



Spring watering interactively improves aboveground net primary productivity and soil microbial biomass in a semi-arid grassland of China

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ABSTRACT

An increasing number of studies have suggested a more important role of precipitation during specific segments of the year than annual amount in determining the aboveground net primary productivity (ANPP). In semi-arid grasslands of China, highly irregular distribution and intensity of precipitation supply induced by current climate changes often causes soil drought or water pulses in spring when plants are at their early growing stage. Here we tested the impact of spring precipitation supply on plant growth and nutrient uptakes, as well as dynamics of carbon (C), nitrogen (N), phosphorus (P) in soil microbial biomass (MB) and abiotic labile forms over the growing season in a semi-arid grassland of China. We conducted a spring rainfall-simulating experiment by manual watering (using drought plots as control) under field conditions from late April to May, and started sampling monthly from June to October. The results clearly showed that spring watering increased ANPP and microbial biomass C (MBC), and these effects were consistent throughout the entire growing season. Treatment effects can be detected in soil microbial biomass but not in abiotic labile pools. Throughout the growing season, soil water content and N availabilities were the main factors controlling soil microbial dynamics across treatments. Nevertheless, markedly higher microbial biomass P (MBP) and lower MB C:P ratio were observed in watering plots in September when plant P uptake had dropped down in watering plots but still kept increasing in drought plots. This suggested a delay of phenological period of plants induced by spring drought and P competition existing between plants and microorganisms. Overall, the present work highlights the importance of spring precipitation and provides implications for understanding current and future ANPP variations. In addition, we suggest to use MBC as a good soil indicator for soil fertility and plant productivity under changing seasonal precipitation patterns.

1. Introduction

Grasslands, accounting for 25.4% of the global land area, play a vital role in terrestrial net primary productivity (35% of global area) and soil organic carbon pool (30% of global area) (Kang et al. 2007). In China, grasslands are the dominant landscape (40%), and of which 78% distributed in the northern temperate and semi-arid zones (Kang et al. 2007; Xu et al., 2010).

In arid and semi-arid grassland ecosystems, precipitation is the major factor limiting aboveground net primary productivity (ANPP) (Bai et al., 2004, 2008). However, conflicting results regarding the relationship between ANPP and precipitation amount have been reported in previous studies, with positive (Fay et al., 2000; Juandedios et al.,

2009; Zhang et al., 2013; Xu et al., 2014), negative (Salve et al., 2011), and poor or no correlations (Duncan and Woodmansee, 1975; Xia et al., 2010). Robinson et al. (2013) suggested that seasonal distribution of precipitation may have a stronger influence on ANPP than total annual precipitation, since it has significant impacts on timing and quantity of soil water available for plant uptake and biogeochemical processes (Weltzin et al., 2003; Densmore-McCulloch et al., 2016). Thus, it is important to know how ANPP responds to precipitation during a specific season of the year, but the information on this issue is still scarce.

In spring, when plants grow at their early growing stage, the semi-arid grasslands in China often subject to drought or precipitation pulses. Even, in the context of global climate change, this tendency is expected to increase (Stocker, 2014). Spring precipitation can affect root

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extension (León et al., 2011), seedling survival (Padilla and Pugnaire, 2007; León et al., 2011), and phenology (Bertiller et al., 1991; Mathias and Chesson, 2013) in perennial grasslands. However, the impact of spring water availability on the total annual ANPP is not clear. For example, a watering experiment in a California grassland showed a rapid and positive plant biomass response to an extended spring rainy season (Suttle et al., 2007). Another spring watering experiment in an arid sagebrush steppe in Oregon (USA) also showed a positive impact on plant productivity, although this was only noticeable 4 years after the beginning of the experiment (Bates et al., 2006). However, Densmore-McCulloch et al. (2016) reported that increased spring precipitation by watering in semi-arid shrub-steppe grasslands did not increase plant production compared with the natural ambient precipitation control. In addition, based on a numerical model, Bai (1999) stated that precipitation from mid-April to mid-June would have a negative influence on total ANPP of semi-arid *Stipa krylovii* grasslands in north China. Due to the complexity of the influence of precipitation on ANPP and the lack of measurements, it is necessary to monitor the plant growth over the growing season as affected by spring precipitation.

Plant physiology and growth and soil microbial processes are often coupled (Xu et al., 2010; Liebisch et al., 2014). As decomposers and nutrient sink-sources, soil microbes play an important role in the biogeochemical cycle and the plant nutrient supply (Singh et al., 1989; Wardle et al., 2004). On the one hand, microbes are sensitive to changes in environmental conditions, such as soil temperature, moisture (caused by precipitation) (Fang and Moncrief, 2001; Hamel et al., 2006), and chemical properties (Bååth and Anderson, 2003) and thus affect plant growth. So far, many researchers have used soil microbial biomass carbon (MBC) as an indicator of soil fertility (e.g. Joergensen and Emmerling, 2006; Bastida et al., 2008). On the other hand, plants could inversely affect soil microbial biomass through root exudates and nutrient competition (Hertenberger et al., 2002; Liebisch et al., 2014). The temporary changes of C, nitrogen (N), and phosphorus (P) ratios in soil microbial biomass may help us decipher the coupling mechanisms and potential limitations of nutrients (Aponte et al., 2010; Kirkby et al., 2011; Griffiths et al., 2012; Bing et al., 2016). Thus, evaluating seasonal changes of MBC, MBN, and MBP, as well as plant growth and their interactions as affected by spring precipitation could greatly improve our understanding of grassland responses under changing climate.

In this context, the objective of this study was to investigate the influence of simulated spring precipitation on seasonal changes of aboveground plant biomass, as well as C, N, P in soil microbial biomass and abiotic labile forms in a semi-arid grassland of China. We hypothesize that increased precipitation in spring increased the size of the soil microbial nutrient pools and ANPP. To better understand the potential relationships between plants and microorganisms, we also monitored plant N and P uptakes.

2. Material and methods

2.1. Description of the study site

The experimental site is located in the Xilin River Basin, Inner Mongolia, China (N 44°15', E 116°32'; 1200 m above sea level). The region belongs to the Eurasian steppe grassland and has a temperate semi-arid continental climate with a mean annual temperature of 3.5 °C and a mean precipitation of 350 mm; evaporation is 4–5 times higher than precipitation. Over 80% of the precipitation is distributed in the plant growing season from late April to early October (Fig. 1). Based on the study of Xiao et al. (1995), *Stipa krylovii* (Perennial Poaceae) is the dominant species, other dominant species in this region are *Aneurolepidium chinense*, *Artemisia frigida*, and *Artemisia commutata*. The soil is a loamy sand dark chestnut soil (classified as Calcic Kastanozem according to the ISSS Working Group RB, 1998), with 77.78% sand, 8.89% silt, and 13.33% clay, containing a total of 15.3 g kg⁻¹ organic C

(TOC), 1.6 g kg⁻¹ N (TN), and 0.33 g kg⁻¹ P (TP). Soil pH is 7.4, with a bulk density of 1.4 g cm⁻³. The site was grazed by sheep from late spring to late autumn in previous years. A uniform area was selected and fenced off for the experiment in early April 2015.

2.2. Field experimental design

The rainfall-simulating experiment by manual watering was conducted from late April to May 2015. The experiment contained three treatments with three completely randomized blocks, resulting in a total of nine plots. Each plot measured 3 × 3 m with a buffer distance of 1 m between plots. The treatments were as follows: (1) watering once on 24 April (W1), (2) watering again on 14 May after soil moisture decreased back to the value before the first watering (12% in soil volume water content, Fig. S1) (W2), and (3) no watering as control treatment (W0). The starting time of the water application was chosen based on the climatic conditions and on field investigation for plant phenology. In each watering manipulation, we used 20 mm of water, which is based on the local precipitation data provided by the municipal meteorological station and approximately equivalent to the historical 50-year (1950–2000) average of total precipitation from 24 April to the end of May. We set these treatments in order to mimic different frequency and intensity of spring precipitation which could occur predicted by current climate change models. The water used for the experiment was collected from a well nearby the experimental site. The water was evenly and slowly sprayed onto the plots to minimize surface runoff. To avoid natural precipitation to the treatments during the period of the spring watering experiment, a temporary waterproof tarpaulin (PVC film), which was anchored tightly on iron stakes at the corners of the experimental site, was set up and removed from all plots before and after each natural precipitation, respectively. Apart from the watering treatment period (from 24 April to 30 May), all experimental plots received the same natural precipitation. Time-domain reflectometry (TDR, Spectrum, USA) was used to monitor soil moisture changes caused by watering and changes in environmental factors during the watering experiment (shown in Fig. S1).

2.3. Soil sampling and analysis

In the same year after the watering experiment, soil sampling was carried out monthly from 1 June to 1 October for the three treatments, which covered the whole growing season. Five soil cores (0–15 cm) were randomly taken from each of the three plots for each treatment by using an auger (5 cm in diameter, avoiding the plot edge), then mixed to obtain one composite sample. In the laboratory, coarse fresh plant debris, roots, and stones were removed by sieving through a 4-mm mesh; the moist samples were then thoroughly homogenized and stored at 4 °C until the measurements of the soil microbial biomass. A portion of soil was air dried and sieved at 2 mm before the determination of physicochemical characteristics.

Soil pH was determined in a water: soil suspension with a mass-volume ratio of 1:2.5. Bulk density and soil water content (SWC) were determined by oven-drying to a constant mass at 105 °C. Soil TOC and TN were determined by dichromate digestion and Kjeldahl digestion, respectively. Soil TP was determined by the vanadium molybdate yellow colorimetric method after HClO₄-H₂SO₄ digestion (Bao, 2000). Particle size distribution was measured by the pipette method (Sheldrick and Wang, 1993). Within 1 week, we determined MBC, MBN, and MBP, as well as K₂SO₄-extractable C (Ext-C), N (Ext-N), and NaHCO₃-extractable P (Ext-P).

Soil microbial biomass C (MBC), N (MBN), and P (MBP) were estimated by fumigation extraction methods, calculating as the difference between fumigated and non-fumigated soils with conversion factors of 0.45, 0.54, and 0.40, respectively (Brookes et al., 1982, 1985; Vance et al., 1987). The K₂SO₄-extractable C (Ext-C), N (Ext-N), and NaHCO₃-extractable P (Ext-P) in non-fumigated soils were used as soil abiotic

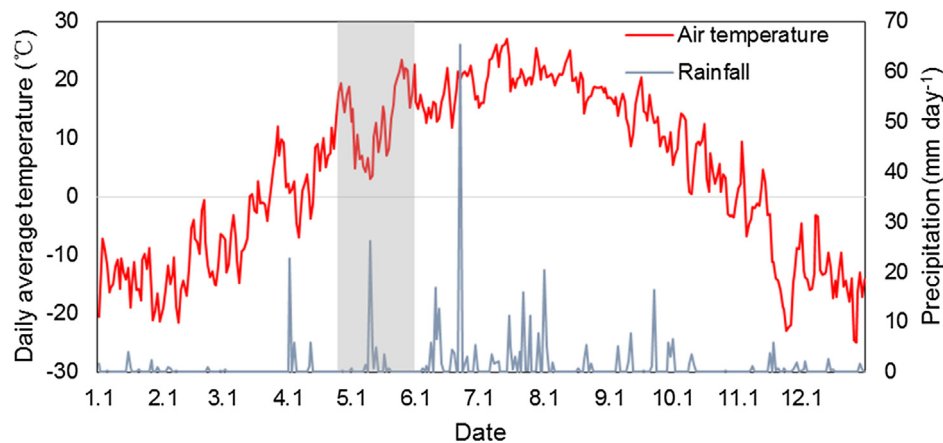


Fig. 1. Daily precipitation and air temperature at the experimental site in 2015. Grey box shows the period of rainfall simulating experiment from 24 April to 30 May.

labile forms (Beck et al., 1997; Hamel et al., 2006). Ext-C and Ext-N were determined using a TOC-N auto-analyzer (multi N/C *3100, Jena, Germany), while Ext-P was determined by the vanadium molybdate yellow colorimetric method.

2.4. Plant sampling and analysis

We performed plant samplings simultaneously with the soil samplings. Briefly, using scissors, we clipped plant parts just above the soil surface on two randomly selected 0.5×0.5 m quadrats in each plot, and enveloped the samples after removing dead plant material. All plant samples were placed at 60°C for 48 h to determine dry biomass. After this, we sieved the plant samples through a 0.25-mm mesh and digested the sub-samples using $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$. N and P concentration in the filtered extracts were analyzed via the Kjeldahl and vanadium molybdate yellow colorimetric method, respectively (Bao, 2000).

2.5. Climatic data

For the study of the response of soil microbes to climatic changes throughout the growing season, we selected the daily mean climatic data in this region as reference, including daily average air temperatures and precipitation. The municipal meteorological station provided the data.

2.6. Statistical analysis

All statistical analyses were performed with the software package SPSS (version 20.0; SPSS Inc., Chicago, IL). For the parameters of C, N, and P in soil microbial biomass and abiotic labile forms, the effects of treatment and sampling time (seasonal variation) were assessed using analysis of variance (ANOVA) (mixed model). Least Significant Difference (LSD) was used to test the interaction differences among treatments and seasonal variations. For microbial ratios and plant factors, we used one-way ANOVA to separately refer the differences among treatments and seasonal variations. In all cases, we considered $P < 0.05$ as significant. Stepwise multiple regression analyses (both forwards and backwards) were used in order to examine the relationships between short-term changes of air temperature, soil and plant factors and MBN and MBP and their ratios during each sampling interval (Table 2). The factors included changes in air temperature (DLT_TEMPERATURE), soil water content (DLT_SWC), Ext-C (DLT_Ext-C), Ext-N (DLT_Ext-N), Ext-P (DLT_Ext-P), as well as aboveground plant biomass (DLT_PLANT-B), plant N uptake (DLT_PLANT-N), and plant P uptake (DLT_PLANT-P).

3. Results

3.1. Seasonal climatic variations

There were 149 continuous vegetation growth days (air temperature $> 5^\circ\text{C}$) from 12 May to 7 October in the experimental year, which covered our sampling period (from 1 June to 1 October) (Fig. 1). Total annual precipitation was 413 mm, with 43 mm occurring during the rainfall simulating experiment (Fig. 1). Precipitation was unevenly distributed throughout the year, resulting in significant seasonal variations in SWC of sampled soils for all three treatments. However, no significant difference was observed among treatments (Fig. 1; Table 1).

3.2. Seasonal variations in soil microbial biomass and nutrients

Significant treatment effects were detected on MBC, MBN, and MBP, but not on Ext-C, Ext-N, and Ext-P (Figs. 2 and 3; Table 1). MBC was consistently higher in W1 and W2 than in W0 throughout the season except for 1 July (Fig. 2a). Irrespective of treatments, all the measured C, N, and P pools had similar change patterns over the growing season except for MBP on 1 September (Figs. 2 and 3). Regarding MBP on 1 September, markedly higher values were observed in W1 and W2 compared with W0 (Fig. 2c).

Similarly, the ratios of MB C:N, C:P, and N:P fluctuated significantly over the growing season (Fig. 4). Treatment effect on MB C:N ratio was rather negligible, even though it was significant on 1 June and 1 September ($< 20\%$) (Fig. 4a). In contrast, MB C:P and N:P ratios were markedly lower in W1 and W2 compared with W0 on 1 September (up to 184% and 219%, respectively) (Fig. 4b and c).

3.3. Plant biomass and N, P uptakes

Throughout the growing season, aboveground plant biomass values and N, P uptakes were consistently higher in W1 and W2 than in W0 (Fig. 5). In W1 and W2, plant biomass reached the maximum value on 1 August, which was earlier than that in W0 (on 1 September) (Fig. 5a). Similarly, plant N, P uptakes in W1 and W2 reached maximum values on 1 August and then declined with time, while these values in W0 kept increasing until 1 September (Fig. 5b, c).

Considering the averaged values of C, N, and P in soil microbial biomass and abiotic labile forms, the total ANPP (maximum values observed during the season) was only found to be significant correlated with the averaged MBC and MBN across treatments (Fig. 6).

Table 1

Summary of average values, and results of repeated-measures ANOVA for the effects of the three spring watering treatments W0, W1, and W2 and seasonal fluctuation on each value ($N = 5$ for averages, and $N = 45$ for repeated-measures ANOVA).

	MBC ^a	MBN	MBP	Ext-C	Ext-N	Ext-P	SWC
	$\mu\text{g g}^{-1}$						g g^{-1}
Treatment (T)	$F = 10.5$ $P < 0.001$	$F = 4.2$ $P = 0.024$	$F = 6.8$ $P = 0.007$	NS	NS	NS	NS
Seasonal Variation (S)	NS ^b	$F = 48.2$ $P < 0.001$	$F = 17.4$ $P < 0.001$	$F = 27.2$ $P < 0.001$	$F = 18.4$ $P < 0.001$	$F = 23.0$ $P < 0.001$	$F = 530.1$ $P < 0.001$
T*S	NS	NS	$F = 6.4$ $P < 0.001$	NS	NS	NS	NS
LSD _{0.05} ^c	121.9	22.5	17.8	18.1	5.0	2.2	0.01

^a MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus; Ext-C, extractable carbon (with $0.5 \text{ mol L}^{-1} \text{ K}_2\text{SO}_4$); Ext-N (with $0.5 \text{ mol L}^{-1} \text{ K}_2\text{SO}_4$), extractable nitrogen; Ext-P, extractable phosphorus (with $0.5 \text{ mol L}^{-1} \text{ NaHCO}_3$); SWC, soil water content.

^b NS means not significant.

^c The LSD refers to the interaction effect between treatment and seasonal variation at $P < 0.05$.

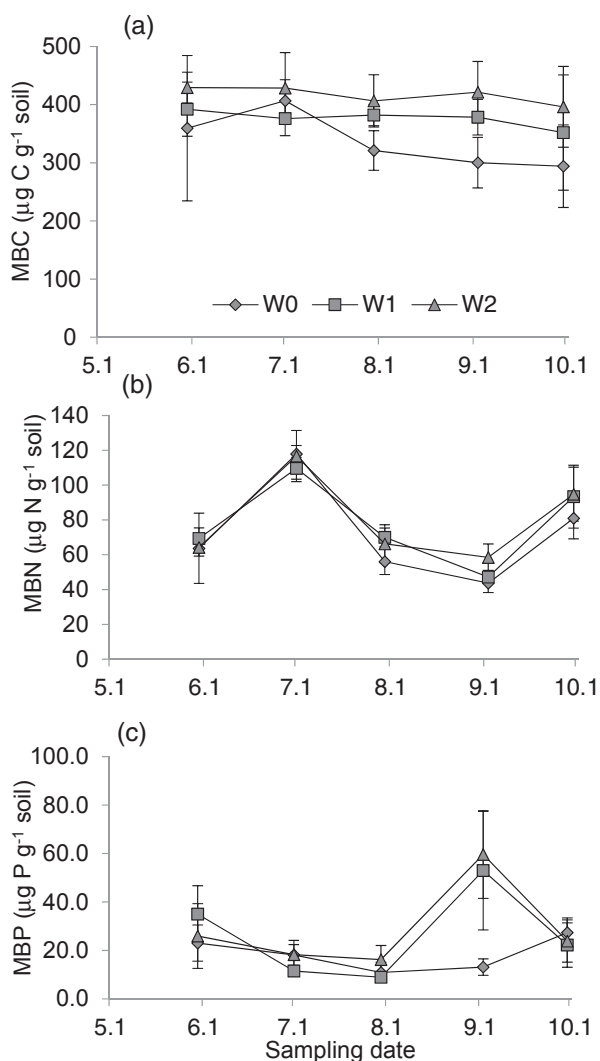


Fig. 2. Seasonal fluctuations of soil microbial biomass (MB) carbon (C) (a), nitrogen (N) (b), and phosphorus (P) (c) in the three spring watering treatments W0, W1, and W2 during the experimental period (June to October 2015). Means and standard deviations of the three field replicates.

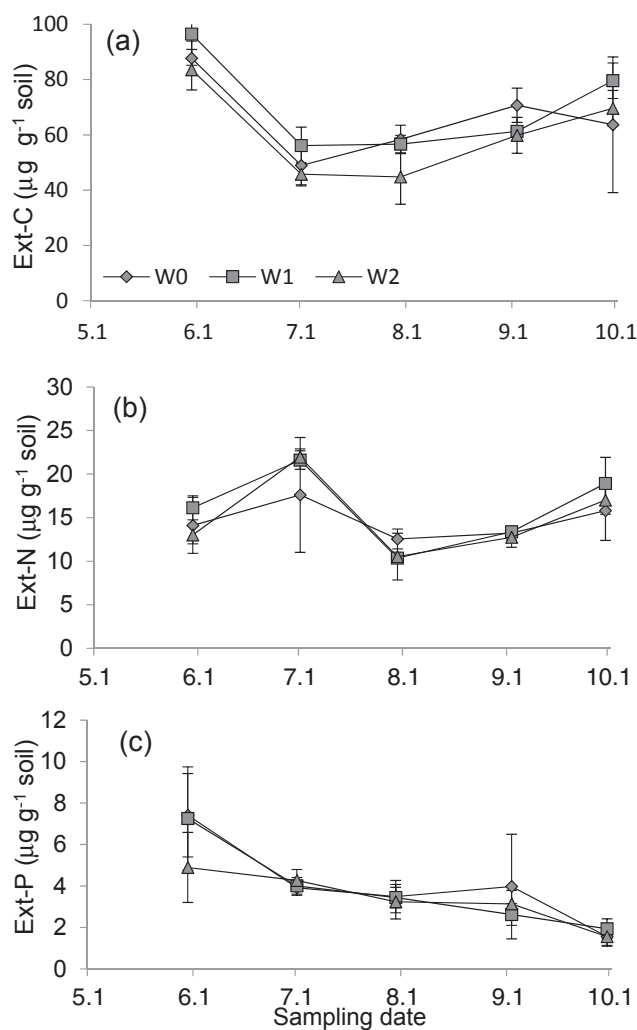


Fig. 3. Seasonal fluctuations of soil extractable C (with $0.5 \text{ M K}_2\text{SO}_4$, Ext-C) (a), N (with $0.5 \text{ M K}_2\text{SO}_4$, Ext-N) (b), and P (with 0.5 M NaHCO_3 , Ext-P) (c) in the three spring watering treatments W0, W1, and W2 during the experimental period (June to October 2015). Means and standard deviations of the three field replicates.

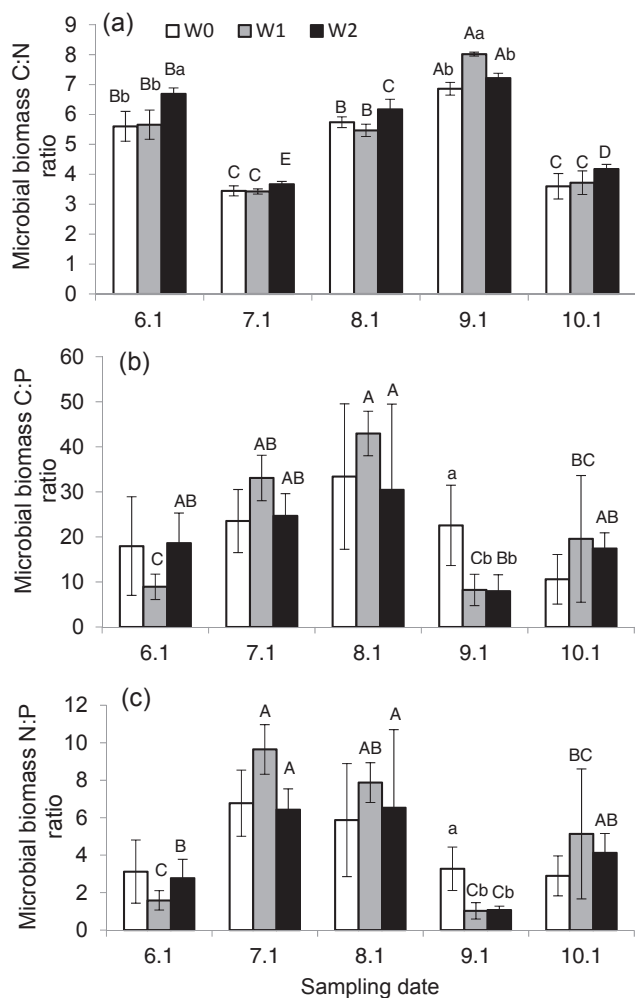


Fig. 4. Seasonal fluctuations of soil microbial biomass C:N ratio (a), C:P ratio (b), and N:P ratio (c) in the three spring watering treatments W0, W1, and W2 during the experimental period (June to October 2015). Bars indicate the standard error ($N = 3$). Different lowercase letters indicate significant difference between treatments at a certain sampling date ($P < 0.05$), while for each treatment, different capital letters indicate significant difference between sampling dates ($P < 0.05$). Note that no statistical differences of MB C:P and MB N:P ratios was found in W0 treatment across the growing season due to the high error bars, however, their change patterns in W0 were similar as those in W1 and W2.

3.4. Factors controlling soil microbial biomass pools and dynamics

Due to the similar seasonal fluctuations of soil microbial biomass across treatments, stepwise multiple linear regression analyses were further carried out to study their controlling factors (Table 2). The main factors impacting the variability of soil microbial biomass and their ratios were SWC and Ext-N, which accounted for up to 67% and 69% of the variability, respectively. In addition, changes in air temperature and aboveground plant biomass accounted for 12% of the variability in MB C:N ratio. Changes in aboveground plant biomass, together with plant N uptake, also affected the variability in MB N:P ratio.

4. Discussion

4.1. Effect of spring watering on soil microbial biomass carbon and grassland productivity

Throughout the growing season, spring watering increased the soil microbial biomass carbon (MBC) (up to 30%), following the order of

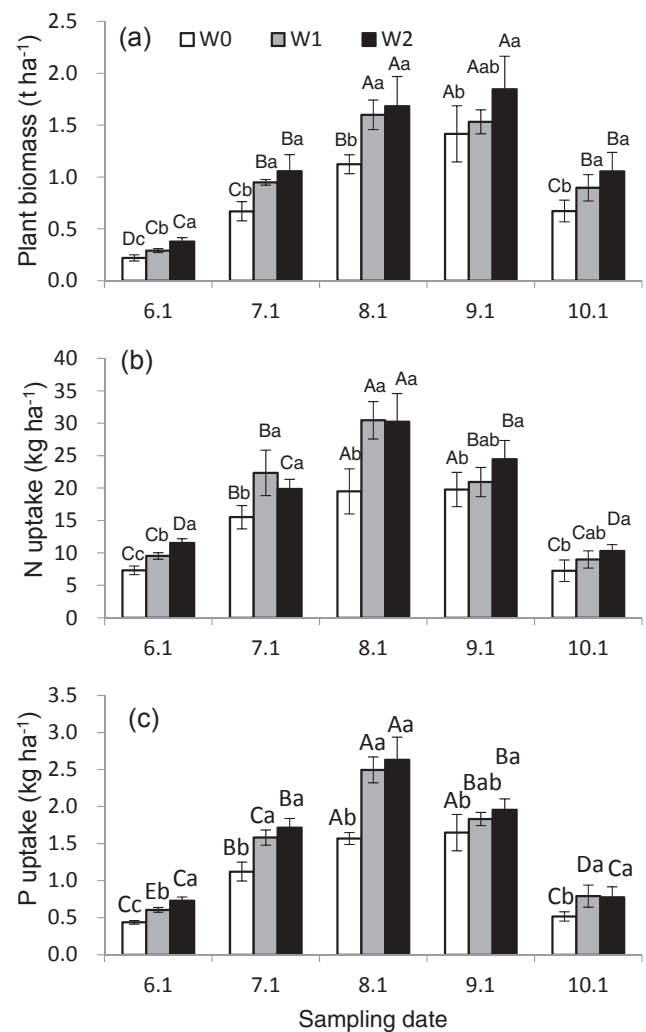


Fig. 5. Changes of aboveground plant biomass (a) and N (b), P (c) uptake in the three spring watering treatments W0, W1, and W2 at each sampling date during the experimental period (June to October 2015). Bars indicate the standard error ($N = 3$). Different lowercase letters indicate significant difference between treatments at a certain sampling date ($P < 0.05$), while for each treatment, different capital letters indicate significant difference between sampling dates ($P < 0.05$).

W2 > W1 > W0 (Table 1). Stimulation of water addition on soil microbial growth has also been reported in many previous studies of water-limited ecosystems (Gallardo and Schlesinger, 1995; Gregger et al., 2012; Liu et al., 2016; Huang et al., 2018). Interestingly, the observed increase in MBC induced by spring watering was consistent throughout the entire growing season, even though there was no longer significant difference in SWC between treatments (Fig. 2a; Table 1). These results suggest that the effect of spring precipitation on the size of soil microbial pools can be indirect and might last for a relatively long time. This finding is of significance since it may provide implications of microbially-mediated C and nutrient cycling under changing climate (Bardgett et al., 2008; Singh et al., 2010; Griffiths et al., 2012). A number of previous studies have linked the increased microbial growth to increasing substrate availability under water addition (Kieft et al., 1987; Stark and Firestone, 1995). In the present study, however, we did not observe significant differences in substrate (i.e. Ext-C) among treatments (Fig. 3a; Table 1). One explanation would be that the increase of substrate availability was not detected since it soon declined with increasing microbial growth.

The consistently increased microbial biomass in watering treatments could be attributed to the interaction between plants and

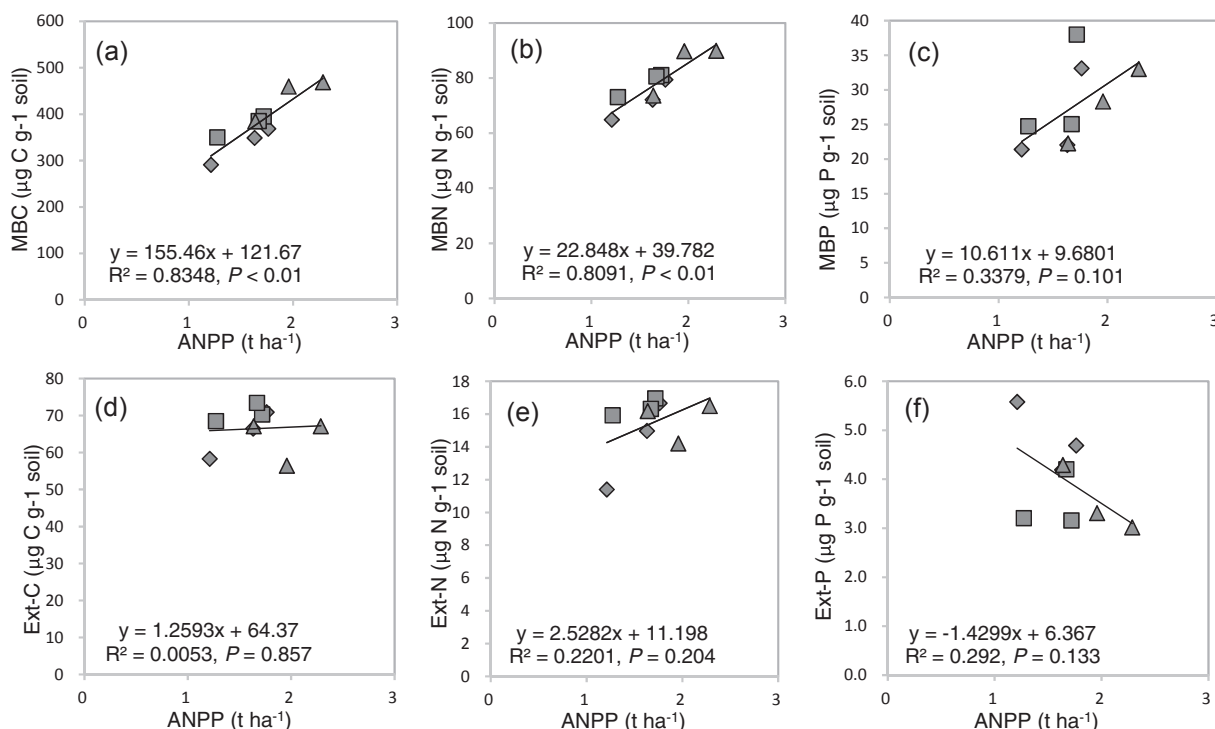


Fig. 6. Correlations between total aboveground net primary productivity (ANPP) and seasonal (June to October 2015) average of soil microbial biomass (MB) carbon (C) (a), nitrogen (N) (b), and phosphorus (P) (c), as well as seasonal average of soil extractable C (with 0.5 M K_2SO_4 , Ext-C) (d), N (with 0.5 M K_2SO_4 , Ext-N) (e), and P (with 0.5 M NaHCO_3 , Ext-P) (f) across the three spring watering treatments W0 (\blacklozenge), W1 (\blacksquare), and W2 (\blacktriangle).

Table 2

r^2 of factors explaining net changes of microbial biomass (MB) nitrogen (N), and phosphorus (P), as well as MB C:N ratio, C:P ratio, and N:P ratio across all the three spring watering treatments W0, W1, and W2 using stepwise multiple linear regression analyses for four intervals during the season.

Parameter	Factor/ r^2			
MBN	DLT_Ext-N	DLT_SWC		
	0.693	0.136		
MBP	DLT_SWC			
	0.509			
MB C:N ratio	DLT_Ext-N	DLT_SWC	DLT_TEMPERATURE	DLT_PLANT-B
	0.533	0.328	0.084	0.037
	DLT_SWC			
	0.668			
MB N:P ratio	DLT_SWC	DLT_Ext-N	DLT_PLANT-N	DLT_PLANT-B
	0.423	0.327	0.112	0.072

microorganisms during the growing season (Hertenberger et al., 2002). Indeed, we found significantly and consistently higher ANPP in watering treatments (up to 30%) compared with the spring drought treatment (W0) (Fig. 5). One explanation would be that increased SWC (Fig. S1) stimulates root growth as well as seedling survival, thereby stimulating subsequent aboveground plant growth (Padilla and Pugnaire, 2007; Quevedo-Robledo et al., 2010; León et al., 2011). Increased plant growth can in turn stimulate soil microbial growth via releasing exudates (Hertenberger et al., 2002). This interaction between plants and microorganisms is evidenced by the significant positive relationships between total ANPP and averaged MBC and MBN across treatments (Fig. 6a and b). Furthermore, we suggest to use MBC as an soil indicator for soil fertility and plant productivity, as it responded, compared to the abiotic factors (i.e., Ext-C, Ext-N, and Ext-P), more sensitively to soil environmental changes (Figs. 2a, 3, and 6).

4.2. Effects of spring watering on seasonal plant- microorganism interactions

In the present study, the ratios of MBC, MBN, and MBP varied significantly throughout the season (Fig. 4). Since MBC was constant, mainly the variation of MBN and MBP accounted for these changing ratios (Table 1). Generally, the MB C:N ratio of fungi is higher than that of bacteria (Anderson and Domsch, 1980). The fluctuations in the MB C:N ratio observed throughout the growing season may indicate a changing microbial community composition. Similar change patterns of MB C:N ratio have also been observed in our previous study in semi-arid grassland (Chen et al., 2018; Huang et al., 2018). We did not observe obvious treatment effects on MB C:N ratio across seasons in the present study, indicating no change of microbial community occurred induced by spring precipitation in monthly-scale.

Regarding MB C:P and MB N:P ratios, a tendency to increase during the rapid plant growth period (from 1 June to 1 August) and to decrease during the late growing season (from 1 August to 1 October) was found for all three treatments (Fig. 4b and c). This may indicate a P competition between plants and microorganisms in this area (Griffiths et al., 2012). More obviously, on 1 September, the ratios were significantly lower in W1 and W2 than in W0 (Fig. 3b and c). In watering treatments, plant P uptake reached the peak relatively earlier, on 1 August, and decreased from then onwards. In contrast, the peak of plant P uptake in spring drought treatment was delayed and the uptake was still increasing until 1 September (Fig. 5c). Thus, the transient increase in MBP and lower MB C:P and MB N:P ratios in W1 and W2 on 1 September could be attributed to the decrease in plant P uptake (Fig. 2c and 5c). A similar interaction between plants and microorganisms for P has been reported by Liebisch et al. (2014), who showed synchronously increased MBP values after cutting of grassland plants.

4.3. Factors controlling soil microbial dynamics across treatments

Since the seasonal change patterns of the soil microbial parameters

were roughly the same in all the three treatments (Figs. 2 and 4). Stepwise multiple linear regression analyses were further carried out to investigate the environmental drivers of microbial variations across treatments. The SWC was one of the main factors controlling seasonal microbial dynamics, indicating the significance of soil water availability are reflected throughout the season in this ecosystem. Thus more work is needed to evaluate the role of precipitation occurring in different durations of the year (Robinson et al., 2013).

Apart from SWC, soil N availability was also a main factor. This finding agrees with those previously reported, stating that arid and semi-arid grasslands are primarily limited by water availability (e.g., Brueck et al., 2010) and that the productivity of these grasslands becomes increasingly N-limited under wetter conditions (Burke et al., 1997; Austin et al., 2004). Besides, air temperature and plant growth also partly accounted for some of the microbial variations (Table 2). Soil temperature could directly affect microbial biomass and may also operate indirectly through modulating substrate availability through plant phenology (Rinnan et al., 2008). Since the air temperature during our experimental period (from 1 June to 1 October) was always above 5 °C (refers to vegetation days) (Fig. 1), the effect of temperature on soil microbial dynamics was therefore more likely through regulating plant-microorganism interaction.

5. Conclusion

Our results clearly showed that spring precipitation could improve ANPP and MBC, and this effect was consistent throughout the growing season. We suggest that MBC could be used as a good indicator for soil fertility because of its significant relationship with ANPP and sensitive response to treatments compared with other biotic and abiotic parameters. Markedly higher MBP and lower MB C:P ratio were observed in watering plots in September when plant P uptake had dropped down in watering plots but still kept increasing in drought plots, suggesting a delay of phenological period of plants induced by spring drought and P competition existing between plants and microorganisms. Throughout the season, soil water availability was also the main factor controlling soil microbial dynamics in this semi-arid ecosystem, which requires more work to better understand ANPP variation through investigating the role of precipitation during different segments of the year.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2020.104478>.

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