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REGULAR ARTICLE

Testing nitrogen and water co-limitation of primary productivity in a temperate steppe

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Abstract
Background and aims Primary productivity in the temperate steppe is assumed to be co-limited by nitrogen (N) and water availability, but empirical evidence is scarce. We examined the N and water limitation status of primary productivity from the species scale to community scale under the framework of resource co-limitation.
Methods We compared the responses of aboveground net primary productivity (ANPP) at different ecological levels to factorial N and water addition in two years in a temperate steppe of northern China.
Results Water addition significantly enhanced total ANPP by 46%, with stronger effects in the dry year. Total ANPP was sub-additively co-limited by N and water availability, being more sensitive to water addition than to N addition in the dry year and equally sensitive to both resources in the year with normal precipitation. The responses of total ANPP to resource additions were largely driven by the changes of grasses rather than the forbs. Species level ANPP showed conservative responses to resource additions.
Conclusions Our results highlight the hierarchical patterns of limitation status in primary productivity at different biological organization levels in this temperate steppe. The sub-additive limitation by N and water in this ecosystem deserves more attention in modelling the dynamics of ecosystem carbon cycle under global change scenarios.

Keywords Co-limitation · Drought · Drylands · Multiple resource limitation · Plant functional group · Precipitation · Primary production

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Introduction

Evidence is mounting that ecosystem primary productivity is co-limited by multiple resources (Elser et al. 2007; Fay et al. 2015; Harpole et al. 2011), and that multiple resource co-limitation plays a large role in structuring ecosystem composition and functioning (Kaspari et al. 2017). Compared with our understanding about the co-limitation of different nutrients, we know less about the interactions between the nutrient limitation and limitations due to other resources, such as water in the semi-arid ecosystems (Hooper and Johnson 1999; La Pierre et al. 2016).

As primary productivity of semi-arid ecosystems responds strongly to nitrogen (N) or water addition (Hooper and Johnson 1999; Harpole et al. 2007; Bai

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et al. 2008), they should not be single-limited by N or water availability. Instead, they should be co-limited by N and water. Following the co-limitation scenarios proposed by Harpole et al. (2011), co-limitation by both resources could be defined as *simultaneous* co-limitation and *independent* co-limitation. Simultaneous co-limitationoccurs under conditions producing a positive response of productivity only if both resources are added simultaneously, which is not the case for N and water in semiarid ecosystems as evidenced by empirical experiments (Harpole et al. 2007; Bai et al. 2008). Alternatively, primary productivity of semi-arid ecosystems may be co-limited by N and water independently, such that single resource additions lead to positive effects on productivity (Harpole et al. 2011; Sperfeld et al. 2016). Theoretically, the independent co-limitation of N and water could produce a range of potential interactions among resources, including *super-additive*, *additive*, or *sub-additive* (Harpole et al. 2011; Sperfeld et al. 2016; Kaspari et al. 2017). These types of resource interactions would then lead to effect sizes of productivity increase fromr combined N and water addition as either larger, equal to, or smaller than the sum of the effect size of two single additions, respectively (Sperfeld et al. 2016). Whether N and water co-limitation in semiarid ecosystems is *super-additive*, *additive*, or *sub-additive* is largely unknown. Such a knowledge gap limits our ability to predict ecosystem dynamics under climate change scenarios.

Precipitation, one of the dominant drivers for primary productivity in semi-arid ecosystems (Hooper and Johnson 1999; Wilcox et al. 2016), is a modulator for the response of primary productivity to N availability (Harpole et al. 2007; Ren et al. 2017). Both the spatial and temporal variations of precipitation alter N and water co-limitation status of semi-arid grasslands. For instance, N limitation intensifies across a precipitation gradient at regional scale (Burke et al. 1997). While the changes of N and water limitation status with spatial variation of precipitation are well addressed (Hooper and Johnson 1999), we still know little about changes in N limitation for productivity associated with temporal variation in precipitation. Given the predicted increases in inter-annual variation of precipitation in the next few decades (IPCC 2013), it is critically needed to understand the temporal variation of resource limitation status for primary productivity.

Resource limitation status is predicted to vary among different plant functional groups and species, due to their differences in resource acquisition and use strategies (Bloom et al. 1985; Craine 2009). Furthermore, primary productivity at community level is more likely to be co-limited by multiple resources than that at functional group or species level, because plants can vary greatly in resource demands (Craine 2009). In a California grassland, Harpole et al. (2007) found that the aboveground net primary productivity (ANPP) of two annual grasses, were strongly increased by combined N and water addition, a third species was enhanced by N addition alone, whereas all forbs showed no detectable response to either single resource addition or combined addition. In a recent meta-analysis, DeMalach et al. (2017) reported that water addition increases community biomass through stimulating the growth of forbs while N addition increases community biomass by enhancing the growth of graminoids. Many studies provide evidence for species-specific variation of N and water limitation status in a single year (Harpole et al. 2007; St Clair et al. 2009), however, it remains unknown to what extent inter-annual variation in precipitation would drive the N and water co-limitation status at species and functional group levels in a semi-arid grassland.

Here, we tested the co-limitation status of N and water for different ecological scales from species level to community level in a semi-arid temperate steppe, and their inter-annual variation between two years with large differences in annual ambient precipitation. Previous results showed that plant physiological traits, such as N uptake and N use efficiency, modulated the impacts of N and water addition on ANPP in this ecosystem (Lü et al. 2014), indicating the close relationship between growth at different ecological scales. We predicted that 1) the co-limitation interaction of N and water availability for total ANPP at community level would be *super-additive* as N is the most limiting element and water availability could enhance soil N availability in this ecosystem (Wang et al. 2006); 2) the positive effects of N addition would be due to the growth of tall grasses, the functional group with better competitive ability for light after eutrophication (Hautier et al. 2009), while the positive effects of water addition would be due to the growth of forbs as indicated by a meta-analysis (DeMalach et al. 2017); 3) such responses at community and plant functional group levels were driven by the responses of dominant species as suggested by the mass-ratio hypothesis (Grime 1998). Results from this study will determine the resource limitation status of the temperate steppe in the context of the resource co-limitation framework (Craine 2009; Harpole et al. 2011).

Materials and methods

Our experiment was carried out in a semi-arid temperate steppe located near the Inner Mongolia Grassland Ecosystem Research Station, China (43°38′ N, 116°42′ E, 1250 m a.s.l.). Mean annual precipitation is 334 mm (1980–2008), ranging from 182 mm in 1980 and 507 mm in 1998. Mean annual temperature is 0.9 °C, ranging from −1.1 °C in 1987 and 2.4 °C in 2002. Annual precipitation in 2007 and 2008 was 240 and 362 mm, 72 and 108% of the long-term mean value, respectively. The growing season in this region is about five months, lasting from May to September. Soils of this site are Haplic Calcisols according to the FAO soil classification system. Mean bulk density of top soil (0–10 cm) is 1.29 g cm^{-3}, with mean pH value of 7.2. Inorganic N and Olsen-P concentration of the top soil is ~7 mg kg^{-1} and ~3 mg kg^{-1}, respectively. The site has been fenced to prevent livestock grazing since 1999. Perennial grasses, including *Stipa grandis* P. Smirn, *Achnatherum sibiricum* (Linn.) Keng, and *Agropyron cristatum* (L.) Gaertn., are the dominant plant species in this ecosystem.

We set up 20 plots, arrayed in five rows of four 4 m × 4 m plots, separated by 1 m aisles. Each plot in every row received one of four treatments in a stratified random design. There were four treatments, including Control (C): no resource addition; N addition (+N), granular urea was added twice a year totaling 17.5 g N m^{-2} $yr.^{-1}$; Water addition (+W), 10 mm of tap water (per square meter) was added with a sprayer weekly from in the growing season each year; and Combined N and water addition (+NW). To reduce water losses by evaporation, water additions were generally carried out after 16:00 pm. In the treatments with water addition, a total of 180 mm water was added each year, which is about 50% of the long-term mean annual precipitation in this region. All the treatments were carried out in both 2007 and 2008, two hydrologically contrasting growing seasons, with a total precipitation of 240 mm in 2007 (dry year, with 192 mm in the growing season) and 362 mm in 2008 (normal year, with 295 mm in the growing season). We selected high rates for both N and water addition in this experiment to alleviate the potential N and water limitation for plant growth in this area. Primary productivity in this ecosystem was previously predicted to be limited by N and water availability (Bai et al. 2008).

In mid-August of both years, aboveground biomass of all living vascular plants within a 1 m × 1 m quadrat from each of the 20 plots was clipped manually with scissors at the soil surface. Plants from each quadrat were sorted to species and then oven-dried at 65 °C for 48 h. Clipped areas did not overlap across those two years. Aboveground net primary productivity (ANPP) was determined as the peak aboveground biomass in mid-August each year (Bai et al. 2009). All the species sampled in both years were classified into three plant functional groups based on their growth form and stature: tall grasses, short grasses, and forbs. The species that were classified into tall grasses group included *Ac. sibiricum*, *Ag. cristatum*, *Leymus chinensis* (Trin.) Tzvel., and *S. grandis*. The species that were classified into short grasses group included *Carex korshinskii* Kom., *Cleistogenes squarrosa* (Trin.) Keng., *Koeleria cristata* (L.) Pers., and *Poa annua* L.. The species that were classified into forbs group included *Allium bidentatum* Fisch. ex Prokh., *Al. japonicurn* Regel, *Al. tenuissimum* L., *Artemisia frigida* Willd., *Axyris amaranthoides* L., *Chenopodium glaucum* L., *Dontostemon dentatus* (Bunge) Ledeb., *Iris tenuifolia* Pall., *Kochia scoparia* (L.) Schrad., *Phlomis umbrosa* Turcz., *Potentilla acaulis* L., *P. bifurca* L., *P. tanacetifolia* Willd. ex Schlecht., *Salsola collina* Pall., *Serratula chinensis* S.Moore., and *Thalictrum petaloideum* L..

We calculated the response ratios of ANPP at community, functional group, and species scales to N and water addition:

N response: ln(+N/C)
W response: ln(+W/C)
NW response: ln(+NW/C)

Log response ratios (LRR) indicate the proportional response to different treatments and tend to be distributed normally. A log ratio of 0 indicates no response of a treatment compared to the control value; values >0 show positive responses and < 0 show negative responses. We calculated 95% confidence intervals (CI) of LRRs, and considered CI that overlapped with 0 to indicate no change from the control. We examined the ANPP responses of five species which were presented in each of those 20 plots, including *Achnatherum sibiricum*, *Agropyron cristatum*, *Carex korshinskii*, *Cleistogenes squarrosa*, and *Stipa grandis*. Together, they accounted for 86 and 76% of total community ANPP in 2007 and 2008, respectively. One-way ANOVAs followed by least square mean comparisons were used to compare the differences of responses among different treatments. Mixed-effects models (lmer function in lme4 packages) were used to quantify the effects of different variables on ANPP at species, functional group, and community levels, with N addition and water addition as fixed factors and block and year being treated as random factors. All statistical analyses were performed using R version 3.0.2 (R Core Team 2015).

Results

Responses at community level

Averaged across all the treatments, total ANPP was 293 g m^{-2} $yr.^{-1}$ in 2007, 20% higher than that in 2008 ($p < 0.001$, Table 1; Fig. 1a). Water addition increased total ANPP by 46% ($P < 0.001$, Table 1; Fig. 1a), with a stronger effect in 2007 than in 2008 (Fig. 1a). Nitrogen addition and water addition significantly interacted to affect total ANPP ($P < 0.05$, Table 1), with positive effects of N addition occurring under ambient water conditions (Fig. 1a).

For the LRR of total ANPP, all the resource additions generated higher ANPP than control in both years (Fig. 1b,c). In the dry year 2007, the two treatments with water addition produced significantly higher ANPP than N addition alone (Fig. 1b). In 2008, there was no significant difference in the size effect across the three treatments (Fig. 1).

Responses at functional group level

Across the two years, water addition significantly increased the ANPP of short grasses by 70% ($P < 0.001$) and tall grasses by 37% ($P < 0.01$), with a marginally positive effect on forb production ($p = 0.08$, Table 1; Fig. 2). Nitrogen addition and potential interactive effects with water addition did not significantly influence the ANPP for any individual plant functional group (Table 1).

All resource addition treatments had positive effects on the ANPP of three functional groups, as indicated by the fact of mean values of LRR > 0 (Fig. 2). However, such positive effects were statistically significant for few cases. In 2007, water addition alone significantly increased the ANPP of tall grasses. In 2008, water addition alone increased the ANPP of short grasses, and combined addition significantly enhanced the ANPP of both short and tall grasses. There was no significant difference in their impacts on ANPP of all plant functional groups across those three resource addition treatments in both years.

Responses at species level

Across 2007 and 2008, water addition significantly increased the growth of *Achnatherum sibiricum* and *Carex korshinskii* (both $P < 0.01$) and marginally increased that of *Cleistogenes squarrosa* and *Stipa grandis* (Table 1; Fig. 3). Nitrogen addition had no significant effect on the growth of all the five species except for a marginally positive effect on *Stipa grandis*

Table 1 Results of mixed effect model with nitrogen addition (N) and water addition (W) as fixed factor and block and year as random factors on aboveground net primary productivity at plant community, functional group, and species levels. *F*-values were shown for N and W and Chi-Square values were shown for block and year

Source	d.f.	Community	Functional groups			Species				
			Short grasses	Tall grasses	Forbs	Achnatherum sibiricum	*Agropyron cristatum*	Carex korshinskii	*Cleistogenes squarrosa*	*Stipa grandis*
N	1	2.75	1.48	1.29	0.67	1.26	0.05	1.26	1.12	3.93^
W	1	116.78***	15.63***	10.65**	3.40^	11.71**	0.09	11.71**	3.83^	3.53^
N*W	1	6.45*	0.25	0.02	2.84	0.65	0.05	0.65	0.42	0.00
Y		11.16***	0.12	2.02	0	0.34	0	0.34	0	2.58
Block		0.48	0	5.71*	0	0	0.01	0	0	0

Statistical significance is depicted as: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$: ^, $0.05 < p < 0.1$

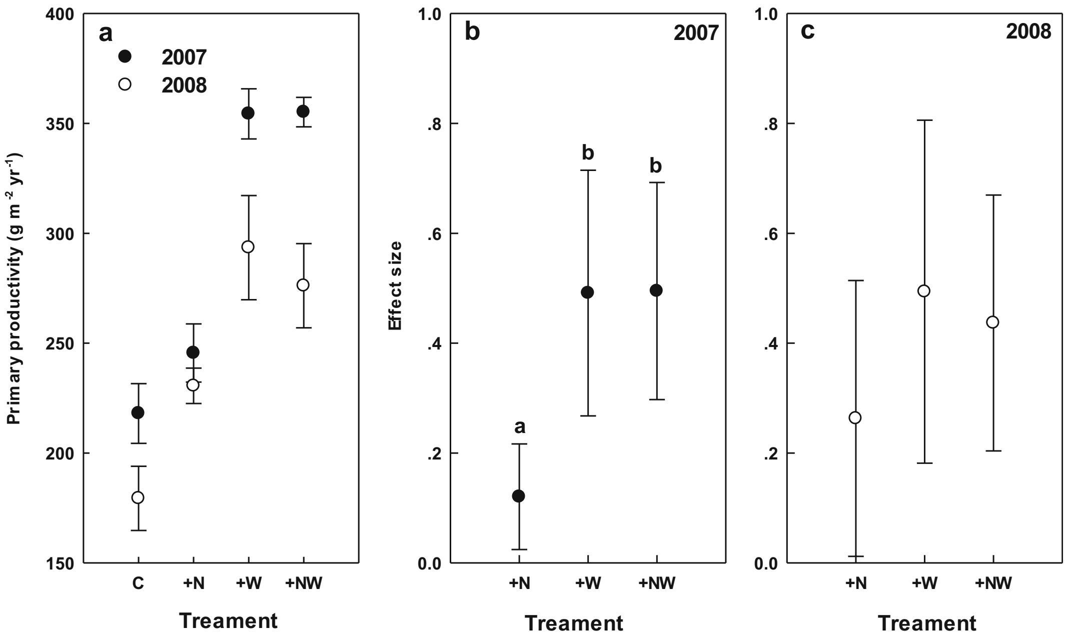

Fig. 1 Effects of nitrogen and water addition on community aboveground primary productivity in 2007 and 2008 (**a**) and their responses to nitrogen addition alone (+N), water addition alone (+W), and combined nitrogen and water addition (+NW) measured as effect sizes (log response ratios), in 2007 (**b**) and 2008 (**c**). LSD Mean differences at $P < 0.05$ among treatments are indicated by different letters. Data are presented as means ±1 SEM for ANPP (**a**) and as means ±95%CI for effect size (**b**, **c**)

(Table 1; Fig. 3). There were no interactive effects of N and water addition on the ANPP of all species across both years.

With respect to the effect sizes, the positive impact of N addition alone was significant for *Stipa grandis* in 2007 (Fig. 3). The two treatments with water addition significantly enhanced the growth of *Achnatherum sibiricum* in 2007 (Fig. 3). Combined N and water addition enhanced the growth of *Carex korshinskii* in 2007 (Fig. 3). There was no significant impact of resource addition treatments on the growth of all the five species in 2008 (Fig. 3).

Discussion

Our results showed that the co-limitation of total ANPP in this semi-arid temperate steppe by N and water was independent and *sub-additive*, in that the effects size of combined N and water addition was smaller than the sum of the effect size of two single additions. The *sub-additive* co-limitation status even did not change across the two years with contrasting precipitation. Total ANPP of this temperate steppe was more sensitive to increases in water availability than that of N availability in the dry year. The co-limitation status of primary productivity seems to be hierarchical across different ecological scales ranging from species to community, in that resource co-limitation is more evident at a higher organizational scale.

While numerous studies have shown that primary productivity is co-limited by multiple nutrients in grasslands (Harpole et al. 2011; Fay et al. 2015), we present additional evidence that primary productivity could be co-limited by nutrients and resources beyond nutrients, such as water. Nitrogen or water addition independently increased ANPP in those two hydrologically different years, indicating that ANPP in this temperate steppe was co-limited by N and water availability. Water availability regulates the spatial and temporal variation of primary productivity in grasslands (Bai et al. 2008; Bai et al. 2010; Burke et al. 1997; Wilcox et al. 2016). Meanwhile, N is the most common limiting nutrient for primary productivity in many terrestrial ecosystems (LeBauer and Treseder 2008). Consistent with our results, many studies have reported positive impacts of N or water addition on primary productivity of semi-arid grasslands in different regions (Bai et al. 2010; Harpole et al. 2007; Heisler-White et al. 2008), indicating that the *independent* co-limitation of primary productivity by N and water in semi-arid grasslands is widespread.

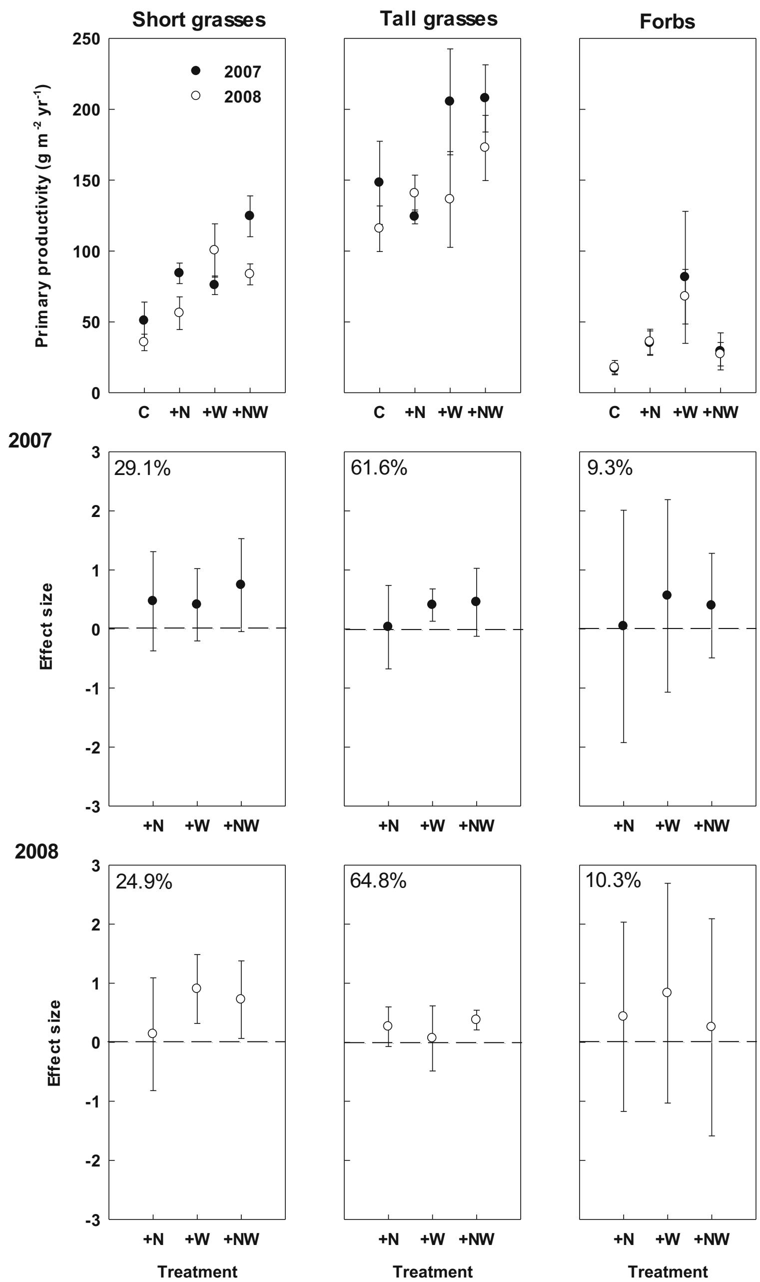

Fig. 2 Effects of nitrogen and water addition on aboveground primary productivity of plant functional groups in 2007 and 2008 (top panel) and their responses to nitrogen addition alone (+N), water addition alone (+W), and combined nitrogen and water addition (+NW) measured as effect sizes (log response ratios), in 2007 (middle panel) and 2008 (bottom panel). The relative biomass contribution (% value) of each plant functional group in control plots of each year was shown. See the meaning of each label in Fig. 1. Data are presented as means ±1 SEM for ANPP and as means ±95%CI for effect size

Inconsistent with our first hypothesis, we found that the interaction of N and water additions resources to alleviate co-limitation was *sub-additive* rather than *super-additive* in the semi-arid temperate steppe. The effect size of combined N and water addition on total ANPP was not greater than that of single resource addition. Some overlaps in the pathways through which N addition and water addition increase ANPP would be the possible cause for the *sub-additive* independent co-limitation by N and water. For example, N addition increases plant growth mainly through enhancing soil N availability and plant water use efficiency (Bai et al. 2008; Gao et al. 2011). Water addition could also increase soil N availability (Wang et al. 2006) besides its direct and positive effect on soil water availability (Harpole et al. 2007). Both water and N additions have been previously shown to enhance soil inorganic N concentration in this ecosystem (Lü et al. 2014).

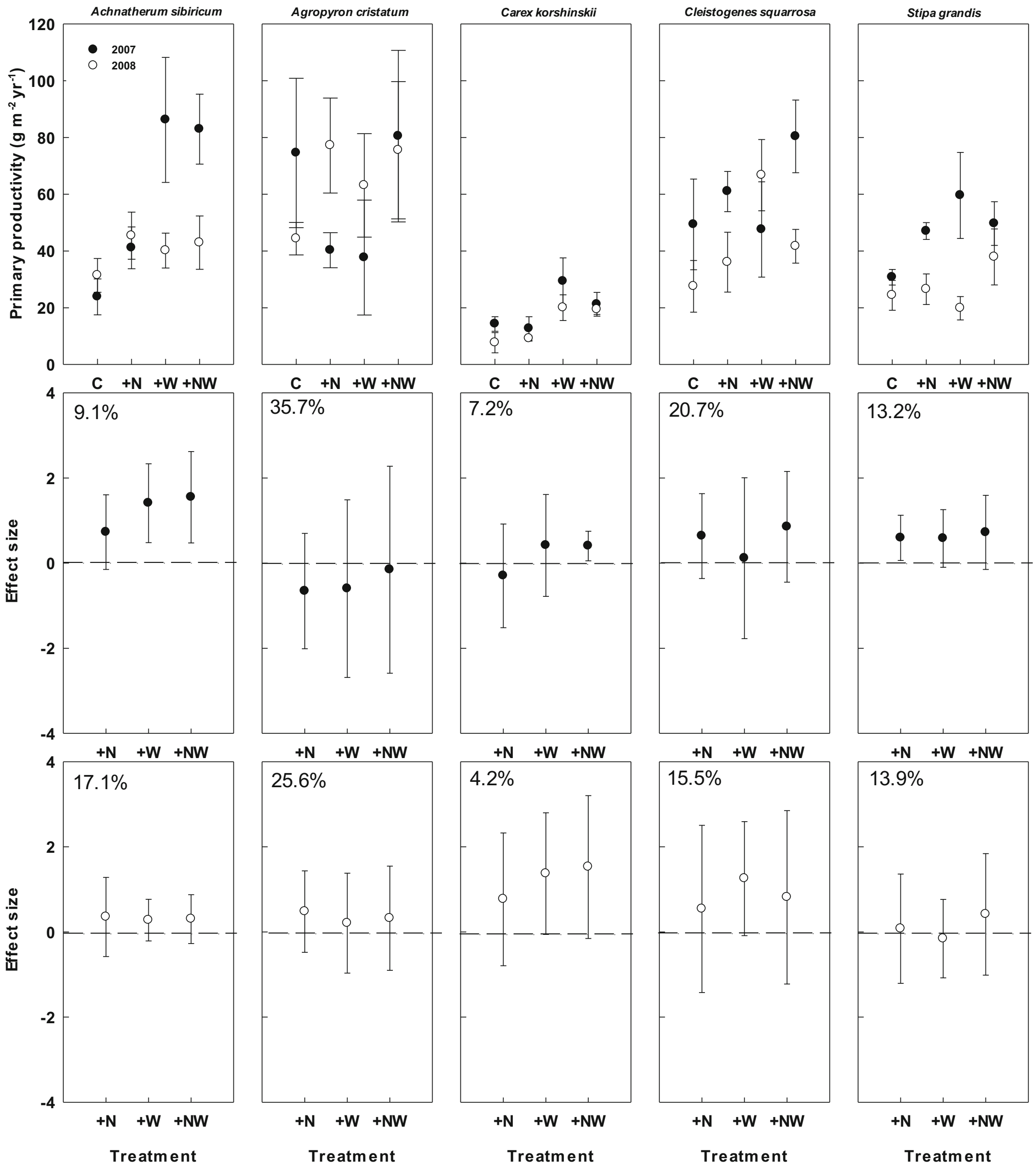

Fig. 3 Effects of nitrogen and water addition on aboveground primary productivity of dominant plant species in 2007 and 2008 (top panel) and their responses to nitrogen addition alone (+N), water addition alone (+W), and combined nitrogen and water addition (+NW) measured as effect sizes (log response ratios), in 2007 (middle panel) and 2008 (bottom panel). The relative biomass contribution (% value) of each species in control plots of each year was shown. Data are presented as means ±1 SEM for ANPP and as means ±95%CI for effect size

Moreover, total ANPP could be limited by other resources beyond N and water (Fay et al. 2015).

The type of co-limitation by N and water found here is different from that of nutrient co-limitation in terrestrial ecosystems. Global synthetic analyses show a strongly *super-additive* impact of N and phosphorus addition on primary productivity in terrestrial ecosystems (Elser et al. 2007; Harpole et al. 2011). The differences in our findings and those of Elser et al. (2007) and Harpole et al. (2011) imply that different mechanisms may underlie the different types of co-limitation between nutrients and that between nutrient and non-nutrient resource, which should be addressed in further studies. Given the vast distribution of semi-arid grassland globally and its importance in driving global carbon cycle (Poulter et al. 2014), the non-additive impacts of increased N and water availability on primary productivity in semi-arid grasslands, as found here, deserve more attention in modeling global carbon cycle under the climate change scenarios.

The co-limitation status of ANPP by N and water did not shift across those two years with different annual precipitation. The positive effects of two water addition treatments (+W and + NW) on total ANPP were greater than that of N addition alone in the dry year 2007. The effect sizes of those three treatments on ANPP showed no detectable variation in 2008, the year with normal precipitation. Such differences between the results of 2007 and 2008 were mainly due to the patterns of ambient precipitation (Lü et al. 2014). Much more large precipitation pulses occurred in the growing season of 2008 than that of 2007, which led to a substantial reduction of soil N availability (Fig. S1) and thus might account for the lower total ANPP of all the treatments in 2008 than that in 2007. Our results suggest that ANPP in this steppe would be more sensitive to increases of water availability than that of N availability in dry years. The effect size of N addition alone (+N) was significantly positive in both 2007 and 2008, indicating that N would be a limiting factor for primary productivity irrespective of the changes of ambient precipitation. Based on a literature survey of fertilization experiments in grasslands, Hooper and Johnson (1999) reported that the primary limiting factor would not shift from water to N across the geographic water availability gradient. Instead, our results suggest that ANPP is N and water co-limited. Together, those results suggest that ANPP in semiarid ecosystems would be co-limited by N and water at both temporal and spatial scales.

At plant functional group level, we found water addition had significant effect on grasses instead of forbs and N addition had no significant impact on all functional groups, which did not support our second hypothesis. Moreover, our results showed that individual species responses to N and water additions were weak, probably due to the short-term duration of our experiment. The growth of two dominant grasses, *Achnatherum sibiricum* and *Stipa grandis*, were sensitive to N and water additions. Their changes drove the responses of tall grasses, the dominant plant functional group in this ecosystem, to water addition in the dry year 2007. Their positive responses to N addition might be counteracted by the species showing a negative response (*Agropyron cristatum*), resulting in a neutral response of tall grasses to N addition in 2007. In the dry year, the growth of tall grasses tended to be primarily limited by water, as indicated by the fact that both treatments with water addition significantly increased their ANPP. In contrast, both treatments with N addition significantly enhanced ANPP of tall grasses in 2008, suggesting N would be the primary limiting factor for their growth in the year with normal precipitation. The dominant status and competitive ability of tall grasses may structure the resource co-limitation status of other plant functional groups in this natural ecosystem. While we reported the *actual* resource limitation status of plant species and functional groups with field experiment here, more works are needed to address their *potential* resource limitation status with combined field and common garden experiments (to exclude interspecific competition). Given the weak responses of individual species to resource addition in natural ecosystem, broad functional groups as we used here appear useful for capturing the idiosyncratic responses of different species.

In conclusion, our results show that ANPP in semi-arid grassland are N and water co-limited, and such status would not change interannually. The co-limitation of primary productivity by N and water in this semi-arid grassland is *sub-additive* rather than *additive*, indicating that the simultaneous increases of N and water availability would not generate more primary productivity than increased availability of single resource. Our results have implications for modeling the primary productivity and carbon cycling in the temperate steppe, which are predicted to experience increases in atmospheric N deposition and precipitation in the next few decades (Galloway et al. 2008; Liu et al. 2013; Sun and Ding 2010). We recognized several limitations in our data set. Evidence would be much stronger if long-term data are available. Our experimental approach did not allow us to easily investigate the co-limitation status of individual species in the field. This study points out the need for further investigation to understand the interaction between N and water with respect to their impacts on primary productivity in drylands.

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