

The role of spring ephemerals and soil microbes in soil nutrient retention in a temperate desert

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Abstract

Aims Nutrient uptake by ephemerals is a key element of nutrient retention in some hardwood forests. However, little information is available regarding the role of ephemerals and soil microbes in deserts.

Methods Seasonal patterns of nitrogen (N) and phosphorus (P) uptake by spring ephemerals and soil microbes were measured in 2011–2013 in a temperate desert. Seasonal dynamics of soil inorganic N and available P, nitrate leaching and soil microbial N and P were also monitored.

Results Ephemerals exhibited a large nutrient pool in their growing season, with net N and P uptakes of 0.49–0.94 g m⁻² and 0.05–0.09 g m⁻², respectively, in normal precipitation years (2011 and 2013). Within 6 months of death, spring ephemerals released 35 % of litter N and 60 % of litter P. N and P microbial immobilizations were 3.6 and 4.5 times greater, respectively, than spring

ephemeral uptake during normal precipitation years, but soil microbes showed a net nutrient release during the dry year (2012).

Conclusions This study demonstrated that the relative importance of soil microbes and spring ephemerals in soil nutrient retention is related to annual precipitation, with higher nutrient retention by soil microbes in normal precipitation years and by spring ephemerals in dry year.

Keywords Plant interaction · Plant phenology · Spring ephemeral · Vernal dam · Soil nutrient retention

Introduction

Plant growth depends on soil nutrient supply, and in turn, the nutrients returning to the soil from plants by litter decomposition or root exudates can also adjust soil nutrient status (Morgan and Connolly 2013). Soil nutrients can be incorporated into the plant biomass and temporarily stored in plants during the growth season. Thus, nutrient allocation and cycling in a plant community can exert profound effects on ecosystem nutrient retention (Vitousek and Reiners 1975; Morgan and Connolly 2013). In temperate zones with clear seasonal climatic variations, plant litter inputs in the autumn seldom decompose and are usually maintained at the soil surface during the cold winter because of low temperature limits to microbial activities. During the following spring, however, increasing temperatures and rainfall stimulate organic matter decomposition, which, while generating increasing nutrient availability, also

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elicits nutrient loss through leaching, stream flow, and volatilization (Zak et al. 1990; Zechmeister-Boltenstern et al. 2002; Tessier and Raynal 2003; Castellano et al. 2012). In certain deciduous hardwood forests, spring ephemerals and soil microbial communities are reported to improve soil nutrient retention due to their fast growth before the canopy closure of woody plants. The phenomenon of nutrient retention by spring ephemerals has been termed “vernal dam” (Muller and Bormann 1976). However, the relative importance of spring ephemerals and soil microbial communities to soil nutrient conservation has been controversial, as several studies have shown that soil microbial biomass nitrogen is much greater than the amount of nitrogen incorporated by spring ephemerals. For example, microbial biomass nitrogen was 8–20 times higher than that in ephemerals in forest ecosystems (Zak et al. 1990; Rothstein 2000; Tessier and Raynal 2003). Moreover, some studies have even shown that nutrient retention by spring ephemerals can be negligible, because of the large nutrient losses from the thick litter floor in forests (Tremblay and Larocque 2001; Mabry et al. 2008). In addition to nutrient retention, other studies have questioned the importance of nutrient release from litter decomposition of spring ephemerals; for instance, nitrogen release of the spring ephemeral *Allium tricoccum* ($0.1\text{--}0.2\text{ g m}^{-2}\text{ yr}^{-1}$) was minuscule compared with that of canopy litterfall ($5.4\text{ g m}^{-2}\text{ yr}^{-1}$) and soil organic matter mineralization ($7\text{ g m}^{-2}\text{ yr}^{-1}$) (Muller and Bormann 1976; Bormann et al. 1977). However, despite the fact that “vernal dams” are not universal across terrestrial ecosystems, the significance of spring ephemerals in nutrient cycling is widely accepted (Eickmeier and Schussler 1993; Farnsworth et al. 1995; Jandl et al. 1997).

Spring ephemerals are an important element of the plant community in some temperate desert ecosystems, especially in Central Asia (Angert et al. 2007; Huang et al. 2015a). The Gurbantonggut Desert is located in Central Asia, and the vegetation in this desert typically comprises sparsely distributed shrubs and a dense cover of herbs. Snow depth in winter usually reaches 30 cm and is an important water source for seed germination and plant growth in spring (Zhou et al. 2009; Fan et al. 2014). Moreover, snow-melt also stimulates soil microbial growth and physiological activities, through which soil nutrients can be immobilized (Schimel and Balser 2007). However, soil nutrients are also at a risk of being lost due to leaching or gas emission in spring (Austin et al. 2004). The concurrent flushes of available

nutrients and ephemeral growth, as well as soil microbial activities in desert ecosystems are rather similar to those in temperate hardwood forests. However, compared with forests, litter accumulation at the soil surface is extremely rare in deserts, and nutrients returning to the soil from litter decomposition are primarily from the current year; therefore, spring ephemerals in desert ecosystems are inferred to be more important to soil nutrient retention and cycling than in forests. However, the importance of spring ephemerals and soil microbial communities in soil nutrient retention has seldom been directly verified in desert ecosystems (Parker et al. 1984; Guo and Brown 1997; Chen et al. 2009).

The “vernal dam” hypothesis and related previous studies suggest two important implications in terms of soil nutrient retention and utilization. First, the temporal niche segregation of spring ephemerals to some extent makes soil nutrients incorporated into the ephemeral biomass and available later on to living plants through litter decomposition, helping soil nutrient retention and improving nutrient use efficiency. Second, soil microbial communities are considered to be more sensitive to the ambient environment; with increases in water availability and soil temperature, soil microbes can immobilize soil nutrients through growth and physiological activities. This is favorable for soil nutrient retention when plant incorporation is limited. Up to 90 % of temperate deserts are located in central Asia, where spring ephemerals account for more than 80 % of the herbaceous biomass and have a growing season from late March to early June. In contrast, summer annuals and shrubs usually reach peak growth in mid-August (Wang et al. 2006; Huang et al. 2015a). We first hypothesized that spring ephemerals could temporarily immobilize a significant amount of nitrogen (N) and phosphorus (P), thus reducing surface soil nutrient loss. Second, as the “vernal dam” hypothesis addresses the availability of the nutrients released from ephemeral litter to standing plants, we hypothesized that the rapid decomposition of spring ephemeral litter could release a large amount of available nutrients for summer annuals and shrubs. Third, as our previous studies demonstrated that soil microbial biomass exhibited large temporal variations and was closely related to soil moisture in this desert ecosystem (Huang et al. 2015b), we hypothesized that soil microbial communities could also contribute to soil nutrient retention through microbial nutrient immobilization. The aims of the current study were 1) to understand whether spring ephemerals in the desert

ecosystem can also alleviate soil nutrient loss during the growing season and release nutrients to the soil after mortality and 2) to verify whether soil microbial communities also play a role in soil nutrient retention and whether this role is comparable to that of spring ephemerals in the desert ecosystem.

Materials and methods

Study site description

The field site was in the vicinity of the Fukang Station of Desert Ecology, Chinese Academy of Sciences, on the southern edge of the Gurbantunggut Desert (44°12′–44°21′ N, 87°50′–87°54′ E, 450 m a.s.l.) in northwestern China. Sand dunes run in a south–north direction, with a mean height of 20 m. Plants mainly grow in lowlands. The climate of the region is characterized as temperate continental and arid, with dry-hot summers and cold winters. The average temperature is 6.8 °C. The average annual precipitation is 160 mm, with more than 60 % falling in April–September. Snow falls from late October to late March, typically reaching a depth of 20–30 cm, and accounts for 24–40 % of the annual precipitation (Zhou et al. 2009). The potential evapotranspiration is more than 2000 mm. The soil is an aeolian sandy soil, with 90 % of the particles being sand grains. The desert plant community is composed of shrubs, spring ephemerals, and summer annuals (Huang et al. 2015a). *Haloxylon ammodendron* and *Haloxylon persicum* are two dominant shrubs that inhabit lowland and upper sand dunes, respectively (Zhou et al. 2009). Spring ephemerals usually germinate in early April and senesce in mid-June (Fig. S1). The spring ephemerals are primarily composed of *Alyssum linifolium*, *Schismus arabicus*, *Lactuca undulata*, *Leptaleum filifolium*, *Erodium oxyrrhynchum*, *Eremurus anderiensis*, *Descurainia sophia*, *Hyalea pulchella*, *Malcolmia scorpioides*, and *Nonea caspica*. Summer annuals at the study area are *Ceratocarpus arenarius*, *Salsola foliosa*, *Orostachys spinosus*, *Salsola passerina*, and *Euphorbia turczaninowii* (Fig. S1). Summer annuals germinate 5–7 days later than spring ephemerals, and exhibit slow growth rates when spring ephemerals are flowering. Plant biomass of spring ephemerals is significantly greater than that of summer annuals (Huang et al. 2015a). In addition to ephemerals and annuals, the soil surface of interplant spaces is covered by biological soil

crusts, which are intimate associations between soil particles and cyanobacteria, algae, fungi, lichen and bryophytes in varying proportions (Li 2012). Its cover reaches 40 % of the study site (Su et al. 2013).

Experimental design

Twelve permanent plots with an area of 10 × 10 m were set up randomly in the lowlands between sand dunes. Three dominant spring ephemerals (*E. oxyrrhynchum*, *A. linifolium* and *S. arabicus*) and two dominant summer annuals (*S. foliosa* and *C. arenarius*) were selected for the present study. The five species accounted for more than 85 % of the aboveground biomass in our three experimental years (2011–2013). Based on a prior plant phenology investigation, plant height and number were investigated every 3 to 7 days in five permanent 1 × 1 m subplots in each plot from early April to mid-October. Aboveground plant biomass was estimated based on the allometric equations of plant biomass and height by the destructive sampling of at least 50 individuals of each species in 2010. The allometric equations for *E. oxyrrhynchum*, *A. linifolium*, *S. arabicus*, *S. foliosa*, and *C. arenarius* were $TAGB = 0.0733e^{0.1327H}$, $TAGB = 0.0082e^{0.1175H}$, $TAGB = 0.0177e^{0.1811H}$, $TAGB = 0.0359e^{0.1779H}$ and $TAGB = 0.115e^{0.2637H}$, where TAGB and H indicate plant aboveground biomass and plant height, respectively. All r^2 values of allometric equations were >0.87. The belowground biomass of each species was estimated based on the root : shoot ratio, and the ratio was 0.24, 0.33, 0.27, 0.13 and 0.12 for *E. oxyrrhynchum*, *A. linifolium*, *S. arabicus*, *S. foliosa* and *C. arenarius*, respectively.

Soil sample collection

Because soil nutrients at the study site were primarily concentrated in the top layers (Li et al. 2011), five cores (10 cm deep and 5 cm inner diameter) of soil were collected at 0–10 cm depth in each plot at monthly intervals from March to October in 2011, 2012, and 2013. Collected samples were stored in a portable refrigerator and transported to the lab for measurement of soil inorganic N and available P, microbial biomass nitrogen (MBN), and microbial biomass P (MBP).

Soil nitrate-N (NO_3^- -N) and ammonium-N (NH_4^+ -N) were extracted with 2 M KCl and measured by an Auto Analyzer 3 (AA3, BRAN-LUEBBE Ltd., Hamburg, Germany). Soil available P was determined by the sodium

hydrogen carbonate solution-Mo-Sb anti spectrophotometric method (State Environmental Protection State Environmental Protection Administration 2014).

MBN and MBP were assessed using the chloroform fumigation extraction method (Brookes et al. 1985, 1984). Paired 20-g fresh soil samples that were either unfumigated or fumigated with alcohol-free CHCl_3 for 24 h, and then were extracted with 0.5 M K_2SO_4 (1:2.5 w/v) for MBN measurement and with 0.5 M NaHCO_3 for MBP measurement. Total N values for fumigated and unfumigated extracts were analyzed using a TOC analyzer (multi N/C 3100, Jena, Germany). The P concentrations of the extracts were determined using the colorimetric ammonium molybdate-ascorbic acid method (State Environmental Protection State Environmental Protection Administration 2014). The efficiency factors for MBN ($K_n=0.54$, Brookes et al. 1985) and MBP ($K_p=0.40$, Brookes et al. 1984) were used for calculations. We determined mean soil mass of the 0–10 cm soil layer by randomly collecting 12 soil samples from 10×10 cm quadrats. Dry mass of each soil sample was determined gravimetrically. MBN and MBP per gram of soil were multiplied by the mean soil mass per unit area in the 0–10 cm soil layer to obtain the MBN and MBP in units of mg m^{-2} .

Plant nutrient measurements

At least 10 individuals of each spring ephemeral (mid-late May) and summer annual (mid-August) species were collected at peak growth, and collected samples were taken to the lab for further analyses. Plants were rinsed and divided into above- and belowground sections, then ground by a ball mill for N and P measurements after oven-drying at 65°C for 3 days.

For measurements of nutrient release from plants, plant litter was collected after plant senescence and oven-dried at 65°C for 3 days. We placed 10 g of dry litter from each species in a litterbag and included 12 replications for each species. Litterbags were randomly laid in each subplot, and iron nails were used to fix bags at the four corners. The grid mesh of the litterbag was 1.2 mm at the upper surface and 0.1 mm at the lower surface, and the area was 10×10 cm. Litter decomposition was allowed to occur from 10th August 2010 to 10th April 2011. At the end of the experiment, each litterbag was carefully placed into an envelope and transported to the lab. In the lab, soil, sand, and arthropods were removed after the litter samples were

oven-dried at 45°C for 48 h. Litter samples were then oven-dried again at 65°C for 48 h and ground with a mortar and pestle for N and P measurements. In addition, the initial N and P concentrations of each species were also measured before the litter decomposition experiment. Total N was analyzed by the Kjeldahl method (Bickelhaupt and White 1982), and total P was measured by a molybdate/ascorbic acid method (John 1970) after $\text{H}_2\text{SO}_4\text{--HClO}_4$ digestion.

Plant nutrient content was determined at peak plant growth for the three spring ephemerals (mid-late May) and two summer annuals (mid-August). Net nutrient uptake dynamics were determined by plant above-ground biomass and root biomass nutrient content in the 1 m^2 subplot and were calculated from the following equations:

$$\begin{aligned} N_{\text{uptake}} (\text{mg m}^{-2}) &= AM_i \times AN_i + RM_i \times RN_i \\ P_{\text{uptake}} (\text{mg m}^{-2}) &= AM_i \times AP_i + RM_i \times RP_i \end{aligned}$$

where N_{uptake} and P_{uptake} are the N and P uptake; AM_i and RM_i are the aboveground and root biomass, respectively, of plant species i per square meter in a certain year; AN_i and AP_i are the N and P concentrations, respectively, of plant species i 's aboveground biomass; and RN_i and RP_i are the N and P concentrations, respectively, of plant species i 's root biomass.

Net nutrient release by plants resulting from litter decomposition from August to 10th April of each year was calculated using the equations below:

$$\begin{aligned} N_{\text{release}} (\text{mg m}^{-2}) &= N_{\text{initial}} \times N_{\text{loss}} \times \text{Biomass} \\ P_{\text{release}} (\text{mg m}^{-2}) &= P_{\text{initial}} \times P_{\text{loss}} \times \text{Biomass} \end{aligned}$$

where N_{release} and P_{release} are the amounts of N and P released, respectively, through litter decomposition; N_{initial} and P_{initial} are the initial concentrations of litter N (mg g^{-1} plants) and P (mg g^{-1} plants), respectively; N_{loss} and P_{loss} are the ratios of litter N and P lost at the end of the decomposition experiment vs. the initial N and P concentrations (%), respectively; and biomass is the plant biomass per square meter (g m^{-2}).

Soil nitrate leaching

The installation of lysimeters was undertaken after a natural precipitation event of 8 mm on September 13th, 2010. Three small drainage lysimeters were buried underground, and an observation area was excavated to measure percolating water. The lysimeter was made of a

PVC chamber (80 cm diameter, 50 cm height), with a bottom covered by gravel and sealed by steel plates, in which a drainage tube with a diameter of 5 cm was fitted to collect percolating water. We chose three plots with a diameter of 80 cm in the interplant spaces, removed the soil, and then inserted PVC chambers into the soil, keeping the upper edge of each PVC chamber even with the soil surface. Soils from different depths of the inter-shrub spaces were placed in the chamber in 10 cm intervals. In particular, for the surface (0–10 cm) soil with biological soil crusts on top, soils were gently dug out and put into chambers both by soil cores (10 cm diameter), attempting to maintain the original soil structure. Particular care was taken for the 0–10 cm soil layer, trying to eliminate disturbances to the soil seed bank and herbaceous plants in the next year. Before starting the experiment, we watered the three chambers completely twice and then sealed the gaps between the soil and the inner wall of the PVC using by liquefied petrolatum to prevent preferential water flow along the wall. The plant community inside and outside of the lysimeters was also investigated in May and August 2011 at peak growth of spring ephemerals and summer annuals, and individual numbers of plants exhibited no differences, suggesting the herbaceous vegetation recovered after installation of lysimeters. After recovering from the disturbances of installation, leached nitrate was collected at snow-melting (in March) and immediately after each precipitation event from April to October, 2011–2013. The volume of collected infiltration water in the bucket was measured and 20–30 ml samples were stored in a freezer and then measured by an Auto Analyzer 3 (AA3, BRAN-LUEBBE Ltd., Hamburg, Germany). Nitrate leaching was calculated based on the formula $CL = \sum CN \times V$, where CL is the cumulated nitrate leaching in a specific month, CN is the NO_3^- -N concentration, and V is the volume of the collected infiltration water in the bucket.

Statistical analyses

Repeated measures ANOVA was used to analyze the effects of year and species on plant biomass and nutrient uptake and release. Tukey's post hoc test was used to determine differences in these variables between species. One-way ANOVA was used to determine seasonal differences in MBN and MBP, soil inorganic N and available P, and vegetation biomass N and P within a year. Before analysis, all data were tested and transformed to

meet the assumptions of ANOVA analysis. All statistical analyses were performed using SPSS version 17.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

The dynamics of soil N and P pools and nitrate leaching

Soil inorganic N and available P concentrations showed significant seasonal variations over 3 years (Fig. 1, $P < 0.05$). Both peaked in March and dropped dramatically until May, corresponding with the rapid growth of desert spring ephemerals (Fig. 2). A significant amount of soil nitrate leaching also occurred from March to May, with the highest leaching occurring in March (Fig. 1, $P < 0.05$). Nitrate leaching was 17.5–58.6 and 0.2–1.5 mg m^{-2} during the spring ephemeral growing season (from March to June 10) and after the mortality of spring ephemerals (from June 11 to October 31), respectively, across 3 years (Table 1).

Herbaceous community composition and nutrient pool dynamics

The herbaceous community comprised two functional groups with regard to plant life history: spring ephemerals and summer annuals (Fig. S1). The three spring ephemerals, *E. oxycorymbosum*, *A. linifolium* and *S. arabicus*, germinated 8–10 days earlier than the summer annuals as a whole. *S. foliosa* and *C. arenarius* were the earliest germinating summer annual species, the three spring ephemerals germinated 5.4–6.4 days earlier than *S. foliosa* and 1–2 days earlier than *C. arenarius*. Biomass of the five species as a whole varied from 9.5 g m^{-2} in the dry year of 2012 to 55.9 g m^{-2} in 2011, which had normal precipitation (Table 2). *E. oxycorymbosum* was the dominant species in the herbaceous community and had the highest plant biomass across all 3 years (Table 2). Spring ephemerals accounted for 59 % of the total biomass in 2011 and 96 % in 2013 (Table 2).

Nitrogen uptake dynamics differed profoundly among the five species (Fig. 2). Over 3 years, the spring ephemeral *E. oxycorymbosum* exhibited significantly greater N uptake than the other four species, with N uptakes of 913, 95, and 392 mg m^{-2} in 2011, 2012, and 2013, respectively (Table 2). Summer annuals exhibited low N uptake from March to June and an accelerated N

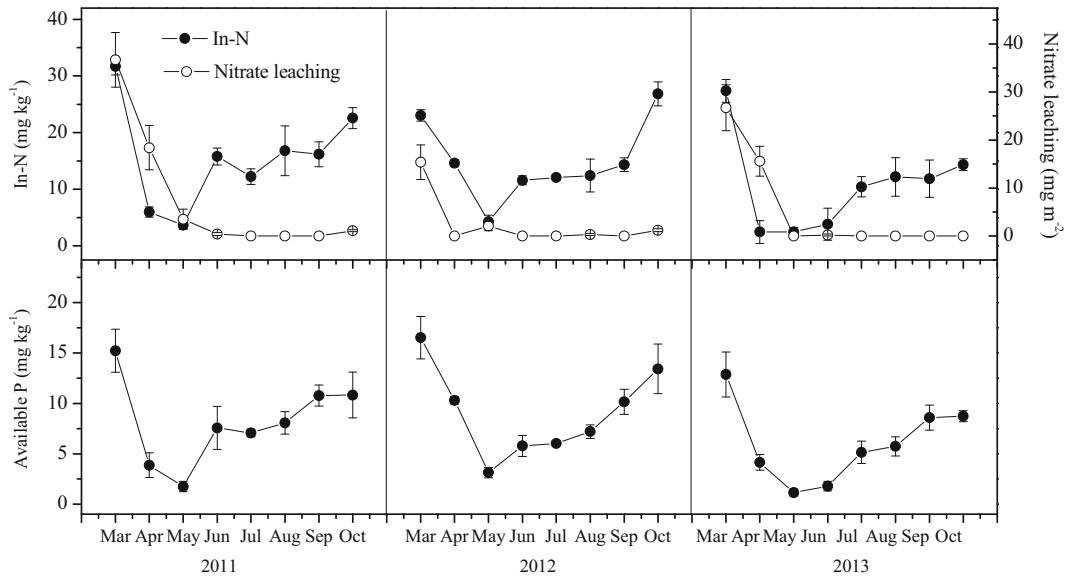


Fig. 1 Seasonal dynamics of soil inorganic nitrogen (In-N), available phosphorus (P), and nitrate leaching in 2011, 2012 and 2013

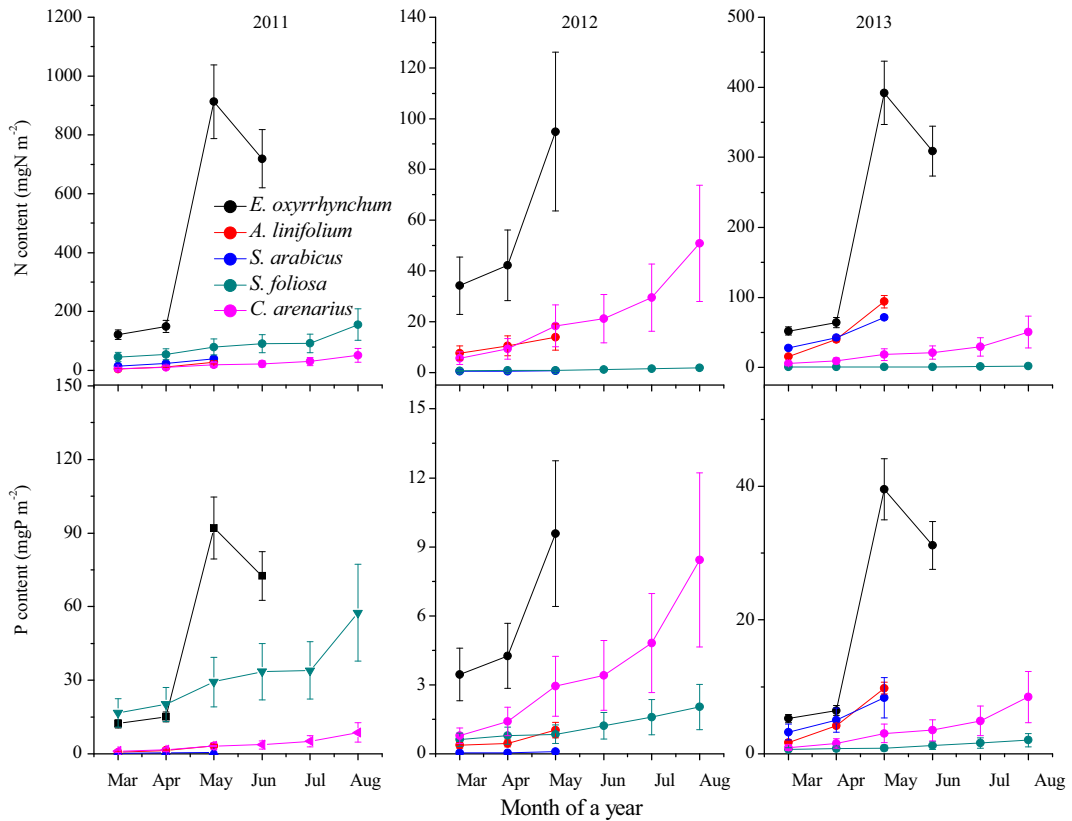


Fig. 2 Plant nitrogen (N) and phosphorus (P) content per square meters (mean ± S.E.) of three dominant spring ephemerals (*Erodium oxycarrhynchum*, *Alyssum linifolium*, *Schismus arabicus*)

and two summer annuals (*Salsola foliosa*, *Ceratocarpus arenarius*) in 2011, 2012 and 2013

Table 1 Soil nutrient balance at the study site across 3 years, 2011, 2012 and 2013

Nutrient	Year	Spring ephemeral growing season (Mar–June 10)				Nutrient releasing by decomposition (August – next April)		
		SEU (mg m ⁻²)	SAU (mg m ⁻²)	MC (g m ⁻²)	N leaching (mg m ⁻²)	SER (mg m ⁻²)	SAR (mg m ⁻²)	N leaching (mg m ⁻²)
N	2011	944 (58) a	208 (36) b	2.6 (0.3) c	59 (10) d	349 (25)	52 (1.5)	1.5 (0.5)
	2012	113 (13) a	52 (9) b	-2.3 (0.6) c	17 (4) b	42 (4)	14.4 (1.9)	1.5 (0.5)
	2013	493 (63) a	52 (8) b	2.2 (0.4) c	42 (8) d	184 (11)	14.4 (0.6)	0.2 (0.2)
P	2011	96 (14) a	58 (3) b	0.26 (0.07) c	–	57 (1)	26.4 (0.4)	–
	2012	9.6 (2.2) a	2.9 (0.2) b	-0.31 (0.06) c	–	7.4 (0.3)	1.2 (0.1)	–
	2013	51 (3) a	2.9 (0.3) b	0.32 (0.06) c	–	31 (1)	1.4 (0.6)	–

SEU nutrient uptake by spring ephemerals; SAU nutrient uptake by summer annuals; MC microbial community consumption of nutrients; SER nutrient release by spring ephemerals; SAR nutrient release by summer annuals. Different small letters indicate a significant difference within a year at $P < 0.05$ level

uptake after the mortality of spring ephemerals (Fig. 2). N uptake from 20 March to 10 June by the three spring ephemerals was 1152, 165 and 545 mg m⁻² in 2011, 2012 and 2013, respectively, accounting for more than 65 % of the total N uptake of the herbaceous community

(Table 2). N uptake by the herbaceous community was greater than N loss through leaching (Tables 1 and 2). P uptake by plants also differed significantly among species (Table 2), with the highest uptake in the spring ephemeral *E. oxycorrhynchum*, ranging from 10 mg m⁻²

Table 2 Plant biomass, nitrogen (N) and phosphorus (P) uptake by spring ephemerals and summer annuals at growth peak, and the nutrient release from plant senescence to snow melting in the next year. Values are means \pm 1 SE ($n = 10$). Different small letters

indicate a significant difference of measured items between species at $P < 0.05$. *E. oxycorrhynchum*: *Erodium oxycorrhynchum*; *A. linifolium*: *Alyssum linifolium*; *S. arabicus*: *Schismus arabicus*; *S. foliosa*: *Salsola foliosa*; *C. arenarius*: *Ceratocarpus arenarius*

Item	Spring ephemerals			Annuals		Total
	<i>E. oxycorrhynchum</i>	<i>A. linifolium</i>	<i>S. arabicus</i>	<i>S. foliosa</i>	<i>C. arenarius</i>	
2011						
Biomass (g m ⁻²)	38 (0.75) a	0.8 (0.03) b	0.1 (0.01) c	14 (2.46) d	2 (0.07) e	56 (3.3)
N uptake (mg N m ⁻²)	913 (17.7) a	29 (6.1) b	2 (0.5) c	158 (14.3) d	51 (6.0) e	1152 (73)
N release (mg N m ⁻²)	338 (2.85) a	11 (0.09) b	0.8 (0.02) c	38 (1.03) d	14 (0.5) e	401 (4.5)
P uptake (mg P m ⁻²)	92 (3.3) a	3 (0.7) b	0.5 (0.2) c	57 (3.6) d	0.8 (0.3) c	154 (9)
P release (mg P m ⁻²)	55 (0.1) a	2 (0.0) b	0.2 (0.03) c	26 (0.0) d	0.4 (0.3) b	84 (0.1)
2012						
Biomass (g m ⁻²)	5.4 (0.53) a	0.9 (0.08) b	0.7 (0.02) c	0.6 (0.05) d	2.4 (0.1) e	9.4 (0.8)
N uptake (mg N m ⁻²)	95 (13.40) a	18 (6.11) b	0.5 (0.3) b	2 (0.1) b	50 (11.2) c	165 (50.1)
N release (mg N m ⁻²)	35 (3.0) a	7 (1.5) b	0.2 (0.1) c	0.4 (0.5) d	14 (1.4) e	56 (4.6)
P uptake (mg P m ⁻²)	10 (2) a	2.0 (7.4) b	0.07 (0.06) c	2.0 (0.5) b	0.8 (0.3) d	15 (3.6)
P release (mg P m ⁻²)	6 (0.2) a	1.3 (0.04) b	0.04 (0.03) b	0.9 (0.0) c	0.3 (0.0) c	8 (0.4)
2013						
Biomass (g m ⁻²)	18 (0.27) a	3.5 (0.05) b	0.2 (0.06) c	0.06 (0.04) c	2 (0.25) d	23 (0.6)
N uptake (mg N m ⁻²)	392 (45.1) a	98 (9.4) b	3 (0.7) c	2 (0.8) c	50 (5.7) d	545 (62)
N release (mg N m ⁻²)	145 (1.3) a	37 (0.4) b	1.4 (0.03) c	0.4 (0.00) c	14 (0.5) b	198 (2)
P uptake (mg P m ⁻²)	40 (5) a	10 (1) b	1 (0.3) c	2 (0.4) d	1 (0.3) c	54 (6)
P release (mg P m ⁻²)	24 (1) a	7 (1) b	0.5 (0.01) c	1 (0.01) d	0.4 (0.01) d	32 (1)

in 2012 to 92 mg m^{-2} in 2011. Over the 3 years, P uptake by spring ephemerals accounted for 62–94 % of the P uptake by the herbaceous community (Table 2). Nutrient uptake by spring ephemerals showed a large interannual variation, while uptake remained constant for summer annuals. Litter decomposition rate reflects the rate at which plant nutrients are returning to the soil. After 6 months of decomposition, *S. arabis* showed the greatest N loss, with 46.5 % of initial nitrogen content being lost; similarly, *A. linifolium* lost more than half of its initial mass and phosphorus (Table S1). The mass, N, and P losses of spring ephemerals were generally larger than those of summer annuals. The spring ephemeral *E. oxyrrhynchum* exhibited the greatest nutrient release (Table 1). Nitrogen release by spring ephemerals from August to the following April was 349 mg m^{-2} in 2011 and 42 mg m^{-2} in 2012 (Table 1), and P release of spring ephemerals reached 57 mg m^{-2} in 2011 (Table 1). In contrast to spring ephemerals, N and P releases of summer annuals were much lower: N release of summer annuals ranged from 14.4 mg m^{-2} in 2012 and 2013 to 52 mg m^{-2} in 2011, while P release of summer annuals varied from 1.2 mg m^{-2} in 2013 to 26.4 mg m^{-2} in 2011 (Table 1).

Dynamics of soil microbial N and P consumption

MBN and MBP exhibited significant variations by month (Fig. 3, $P < 0.05$). MBN and MBP increased after snow-melting (early April) and peaked in May (Fig. 3). The yearly mean MBN and MBP values were 0.24 – 5.67 and 0.1 – 1.0 g m^{-2} , respectively (Fig. 3). Subtracting the MBN just before snow-melting (March in 2011, 2012 and 2013) from the peak MBN (April in 2011 and 2013, May in 2012) in the spring ephemeral growth period gave an estimation of net N uptake by soil microbes; this value was 2.6 g m^{-2} in 2011, -2.0 g m^{-2} in 2012 and 2.2 g m^{-2} in 2013. Nitrogen immobilization by soil microbes was 2.7 and 4.5 times that of N uptake by spring ephemerals in the normal precipitation years of 2011 and 2013, respectively, while soil microbial activity led to a N release in the drought year of 2012 (Table 1). Over the 3 years, nitrate leaching ranged from 17.5 to 58.6 mg m^{-2} ; this was significantly less than N uptake by spring ephemerals (Table 1). After the senescence of spring ephemerals, N and P releases by spring ephemerals were significantly greater than those of summer annuals (Table 1). More importantly, N loss through nitrate leaching was extremely low compared

with which occurred during the spring ephemeral growing season (Table 1).

Discussion

Desert soil is poorly developed and characterized by a considerably lower nutrient content than that of other terrestrial ecosystems; therefore, nutrient conservation is especially important for plant growth and productivity in desert ecosystems (McCalley and Sparks 2009). At present, studies directly investigating the role of spring ephemerals or annuals in soil nutrient retention mechanisms in desert ecosystems are rare (Parker et al. 1984; Guo and Brown 1997; Chen et al. 2009). For instance, Chen et al. (2009) investigated soil nitrogen dynamics and their relationship to the plant community in the Badain Jaran Desert, and showed that annuals could absorb 0.46 – 3.78 g m^{-2} of N at peak growth, and that litter production and soil nutrient content were higher in areas dominated by annual plants than in areas dominated by shrubs. In the present study, spring ephemerals exhibited net N uptakes of 943, 113, and 493 mg m^{-2} , and P uptakes of 96, 9.6, and 51 mg m^{-2} in 2011, 2012, and 2013, respectively. These N uptake values are similar to that of *Erodium americanum* (100 mg m^{-2}) in a hardwood forest in central New Hampshire (Muller and Bormann 1976; Eickmeier and Schussler 1993; Rothstein 2000), and are also comparable to that of *Allium tricoccum* (410 mg m^{-2}) in a hardwood forest in northern Lower Michigan (Rothstein 2000). However, the values are lower than the net N uptake of understory vegetation ($>2.53 \text{ g m}^{-2}$) in a hardwood forest in the Catskill Mountains (Jack and Dudley 2003). The temporal niche of spring ephemerals in this desert is similar to that in hardwood forest ecosystems; this might indicate that spring ephemerals in the two ecosystems have the same functional role in ecosystem nutrient retention. Although spring ephemerals dominate in the Gurbantunggut Desert and represent the major surface cover before the flowering of annuals and perennials (Huang et al. 2015a), notably few studies have considered their roles in nutrient retention in desert ecosystems (Chen et al. 2009). Our results demonstrate that desert spring ephemerals can indeed contain a significant amount of nutrients due to their considerably higher biomass than summer annuals in this desert ecosystem. Some Eurasian annuals, belong to the same genus as those in our study, such as *Erodium cicutarium*

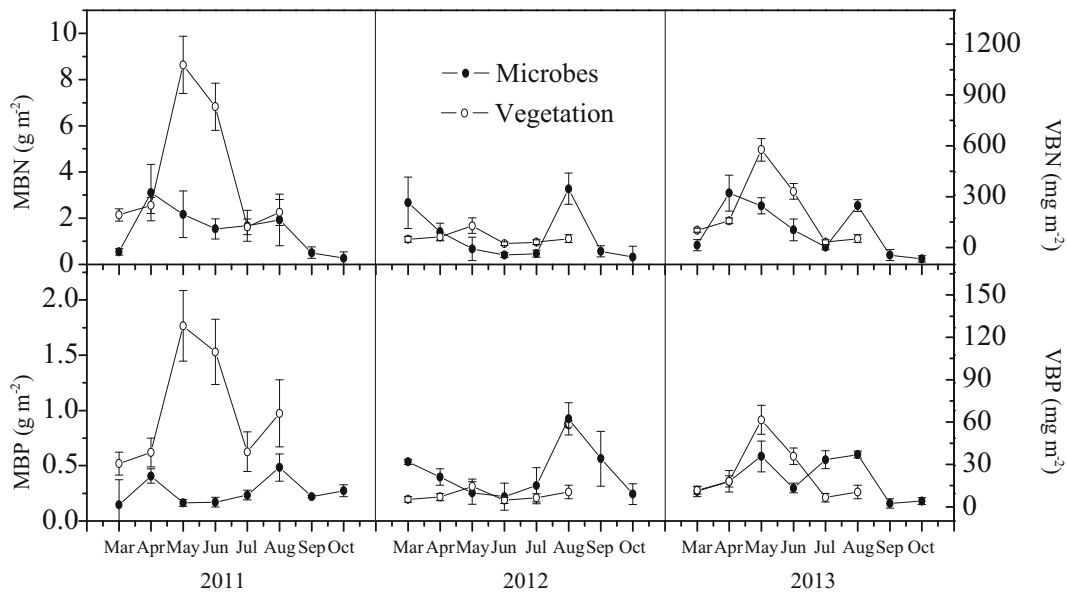


Fig. 3 Seasonal dynamics of microbial biomass nitrogen (MBN), phosphorus (MBP), vegetation biomass nitrogen (VBN) and phosphorus (VBP) in 2011, 2012 and 2013

and *E. oxycorynchum*. *E. cicutarium* is an invasive species and exerts significant influences on vegetation structure and native perennial diversity in North America (Robert et al. 2011). Considering the comparable ratios of the ephemeral biomass to community biomass in their respective communities, we expect a considerable amount of nutrient uptake by the Eurasian (winter) annuals in North America. However, because of the phenological divergences and competitive capacity of ephemerals in a plant community, the relationship between ephemerals and perennials in North America may be different from that found in the present study (Robert et al. 2011).

Net N uptake by desert spring ephemerals is 6.4–16 times greater than N loss through leaching. Rapid water infiltration through sandy soil during snowmelt can remove a large amount of dissolved nutrients from the plant rhizosphere (West and Skujins 1978). In our study, elevated N and P uptakes by spring ephemerals coincided with the decline in soil N and P concentrations in May and June. The rapid growth of spring ephemerals occurs after snow-melting, coinciding with higher soil moisture and nutrient availability. The rapid litter decomposition of ephemerals released nutrients into the soil that may be utilized for the rapid growth of summer annuals, promoting nutrient cycling and retention in the plant community. Although no study has estimated soil nutrient loss in the absence of spring ephemerals in this

desert ecosystem, snow-melting and large precipitation pulses can induce soil oxygen shortages and water infiltration into deeper soil layers, generating large nutrient losses from surface soil. For instance, N loss through leaching can be as high as $1.9 \text{ g m}^{-2} \text{ year}^{-1}$ without the presence of ephemerals in a Colorado pasture (Reed et al. 2012). Moreover, the presence of spring ephemerals can significantly decrease soil temperature (Huang et al. 2015a), which can alleviate N loss through volatilization (Schlesinger and Peterjohn 1991; Heckathorn and Delucia 1995). Compared with other low snowfall temperate deserts, spring ephemerals may increase plant community productivity (Huang et al. 2015a) and extend community phenology (Fig. S1), reducing soil nutrient losses in this desert ecosystem. In the present study, soil inorganic N and available P decreased from March to May, while spring ephemeral biomass increased over the same period. The inverse temporal dynamics of ephemeral growth and soil inorganic N suggest that spring ephemerals act as a temporary nutrient sink in this desert ecosystem.

In the present study, nutrient uptake by spring ephemerals was significantly greater than that of summer annuals, indicating that spring ephemerals are more important than annuals in terms of surface soil nutrient conservation in this desert ecosystem. Rapid nutrient uptake by spring ephemerals results from a significantly greater plant biomass; over the 3 years of investigation,

spring ephemerals accounted for 59–96 % of the entire herbaceous biomass. Moreover, the special environmental cues in this desert ecosystem, including thick snow cover, low soil temperature and high soil moisture content in spring, also contribute to the rapid nutrient uptake in spring ephemerals (Huang et al. 2015a). For instance, out of the three consecutive years of this study, the biomass of spring ephemerals was greatest in 2011, coinciding with a snow thickness of 32 cm and leading to the greatest nutrient pool among the 3 years. A high ratio of ephemeral biomass has also been validated in other desert ecosystems: for instance, ephemeral biomass varied from 9.4 to 95.2 g m⁻² in the Sonoran Desert (Patten 1978), values which are comparable to those of the present study site. These results may indicate that ephemerals are important to soil nutrient dynamics in desert ecosystems.

The growth of summer annuals peaked after nearly 2 months of spring ephemeral senescence. The leaves of two spring ephemerals (*A. linifolium* and *S. foliosa*) decomposed completely in the dry desert, and in the case of *E. oxycorymbum*, nearly 37 % of initial N and 60 % of initial P were released after the plants died. This result suggests that spring ephemerals can facilitate the nutrient utilization of summer annuals in this desert ecosystem. In contrast, an 18-year investigation of the winter and summer ephemeral communities in the Chihuahuan Desert showed that when the plant density of winter ephemerals was very high, the density of summer ephemeral in the following season was always low, and vice versa (Guo and Brown 1997). This negative interaction between plant densities may be because plants growing in one season deplete soil available nitrogen and immobilize it for sufficiently long time that the germination and survival of plants in the following season are subsequently inhibited (Guo and Brown 1997). In our study, though we did not directly investigate what ratio of nutrients released by spring ephemerals was incorporated into summer annual biomass, we did find that nitrogen uptake by spring ephemerals was 11.5 times that of nitrogen loss through leaching. Moreover, ephemerals released 35 % of litter N and 60 % of litter P within 6 months of mortality. This indirectly suggests that spring ephemerals can retain nutrients at the soil surface and improve soil nutrient use efficiency in the Gurbantunggut Desert.

We found that soil microbial biomass N and P increased in early spring, suggesting that soil microbial growth in the temperate desert was stimulated following pulses of water and nutrients. For the duration of the 3-

year study, MBN at snowmelting was 5.9 times that found in October. Nitrogen uptake by soil microbes was nearly 3.6 times that by spring ephemerals in the average precipitation years (2011 and 2013), suggesting that soil microbes also act as a major nutrient sink in this desert. The remarkable nutrient pool provided by soil microbes in this desert is consistent with that of some hardwood forests where soil microbes are a considerable vernal N reservoir (Rothstein 2000). The significantly elevated spring MBN and MBP values suggest an important role of soil microbes in soil nutrient immobilization; more importantly, soil microbial growth is the most important factor in soil nutrient retention prior to the significant nutrient uptake by spring ephemerals. This is consistent with results from some forests (Zak et al. 1990; Zechmeister-Boltenstern et al. 2002; Tessier and Raynal 2003); for instance, approximately 89 % of applied ¹⁵NH₄⁺ was immobilized in microbial biomass in a hardwood forest (Zak et al. 1990). Compared with other terrestrial ecosystems, information on nutrient retention by soil microbes is scarce for deserts (Mart et al. 1997; Schade et al. 2002). The mean microbial biomass nitrogen was 37.5–85.4 mg kg⁻¹ in the Gurbantunggut Desert, similar to the soil microbial biomass nitrogen of 4.4–11.5 mg kg⁻¹ in the north Negev Desert (Alon and Steinberger 1999) and 3.7–52.9 mg kg⁻¹ in the Nevada Desert (Billings et al. 2004). Moreover, some herbaceous species in these desert ecosystems belong to the same genera and have similar phenological characteristics. Therefore, we can infer that soil nutrient retention by microbial communities may be universal in desert ecosystems. Soil microbial communities in desert ecosystems have also shown an elevated growth with increasing water availability (Bell et al. 2008; Huang et al. 2015b). Therefore, we surmise that microbial nutrient immobilization under increasing water availability is possible in deserts. However, soil microbial nitrogen exhibited a dramatic decrease throughout the ephemeral growth season in the dry year of 2012, consistent with the behavior of soil microbes in the Michigan woods. This result demonstrates that low soil moisture can increase microbial mortality, which hinders soil nutrient retention in desert ecosystems (Rothstein 2000).

Conclusions

The seasonal nutrient uptake pattern of spring ephemerals is keeping with the seasonal dynamics of the soil

nutrient pool size and N mineralization dynamics throughout the spring ephemeral growing season. Desert ephemerals can take advantage of soil moisture from melting snow and provide a nutrient sink, eliminating nutrient losses from the soil surface. After the senescence of spring ephemerals, released nutrients due to litter decomposition are utilized by summer annuals and shrubs. Moreover, MBN and MBP peaked 1 month earlier than spring annuals and were significantly higher than nutrient uptake in spring ephemerals in the normal precipitation years; in contrast, soil microbes exhibited a net nutrient release in the dry year. This result suggests that soil microbes are the most important agent in soil nutrient retention in early spring in normal precipitation years and that spring ephemerals are more important in the dry years. Our study also demonstrated that nutrient retention differs between spring ephemerals and summer annuals and that spring ephemerals are more important because of their significantly greater biomass in the plant community. However, summer annuals exhibited obvious divergences in plant phenology from spring ephemerals, and they exhibited a longer growing season. This suggests that summer annuals have the capacity to absorb and retain nutrients for a longer period. Moreover, with increasing precipitation in summer due to climate change, summer annuals may exhibit an increasing biomass ratio in the plant community. In this case, their relative importance in nutrient retention in the plant community of the desert ecosystem may increase.

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References

- Alon A, Steinberger Y (1999) Effect of nitrogen amendments on microbial biomass, above-ground biomass and nematode population in the Negev Desert soil. *J Arid Environ* 41: 429–441
- Angert AL, Huxman TE, Barron-Gafford GA, Gerst KL, Venable DL (2007) Linking growth strategies to long-term population dynamics in a guild of desert annuals. *J Ecol* 95:321–331
- Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235
- Bell C, McIntyre N, Cox S, Tissue D, Zak J (2008) Soil microbial responses to temporal variations of moisture and temperature in a Chihuahuan Desert grassland. *Microb Ecol* 56:153–167
- Bickelhaupt DH, White EH (1982) Laboratory manual for soil and plant tissue analysis. SUNY College of Environmental Science and Forestry, Syracuse
- Billings SA, Schaeffer SM, Evans RD (2004) Soil microbial activity and N availability with elevated CO₂ in Mojave Desert soils. *Glob Biogeochem Cycl* 18, GB002137
- Bormann FH, Likens GE, Melillo JM (1977) Nitrogen budget for an aggrading northern hardwood forest ecosystem. *Science* 196:981–983
- Brookes PC, Powlson DS, Jenkinson DS (1984) Phosphorus in the soil microbial biomass. *Soil Biol Biochem* 16:169–175
- Brookes PC, Landman A, Pruden G, Jenkinson DS (1985) Chloroform fumigation and the release of soil nitrogen-A rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol Biochem* 17:837–842
- Castellano MJ, Lewis DB, Kaye JP (2012) Response of soil nitrogen retention to the interactive effects of soil texture, hydrology, and organic matter. *J Geophysical Res: Biogeosci* 118:1–11
- Chen BM, Wang GX, Peng SL (2009) Role of desert annuals in nutrient flow in arid area of Northwestern China: a nutrient reservoir and provider. *Plant Ecol* 201:401–409
- Eickmeier W, Schussler E (1993) Responses of the spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the “vernal dam” hypothesis. *Bull Torrey Bot Club* 120:157–165
- Fan LL, Tang LS, Wu LF, Ma J, Li Y (2014) The limited role of snow water in the growth and development of ephemeral plants in a cold desert. *J Veg Sci* 25:681–690
- Farnsworth E, Nunez J, Farfan J, Careaga S, Bazzaz F (1995) Phenology and growth of three temperate forest life forms in response to artificial soil warming. *J Ecol* 83:967–977
- Guo QF, Brown JH (1997) Interactions between winter and summer annuals in the Chihuahuan Desert. *Oecologia* 111:123–128
- Heckathorn S, Delucia E (1995) Ammonia volatilization during drought in perennial C₄ grasses of tallgrass prairie. *Oecologia* 101:361–365
- Huang G, Li Y, Padilla FM (2015a) Ephemeral plants mediate responses of ecosystem carbon exchange to increased precipitation in a temperate desert. *Agr For Met* 201:141–152
- Huang G, Li Y, Su YG (2015b) Effects of increasing precipitation on soil microbial community composition and soil respiration in a temperate desert, Northwestern China. *Soil Biol Biochem* 83:52–56
- Jack TT, Dudley JR (2003) Vernal nitrogen and phosphorus retention by forest understorey vegetation and soil microbes. *Plant Soil* 256:443–453
- Jandl R, Kopeszki H, Glatzel G (1997) Effect of a dense *Allium ursinum* (L.) ground cover on nutrient dynamics and mesofauna of a *Fagus sylvatica* (L.) woodland. *Plant Soil*: 245–255.
- John MK (1970) Colorimetric determination of phosphorus in soil and plant materials with ascorbic acid. *Soil Sci* 109:214–220
- Li XR (2012) Eco-hydrology of biological soil crusts in desert regions of China. Higher Education Press, Beijing

- Li CJ, Li Y, Ma J (2011) Scale characteristics of spatial heterogeneity of soil chemical properties in Gurbantunggut Desert. *J Des Res* (In Chinese) 48:302–310
- Mabry CM, Gerken ME, Thompson JR (2008) Seasonal storage of nutrients by perennial herbaceous species in undisturbed and disturbed deciduous hardwood forests. *Appl Veg Sci* 11:37–44
- Mart E, Grimm NB, Fisher S (1997) Pre- and post-flood retention efficiency of nitrogen in a Sonoran Desert stream. *J N Am Benthol Soc* 16:805–819
- McCalley CK, Sparks JP (2009) Abiotic gas formation drives nitrogen loss from a desert ecosystem. *Science* 326:837–840
- Morgan JB, Connolly EL (2013) Plant-soil interactions: nutrient uptake. *Nature Education Knowledge* 4:2
- Muller RN, Bormann FH (1976) Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics in the northern hardwood forest. *Science* 193:1126–1128
- Parker L, Santos P, Phillips J, Whitford W (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan Desert annual *Lepidium lasiocarpum*. *Ecol Monogr* 54:339–360
- Patten DT (1978) Productivity and production efficiency of an Upper Sonoran Desert ephemeral community. *Am J Bot* 65: 891–895
- Reed SC, Coe KK, Sparks JP, Housman DC, Zelikova TZ, Belnap J (2012) Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nat Clim Chang* 2:752–755
- Robert JS, Jennifer LF, Edith BA (2011) Can resource-use traits predict native vs. exotic plant success in carbon amended soils? *Ecol Appl* 21:1211–1224
- Rothstein DE (2000) Spring ephemeral herbs and nitrogen cycling in a northern hardwood forest: an experimental test of the vernal dam hypothesis. *Oecologia* 124:446–453
- Schade JD, Marti E, Welter JR, Fisher SG, Grimm NB (2002) Sources of nitrogen to the riparian zone of a desert stream: implications for riparian vegetation and nitrogen retention. *Ecosystems* 5:68–79
- Schimel J, Balser TC (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88: 1386–1394
- Schlesinger W, Peterjohn W (1991) Processes controlling ammonia volatilization from Chihuahuan Desert soils. *Soil Biol Biochem* 23:637–642
- State Environmental Protection Administration (2014) Soil quality-determination of available phosphorus-sodium hydrogen carbonate solution-Mo-Sb anti spectrophotometric method. China Environmental Science Press, Beijing
- Su YG, Wu L, Zhou ZB, Liu YB, Zhang YM (2013) Carbon flux in deserts depends on soil cover type: a case study in the Gurbantunggute desert, North China. *Soil Biol Biochem* 58: 332–340
- Tessier JT, Raynal DJ (2003) Vernal nitrogen and phosphorus retention by forest understory vegetation and soil microbes. *Plant Soil* 256:443–453
- Tremblay NO, Larocque GR (2001) Seasonal dynamics of understory vegetation in four eastern Canadian forest types. *Int J Plant Sci* 162:271–286
- Vitousek PM, Reiners WA (1975) Ecosystem succession and nutrient retention: a hypothesis. *BioSci* 25:376–381
- Wang XQ, Jiang J, Wang YC, Luo WL, Song CW, Chen JJ (2006) Responses of ephemeral plant germination and growth to water and heat conditions in the southern part of Gurbantunggut Desert. *Chin Sci Bull* 51:110–116
- West NE, Skujins J (1978) Nitrogen in desert ecosystems Dowden, Hutchinson & Ross. Academic Press, Stroudsburg
- Zak DR, Groffman PM, Pregitzer KS, Christensen S, Tiedje JM (1990) The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. *Ecol Evol* 71:651–656
- Zechmeister-Boltenstern S, Hahn M, Meger S, Jandl R (2002) Nitrous oxide emissions and nitrate leaching in relation to microbial biomass dynamics in a beech forest soil. *Soil Biol Biochem* 34:823–832
- Zhou H, Li Y, Tang Y, Zhou B, Xu H (2009) The characteristics of the snow-cover and snowmelt water storage in Gurbantunggut Desert. *Arid Zone Res* 26:312–317