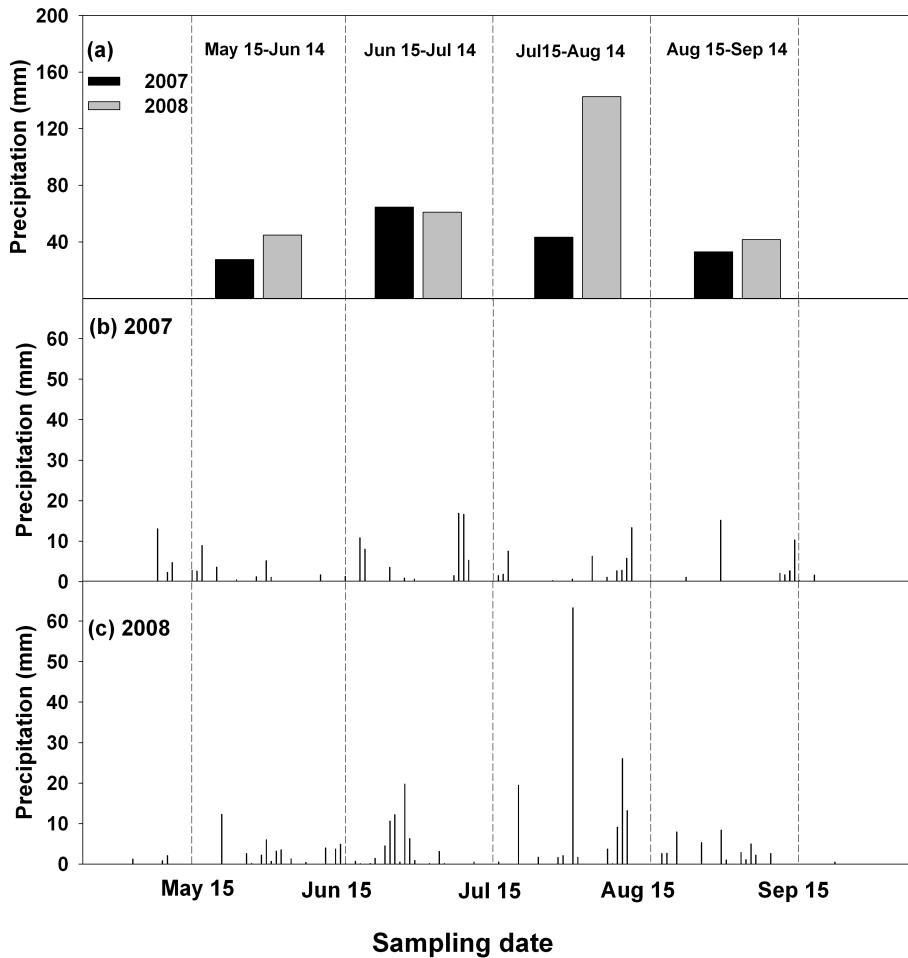


Fig. 1. Monthly (a) and daily precipitation during the growing season in 2007 (b) and 2008 (c). Dashed lines indicate sampling dates.

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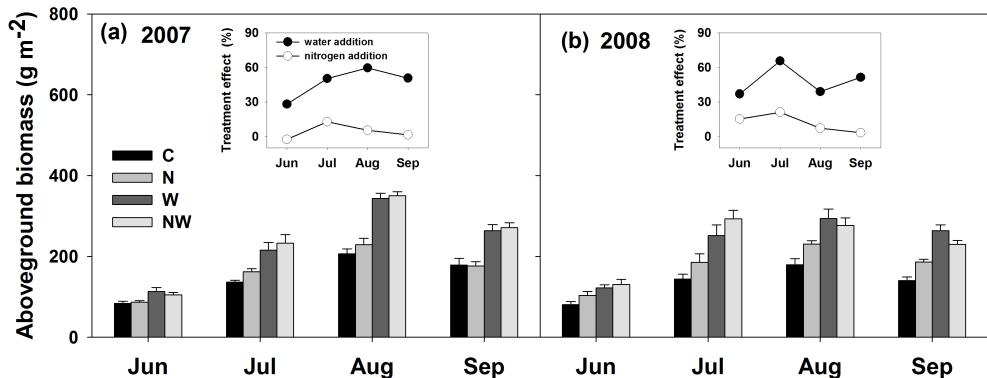


Fig. 2. Responses of aboveground biomass to water addition and nitrogen addition during the growing season in 2007 (a) and 2008 (b). Main effects of each treatment are shown in the insets. Data are presented as mean \pm SE ($n = 5$). Treatments are as follows, C = control, N = nitrogen addition, W = water addition, NW = water + nitrogen addition.

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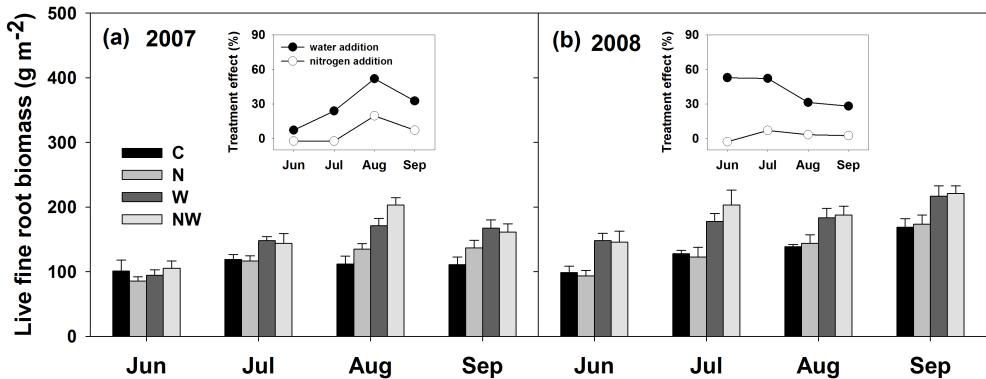


Fig. 3. Responses of live fine root biomass to water addition and nitrogen addition during the growing season in 2007 (a) and 2008 (b). Main effects of each treatment are shown in the insets. Data are presented as mean \pm SE ($n = 5$). C = control, N = nitrogen addition, W = water addition, NW = water + nitrogen addition.

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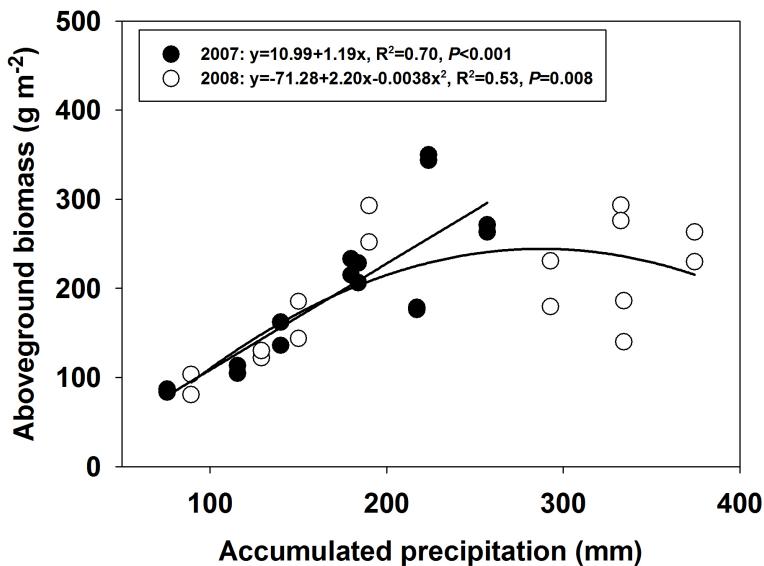


Fig. 4. The relationship between aboveground biomass and accumulated precipitation in 2007 (solid circles) and 2008 (open circles).

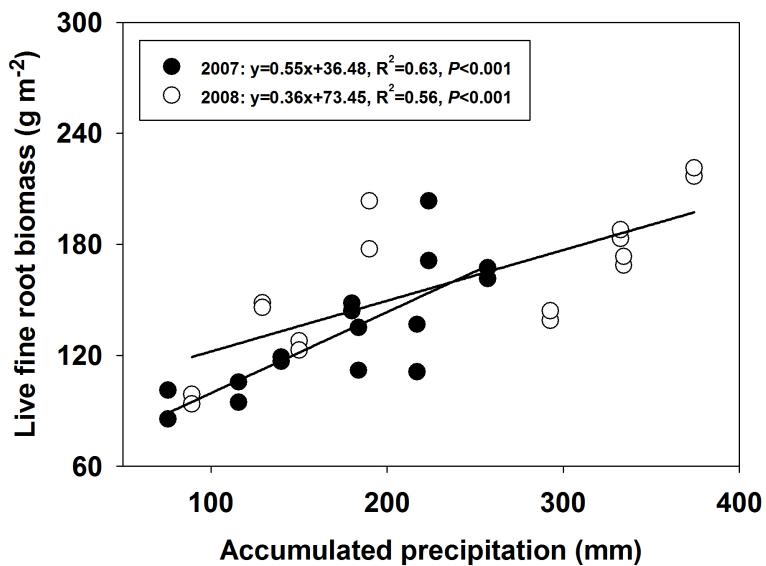


Fig. 5. The relationship between live fine root biomass and accumulated precipitation in 2007 (solid circles) and 2008 (open circles).

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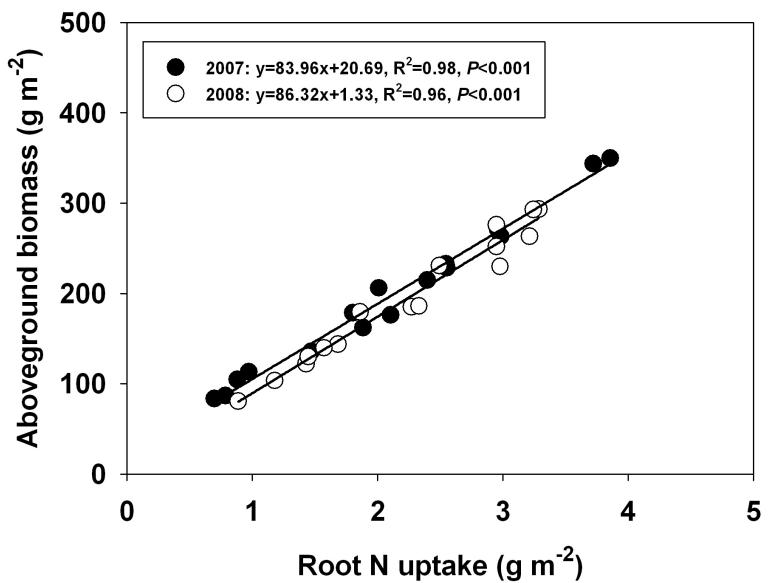


Fig. 6. The relationship between root N uptake and aboveground biomass in 2007 (solid circles) and 2008 (open circles).