Life history responses of two ephemeral plant species to increased precipitation and nitrogen in the Gurbantunggut Desert

Yanfeng Chen[1,2], Lingwei Zhang[3], Xiang Shi[4], Huiliang Liu[1,5] and Daoyuan Zhang[1,6]

[1] Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urümqi, Xinjiang, China
[2] University of Chinese Academy of Sciences, Beijing, China
[3] College of Grassland and Environment Sciences, Xinjiang Agricultural University, Urümqi, Xinjiang, China
[4] College of Agriculture, Shihezi University, Shihezi, Xinjiang, China
[5] Yili Botanical Garden, Xinjiang Institute of Ecology and Geography, Xinyuan, Xinjiang, China
[6] Turpan Eremophytes Botanical Garden, Chinese Academy of Sciences, Turpan, Xinjiang, China

Corresponding author
Huiliang Liu,
liuhuiliang@ms.xjb.ac.cn,
lhl2033904@163.com

ABSTRACT

Precipitation change and nitrogen deposition are not only hot topics of current global change but also the main environmental factors affecting plant growth in desert ecosystems. Thus, we performed an experiment of increased precipitation, nitrogen, and precipitation plus nitrogen on the ephemeral annual species *Nepeta micrantha* and *Eremopyrum distans* in the Gurbantunggut Desert. We aimed to determine the life history responses of *N. micrantha* and *E. distans* to environment changes, and the germination percentage of the offspring (seeds) was also tested in the laboratory. The results showed that increased nitrogen and precipitation plus nitrogen increased the growth of both plant species, whereas increased precipitation inhibited the growth of *N. micrantha* but increased the growth of *E. distans*. This differential response of these two species to precipitation and nitrogen also affected the germination of their offspring. In response to increased nitrogen and precipitation plus nitrogen, the germination percentage of the offspring produced by two species decreased in conjunction with the plants exhibiting high reproduction, which may prevent overcrowding during the following year; however, the *N. micrantha* plants produced more nondormant offspring in conjunction with low reproduction under relatively greater amounts of precipitation, and *N. micrantha* offspring could occupy their habitat via rapid germination in suitable environments. Therefore, with increased precipitation and nitrogen deposition, these differences in offspring dormancy may affect their ecological niche in the community.

INTRODUCTION

Anthropogenic activity and climate change have a continuing effect on global and regional environments, including widespread changes in precipitation and nitrogen deposition

(*Stocker et al., 2013*). Plants are an important component of terrestrial ecosystems and play an important role in their regulation. Therefore, understanding plant responses to precipitation and nitrogen deposition is important for maintaining ecosystem stability (*Cabaço & Rui, 2012*). Especially in arid and semiarid areas where environmental conditions are extremely harsh, slight disturbances are likely to cause a severe changes in plant growth (*Knapp & Smith, 2001*; *Huxman et al., 2004*; *Diffenbaugh, Giorgi & Pal, 2008*). Moisture is the most important limiting factor for plant growth in arid and semiarid regions, and precipitation is the primary source of soil moisture (*Dube & Pickup, 2001*; *Cheng et al., 2006*). In the Gurbantunggut Desert of northwestern China, the annual precipitation is predicted to increase by 30% during the next 30 years (*Bai et al., 2008*; *Liu et al., 2010*; *Huang et al., 2017*). Nitrogen deposition from the nearest city to the study area is 35.4 kg ha^{-1} yr^{-1}, and the nitrogen deposition in the Gurbantunggut Desert is predicted to double in the future (*Liu et al., 2013*; *Xu et al., 2015*). Therefore, researching plant responses to precipitation and nitrogen deposition in this desert ecosystem is highly necessary to adapt to climate change.

Precipitation is a key climate factor that affects plant growth, especially in desert ecosystems (*Hsu, Powell & Adler, 2012*; *Beer et al., 2010*). During the seedling stage, seedling emergence of desert annual plants increased significantly and exhibited faster germination time with increased precipitation in the Mu Us Desert (*Zheng et al., 2005*), but the contrary was the case with the decreasing of soil moisture (*Liu et al., 2018*). During the growth stage, increased precipitation not only promoted the production of new leaves and branches (*Zhang et al., 2015*), but also increased biomass accumulation in desert annual species (*Shemtov & Gutterman, 2003*). But the promotion of precipitation often intensify competition among species. Small-stature plants can be overshadowed by taller plants and the ground cover by small-stature plants decreases with increased precipitation (*Harpole, Potts & Suding, 2007*; *Zavaleta et al., 2003*). The moisture requirement for non-native annual grasses is typically lower than that of native plants leading to an increased advantage in non-native annual grass competition in the Mojave Deserts (*Horn, Nettles & Clair, 2015*). Thus, desert annual herbs respond very rapidly to precipitation changes throughout the whole growth period and species show differential responses to increased precipitation in the community.

Although desert plants are primarily limited by precipitation, previous studies have indicated the potential for co-limitation by nitrogen in desert ecosystems (*Hall et al., 2011*). Hence, nitrogen fertilization is commonly used to improve plant growth in semiarid/arid ecosystems (*Frink, Waggoner & Ausubel, 1999*). In the Mojave Desert, soil nitrogen addition increased the dominance of alien annual plants, but inhibited the growth of natives (*Jordan, 1996*). At the Sevilleta, the cover of two dominant species (black grama and blue grama) is not changing directionally by changes in nitrogen deposition, but are likely caused by other factors (*Baez et al., 2007*). In the Chihuahuan Desert grassland, nitrogen limitation only becomes evident on plant growth following periods of above average precipitation (*Ladwig et al., 2012*). Therefore, these different responses of desert plants to nitrogen likely derive from the variations in species specificity and other factors, especially in precipitation regime.

Water is not only a material for photosynthesis (*Maberly, 2014*), but also a solvent for nitrogen (*Gebauer & Ehleringer, 2000*; *Lloret, Casanovas & Penuelas, 2010*). Similarly, the effects of precipitation plus nitrogen on plants have been reported largely in terms of plant richness (*McHugh et al., 2017*; *Simkin et al., 2016*), diversity (*Bobbink et al., 2010*; *McHugh et al., 2017*), community coverage (*McHugh et al., 2017*), community biomass (*Xu et al., 2018*), and plant-plant interactions (*Wang et al., 2016a*; *Wang et al., 2016b*). However, the effects of precipitation plus nitrogen on whole life history have rarely been reported. The only reports to date have focused on certain aspects of plant life history; for example, the nitrogen plus precipitation significantly advanced the onset of the flowering and fruiting times (*Huang, Li & Li, 2018*) and was shown to increase root growth (*Zhang et al., 2017*), leaf number (*Barker et al., 2006*; *Huang, Li & Li, 2018*), seed yield (*Altenbach et al., 2003*; *Fuertes-Mendizabal et al., 2010*), and biomass accumulation (*Al-Solaimani et al., 2017*). No research on the entire life history has been performed with respect to the effect of precipitation plus nitrogen deposition.

Ephemeral plants are a unique group of plants and widely distributed in the Gurbantunggut Desert (*Lu et al., 2014*). Ephemeral plant coverage can reach 40% of this area in May, while coverage by shrubs and long-living herbs on the surface of the dunes reaches less than 10% (*Wang et al., 2003*). Therefore, ephemeral plants are the primary contributors to the stabilization of the sand surface during early spring. By utilizing winter snowmelt and spring rainfall, ephemeral plants complete their life cycle quickly (*Lu et al., 2016*). Compared with other annual and perennial herbs, ephemeral plants grow more quickly and exhibit greater light use efficiency, and they allocate a greater percentage of their biomass to reproduction (*Yuan & Tang, 2010*). Thus, ephemeral plants are extremely sensitive to climate change. Previous research on the effects of precipitation and nitrogen on ephemeral plants has focused primarily on plant survival, biomass accumulation (*Lu et al., 2014*) and nutrient use (*Wang et al., 2016a*; *Wang et al., 2016b*). The information about plant responses to climate change throughout the entire life history is lacking.

The importance of root traits as drivers of ecosystem function has attracted widespread concern (*Bardgett, Mommer & De Vries, 2014*). In arid-semiarid ecosystems, the root morphology can influence the ability of the plants to regulate their own growth in response to environmental change (*Ogle & Reynolds, 2004*; *Shen, Reynolds & Hui, 2010*; *Griffin-Nolan et al., 2018*). For example, *Paz, Pinedagarcía & Pinzónpérez (2015)* reported that 23 species exhibit wide variation in their root morphology, which ultimately governs plant mass by absorbing water and nutrients. Two common annual ephemeral plants in the Gurbantunggut Desert during early spring include *Eremopyrum distans* and *Nepeta micrantha* (*Wang et al., 2010*; *Ding et al., 2016*). *E. distans* is a member of the Gramineae and has a fibrous root system (*Wang et al., 2010*). *N. micrantha* is a member of the Labiatae and has a taproot system (field observations by the first author from 2014 to 2016). Therefore, the root morphology forms of *E. distans* and *N. micrantha* are significantly different. On the basis of the sensitivity response of ephemeral plants to environmental change, the effects of roots in regulate the response of plant to environmental change and the significant differences in root morphology of *E. distans* and *N. micrantha*, we hypothesized that the life histories of *E. distans* and *N. micrantha* differ in response to

increased precipitation and nitrogen and precipitation plus nitrogen in the field. To test this hypothesis, we compared the phenology, morphological traits, biomass accumulation and allocation, and offspring (seed) germination of *E. distans* and *N. micrantha* plants during the life history.

MATERIALS AND METHODS

Study site

The study site is located on the southern edge of the Gurbantunggut Desert, which is the second largest desert in China (*Wang et al., 2004*). This desert has a typical temperate continental climate with hot summers and cold winters; the highest annual temperature is 42.6 °C, the lowest annual temperature is −41.6 °C, and the annual precipitation is generally 70–100 mm. The evapotranspiration can reach approximately 2,000 mm, which is 20–30 times the precipitation (*Ji, Ye & Wei, 2000*). During the winter, the Gurbantunggut Desert has a stable snow layer and a maximum snow depth of more than 20 cm, which lasts from three to five months (*Zhou, Zhou & Dai, 2009*; *Li et al., 2010*). During the early spring, the snow melts rapidly and provides sufficient water for the growth of ephemeral plants (*Wang et al., 2003*).

Experimental design
Increased precipitation and nitrogen treatments

To simulate the current precipitation amounts in the Gurbantunggut Desert as well as the future and extreme amounts expected, an experiment was established to simulate precipitation increases of +0%, +30%, and +50% based on empirical precipitation data from the study area during the spring and summer. Owing to the rapid development of the economy, the Gurbantunggut Desert has been surrounded by farmland and factories; therefore, it receives a large exogenous input of nitrogen. The nitrogen deposition from a nearby city (Urumqi) has reached 35.4 kg ha^{-1} yr^{-1}(*Wei, 2015*). According to *Galloway et al. (2008)*, global nitrogen deposition will increase rapidly doubling the amount recorded in 1990 within 30 years. Thus, we simulated three N deposition levels in the experiment: N0 (control treatment, no additional nitrogen input, the value is the current actual nitrogen input), N1 (the current deposition rate in a polluted area, 3 g N m^{-2} yr^{-1}), and N2 (the predicted future rate of 6 g N m^{-2} yr^{-1}). The field experiment consisted of three levels of precipitation (+0%, +30%, and +50%; CK, W1, and W2, respectively), three levels of N (0, 3, and 6 g N m^{-2} yr^{-1}; CK, N1, and N2, respectively), and the precipitation plus nitrogen (W1N1 and W2N1). A total of seven treatments (CK, W1, W2, N1, N2, W1N1, and W2N1) were set up with eight replicates for per treatment for a total of 56 plots. The plots were distributed at the bottom of the flat dunes, and the size of each plot was 1 m ×1 m and encompassed 12 plants. To avoid interference, we removed other species from the plots in November 2016 and again in April 2017. We installed plastic film around the plots to avoid affecting the environment. Furthermore, in order to collect rainfall for the increased precipitation experiments, four precipitation collection vessels were installed in the field. Each precipitation collection vessel was assembled from plastic boards (4 m × 4 m) and iron

poles. Each board was installed at an angle of 30° from the ground to collect precipitation, and one bucket was placed on the lower corner of the board.

On September 1, 2014, we installed a weather and soil moisture monitoring device (Caipos GmbH, Schiller Strasse Gleisdorf, Austria) to monitor the precipitation, temperature, and soil moisture. When a precipitation event occurred, the monitoring device collected data from wireless sensors, uploading the measurements directly to a web-based platform every hour. We conducted an increased precipitation experiment on the second day after each natural precipitation events (including some snow fall in early spring). We used a watering can to apply rainwater on the plots designated for testing increased precipitation.

With respect to nitrogen applications, we referred to the methods of *Zhou et al.*'s (*2011*) and applied nitrogen twice per year in late March (snowmelt) and late October (before snowfall). When the nitrogen was applied, NH_4NO_3 and NH_4Cl were dissolved in the water at $NH_4:NO_3 = 2:1$, and the solution was manually applied evenly on the sample surface area; the same amount of water was applied on the control soils.

Experimental material

We sowed seeds in the designated plots in the beginning of October, 2016. One hundred *E. distans* and *N. micrantha* seeds were evenly sown each 1 m ×1 m plot. On March 10, 2017, 12 of the largest plants in each 1 m ×1 m plot were marked, after which excess seedlings and other species were removed.

Measurements and sampling
Phenology

We followed the methods of *Lu et al. (2014)* and observed the experimental plots every 3 days from germination until death, and we recorded the emergence date (the number of days until all the seeds in each treatment had emerged), flowering date (the number of days until all the plants in each treatment had flowered), fruiting date (the number of days until the occurrence of the first green fruit on all the plants in each treatment) and maturation date (the number of days until the first fruits of all the individuals plants in each treatment had turned a khaki color and were ready to disperse naturally) were determined. The post germination life span (the interval from the emergence of the first individual to the death of the last individual in each treatment) was then determined.

Plant traits

When the plants reached maturity, their traits (plant height; leaf area; root length; and the numbers of flowers, fruits, and seeds) were measured. We measured the leaf area of fresh leaves using a LI-COR 3000 leaf area meter directly. However, we measured the leaf area of the curling leaves after they were rehydrated. The total leaf area was calculated as the area of the fresh leaves plus that of the curled leaves. The root of *N. micrantha* has a tap root system and consists mainly of the main root and a small number of lateral roots that are growing on the main root, so, we measured the length of main root to represent the root length. However, root of *E. distans* has a fibrous root system, and it consists of many

fibrous roots. Therefore, the root length of *E. distans* is expressed by taking the average of the fibrous roots.

Dry mass accumulation and allocation

After the plant traits were measured, the plants in all the treatments were harvested and separated into roots, stems, leaves, and reproductive organs (flowers, fruits, and seeds), and the roots were carefully washed free of soil. We harvested the seeds or fruits at maturity, i.e., when the fruits were dry, yellow, and dehiscing. As a result of the different precipitation and nitrogen treatments, the seeds or fruits reached maturity at different times. Thus, we harvested the plants as soon as their seeds or fruits had turned yellow. Various organs (fruits, leaves, stems, and roots) from the plants were weighed separately using a Sartorius BS210S electronic balance (0.0001 g) after they were dried at 75 °C for 48 h. The total biomass was calculated as the masses of the various organs (roots, stems, leaves, fruits and seeds) per plant. The biomass allocation of the roots, stems, leaves, and reproductive organs (flowers, fruits, and seeds) was expressed as a percentage as follows:

Root percentage = (roots mass)/(total mass) × 100%;

Stem percentage = (stems mass)/(total mass) × 100%;

Leaf percentage = (leaves mass)/(total mass) × 100%;

Reproductive percentage = (reproductive mass)/(total mass) × 100%.

Offspring(seed) germination

Mature fruits from the different treatments were collected on May 21 and June 1, 2017. We removed the shells and retained the seeds from *E. distans* and *N. micrantha* for the germination experiment. With respect to *E. distans*, germination tests were conducted at an alternating temperature regimen of 25 °C/10 °C (12 h of light/12 h of darkness) starting on June 20, 2017. With respect to *N. micrantha,* germination tests were conducted at a constant temperature regime of 14 °C (24 h of darkness) starting on June 20, 2017 (these temperature and light settings were determined via another germination experiment on *E. distans* and *N. micrantha*; Y Chen, 2019, unpublished data). Twenty-five seeds were placed on two layers of Whatman No. 1 filter paper that was moistened with 3 mL of distilled water in each of the four 7 cm Petri dishes. Water was added as needed to keep the filter paper moist during the test period. A seed was considered to have germinated when its radicle had emerged. The germinated seeds were counted and removed daily for 30 days. The final percentage of germination (FPG) was estimated as follows: FPG = GN/SN, where GN is the total number of germinated seeds and SN is the number of viable seeds. If the intact seeds did not germinate after the germination experiment, their viability was tested by using a 1% triphenyltetrazolium chloride TTC solution (*Baskin & Baskin, 2014*).
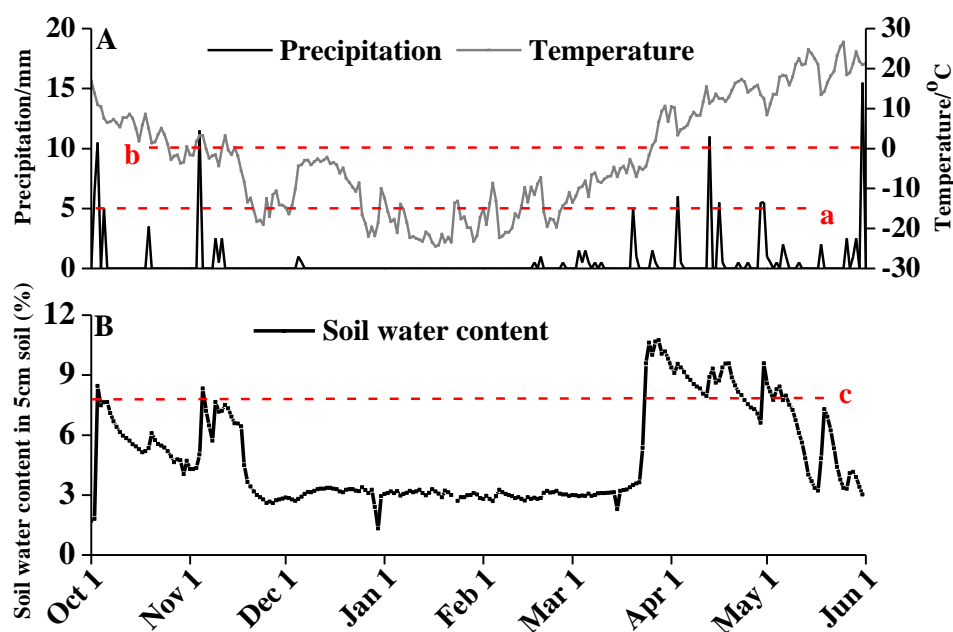
Figure 1 **Precipitation, temperature (A), and soil water content (B) of study area from October 1, 2016 to June 1, 2017.** Red lowercase letter a indicates that precipitation amount exceed 5 cm, red lowercase letter b indicates precipitation amount exceed 10 cm, and red lowercase letter c indicates soil water content above 8%.

Statistical analyses

Data collation and analysis were performed using Microsoft Excel and SPSS 16.0 (SPSS Inc., Chicago, Illinois, USA) software, respectively, and figures were constructed with Origin 8.0 software (Origin Lab, Northampton, MA). Plant traits (plant height, leaf area, leaf number, root length and seed number), dry mass accumulation and allocation (total dry mass and proportion allocated to roots, stems, leaves and reproductive organs) and the final percentage of germination were analyzed as dependent variables, and increased precipitation, nitrogen and precipitation plus nitrogen were considered as fixed effects with a one-way ANOVA. Tukey's test was performed for multiple comparisons to determine significant differences among treatments, and we performed a Bonferroni correction to avoid type I error problems. The allocation results for the roots, stems, leaves and reproductive organs (percentage data) were transformed (log10) before a one-way ANOVA was conducted. Pearson correlations were calculated for data involving the phenology, plant traits, and biomass accumulation and allocation from all treatments.

RESULTS

Precipitation and temperature

From October 2016 to June 2017, the average daily temperature decreased first and then increased, with a minimum of $-24.48\,°C$ on January 17, 2017 and a high of $26.6\,°C$ on May 25, 2017 (Fig. 1A). The snow thickness was 20.23 ± 0.40 cm on February 16, 2017, and the

snow began to melt on March 20, 2017. Water from the snowmelt caused a sharp increase in soil moisture at the end of March. The soil moisture content remained at approximately 8% from late March until late April (Fig. 1B).

Phenology

Increased precipitation (W1 and W2), nitrogen (N1 and N2), and precipitation plus nitrogen (W1N1 and W2N1) delayed the flowering date, fruiting date, and withering date and prolonged the life cycles of *N. micrantha* and *E. distans* significantly ($P < 0.01$) (Table 1).

Plant traits

Increased precipitation (W1 and W2) significantly decreased the height, root length and leaf area ($P < 0.01$) of *N. micrantha* but had nearly no effect on leaf number; Increased nitrogen and precipitation plus nitrogen have almost no effect on the height, root length and leaf number, but N1 significantly increased the leaf area and leaf number of *N. micrantha* ($P < 0.01$, Figs. 2A, 2C, 2E, 2G), and W1N1 significantly decreased the leaf area of *N. micrantha* ($P < 0.01$, Fig. 2E). Conversely, increased precipitation, increased nitrogen, and precipitation plus nitrogen treatments significantly increased the height, leaf area, leaf number of *E. distans* ($P < 0.01$), with the exception of W2 significantly inhibited the root length of *E. distans* ($P < 0.01$, Figs. 2B, 2D, 2F, 2H).

To *N. micrantha*, W1, N2, W1N1 and W2N1 had nearly no effect on the seed number, but N1 significantly increased seed number ($P < 0.01$, Fig. 3A); however, W2 significantly reduced seed number ($P < 0.01$). To *E. distans*, increased precipitation, increased nitrogen and precipitation plus nitrogen significantly increased fruit number, and the increase of W1N1 in fruit number was the greatest ($P < 0.01$, Fig. 3B).

Biomass accumulation and allocation

Increased precipitation (W1 and W2) decreased the total biomass of *N. micrantha* ($P < 0.01$, Fig. 4A), and the decrease of W2 is more significant than W1. The effect of N1 on the total biomass of *N. micrantha* is not significant ($P = 0.98$), but N2 significantly increased the total biomass of *N. micrantha* ($P < 0.01$), and precipitation plus nitrogen (W1N1 and W2N1) also significantly increased the total biomass of *N. micrantha* ($P < 0.01$, Fig. 4A). Increased precipitation, increased nitrogen and precipitation plus nitrogen significantly increased the total biomass of *E. distans*, and the increase of W1N1 in the total biomass is more significant than other treatments ($P < 0.01$, Fig. 4B).

The correlation analysis also revealed a positive correlation between plant traits (height, root length, leaf area, number of leaves, and number of seeds) and the total biomass accumulation of *E. distans* and *N. micrantha*, with the exception of the height of *N. micrantha* (Table 2). Increased precipitation, nitrogen, and precipitation plus nitrogen significantly increased the reproduction percentage of *E. distans* ($P < 0.01$), but N2, W1N1 and W2N1 slightly decreased the reproductive percentage of *N. micrantha* and W1, W2 and N1 slightly increased the reproductive percentage of *N. micrantha* (Fig. 5A). W1, W2 and N1 decreased the leaf percentage of *N. micrantha* ($P < 0.01$), but N2, W1N1 and W2N1 increased the leaf percentage of *N. micrantha* ($P < 0.01$). Increased precipitation, nitrogen,

Table 1 **Effects of increased precipitation and nitrogen and precipitation plus nitrogen treatments on the phenology of *Nepeta micrantha* and *Eremopyum orientale* (mean ± 1s.e).**

	Phenology	CK	W1	W2	N1	N2	W1N1	W2N1
	Emergence date	16 April	16 April	16 April	16 April	16 April	16 April	16 April
	Four-leaf rosette date	20 April	20 April	20 April	19 April	20 April	19 April	19 April
Nepeta micrantha	**Flowering date**	6 May	6 May	6 May	9 May	5 May	8 May	7 May
	Fruiting date	14 May	15 May	15 May	15 May	14 May	15 May	15 May
	Withering date	24 May	25 May	25 May	25 May	24 May	25 May	25 May
	Life cycle (d)	47.80 ± 0.006[b]	48.80 ± 0.467[ab]	49.40 ± 0.340[a]	49.30 ± 0.300[a]	48.40 ± 0.340[ab]	48.70 ± 0.396[ab]	49.20 ± 0.442[a]
	Emergence date	10 Oct	10 Oct	10 Oct	10 Oct	10 Oct	10 Oct	10 Oct
	Four-leaf rosette date	23 April	23 April	23 April	23 April	23April	23April	23 April
Eremopyrum orientale	**Flowering date**	∼	∼	∼	∼	∼	∼	∼
	Fruiting date	13 May	14 May	13 May	13 May	13 May	14 May	14 May
	Withering date	21 May	21 May	22 May	22 May	22 May	22 May	22 May
	Life cycle (d)	224 ± 0.008[b]	224 ± 0.009[b]	225 ± 0.011[a]	225 ± 0.008[b]	225 ± 0.007[b]	225 ± 0.008[a]	225 ± 0.011[a]

Notes.

CK; W1, increase 30% in precipitation; W2, increase 50% in precipitation; N1, increase 3 g N m−2 yr−1; N2, increase 6 g N m−2 yr−1; precipitation plus nitrogen : W1N1, W1 + N1; W2N1, W2 + N1. Oct, October. Different lowercase letters indicate significant differences ($P < 0.05$) among increased precipitation and nitrogen and precipitation plus nitrogen.
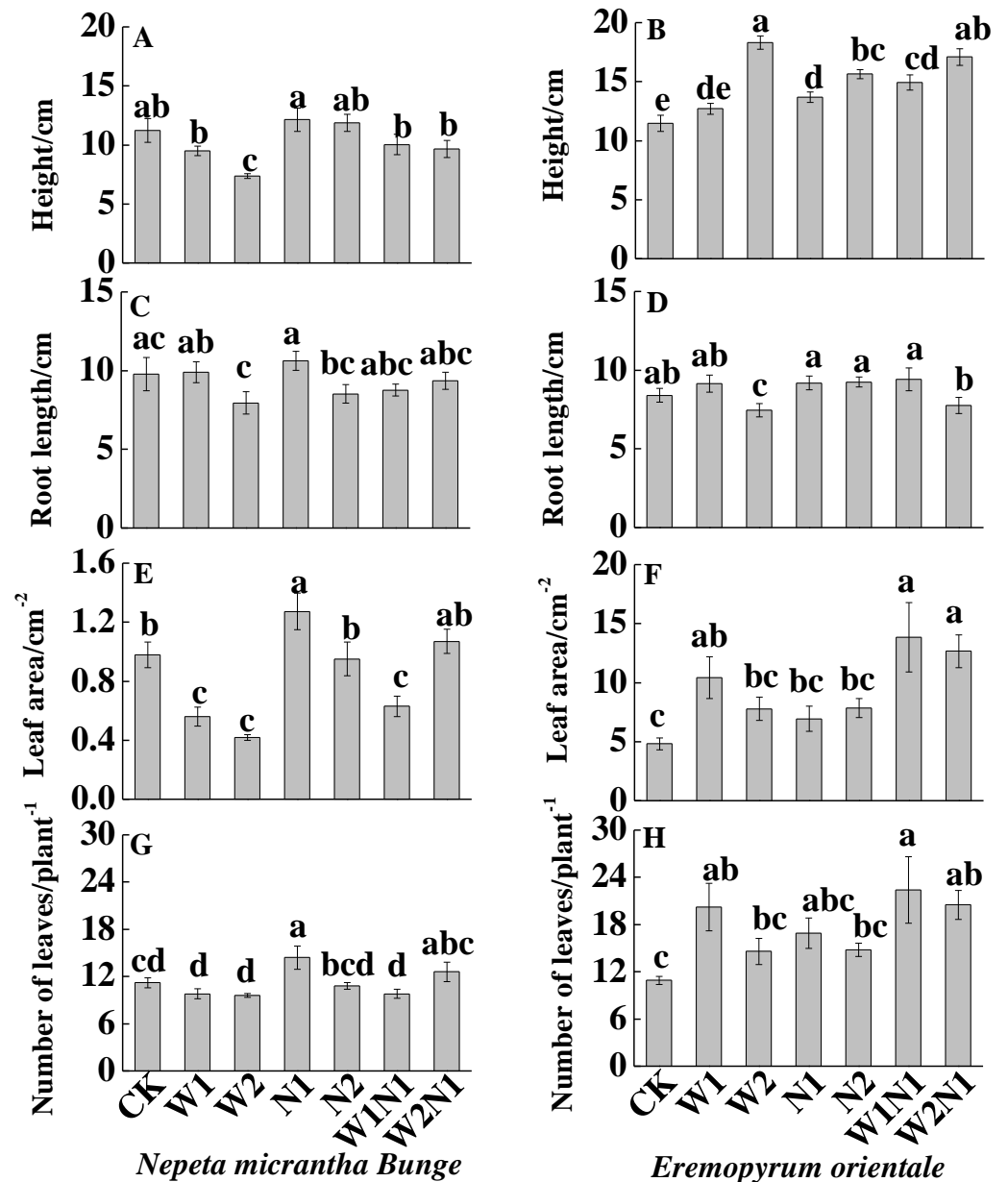
Figure 2 Effects of increased precipitation and nitrogen and precipitation plus nitrogen treatments on plant traits (mean ± 1s.e.) of *Nepeta micrantha* (A, C, E, G) and *Eremopyrum distans* (B, D, F, H). CK, control treatment; W1, increase 30% in precipitation; W2, increase 50% in precipitation; N1, increase 3 g nitrogen m^{-2} yr^{-1}; N2, increase 6 g nitrogen m^{-2} yr^{-1}; precipitation plus nitrogen: W1 + N1, W1N1; W2 + N1, W2N1. Different lowercase letters indicate significant differences among increased precipitation and nitrogen and precipitation plus nitrogen treatments.

and precipitation plus nitrogen decreased the leaf percentage of *E. distans* (Fig. 5B). Increased precipitation, nitrogen, and precipitation plus nitrogen had little effect on the stem percentage of *N. micrantha* and *E. distans*, with the exception of precipitation plus nitrogen increased the stem percentage of *E. distans*. The root percentage of *N. micrantha*
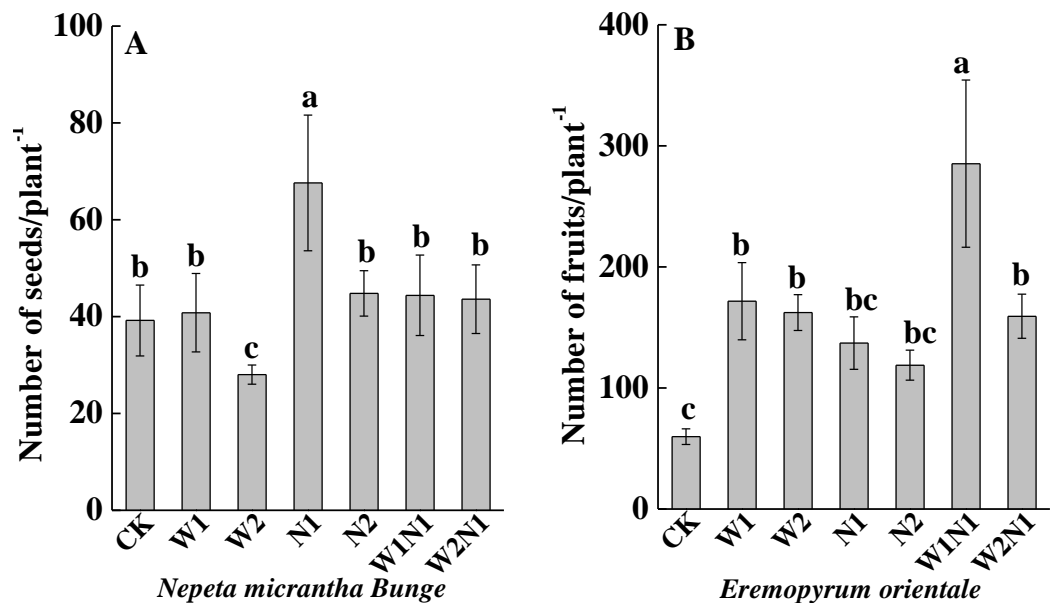
Figure 3 Effects of increased precipitation and nitrogen and precipitation plus nitrogen on seed number per plant (mean ± 1s.e) of *Nepeta micrantha* (A) and *Eremopyrum distans* (B). CK, control treatment; W1, increase 30% in precipitation; W2, increase 50% in precipitation; N1, increase 3 g nitrogen m^{-2} yr^{-1}; N2, increase 6 g nitrogen m^{-2} yr^{-1}; precipitation plus nitrogen: W1 + N1, W1N1; W2 + N1, W2N1. Different lowercase letters indicate significant differences among increased precipitation and nitrogen and precipitation plus nitrogen treatments.

increased significantly with increased precipitation, nitrogen, and precipitation plus nitrogen ($P < 0.01$), and increased nitrogen increased the root percentage of *E. distans*, but W2 treatment decreased the root percentage of *E. distans*; however, the other treatments (W1, W1N1, and W2N1) had little effect on the root percentage of *E. distans*.

Seed germination of the offspring

W1, W2, N1, W1N1 and W2N1 significantly increased the germination percentage of seeds produced by *N. micrantha* plants ($P < 0.01$), and the increase of W2 is more significant than W1, but N2 significantly reduced the germination percentage of seeds produced by *N. micrantha* plants ($P < 0.01$, Fig. 6A). Increased precipitation, nitrogen, and precipitation plus nitrogen significantly reduced the germination percentage of seeds produced by *E. distans* plants, and the reduce of W1N1 is more significant than W2N1 ($P < 0.01$, Fig. 6B).

DISCUSSION

Increased precipitation, nitrogen, and precipitation plus nitrogen prolonged the life cycle of both *N. micrantha* and *E. distans*, which allows plants to absorb water and nitrogen for a longer period of time and promoted vegetative growth (*Cleland et al., 2006*; *Sherry et al., 2007*; *Han et al., 2016*). Plant traits are external manifestations of plants and are easily affected by environmental factors (*Jones, 1985*). W2 significantly inhibited the root
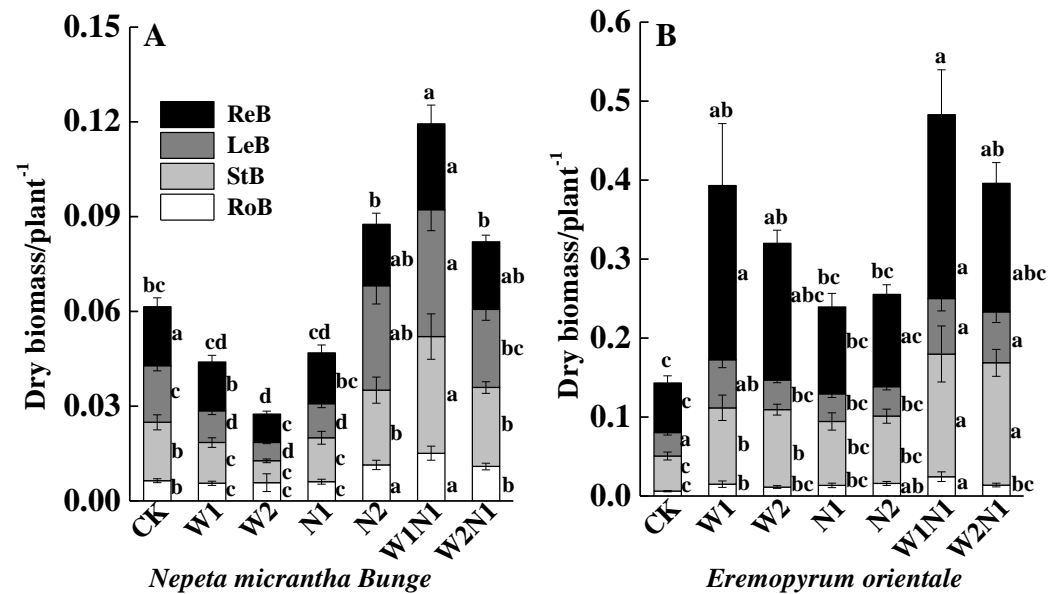
Figure 4 Effects of increased precipitation and nitrogen and precipitation plus nitrogen on dry mass accumulation (mean ± 1s.e) of *Nepeta micrantha* (A) and *Eremopyrum distans* (B). CK, control treatment; W1, increase 30% in precipitation; W2, increase 50% in precipitation; N1, increase 3 g nitrogen m^{-2} yr^{-1}; N2, increase 6 g nitrogen m^{-2} yr^{-1}; precipitation plus nitrogen: W1 + N1, W1N1; W2 + N1, W2N1. ReM, Reproduction mass; LeM, Leaf mass; StM, Stem mass; RoM, Root mass. Different lowercase letters indicate significant differences among increased precipitation and nitrogen and precipitation plus nitrogen treatments.

length of *N. micrantha* and *E. distans* compared to the control, this indicates that increased precipitation in the upper soil profile stimulated roots to stop growing into the deeper layers of soil. However, the relatively dry soil of the control promoted root growth into deeper soil. Studies on *Stipa bungeana* in the desertified grasslands of the Ordos Plateau in Inner Mongolia (China) also have found that root length corresponded to depth of water in the soil profile (*Cheng et al., 2006*). Thus, root is probably the sensitive organ to be affected by precipitation, and significant differences of plant traits in response to increased precipitation and nitrogen are most likely related to the roots (*Eviner & Chapin, 2003*; *Griffin-Nolan et al., 2018*). *E. distans* has a fibrous root system and a sand traps around the roots, it expanding the contact range between the root system and the soil (*Verma et al., 2005*), which are very beneficial for moisture-holding and nitrogen uptake (*Wang & Wang, 2009*). Thus, increased precipitation, nitrogen, and precipitation plus nitrogen significantly increased the height, leaf area, leaf number and seed number of *E. distans*. By contrast, *N. micrantha* has a taproot system consisting of a fixed main root and few lateral roots (*Ding et al., 2016*). Fibrous root systems are more efficient than taproot system at capturing mobile ions from spatially and temporally heterogeneous soils (*Dunbabin, Rengel & Diggle, 2004*). Therefore, most plant traits of *N. micrantha* showed no or negative response to increased precipitation. The reason is the loss of nitrogen caused by the increased precipitation. A previous study on soil nitrogen at the same field site also

Table 2 Pearson correlations among life history traits of Nepeta micrantha and *Eremopyum orientale*.

		He	Rl	Nl	Ns	La	Rom	Sm	Lm	Rem	Tm
	He	1									
	Rl	−.302*	1								
	Nl	0.097	.500**	1							
	Ns	0.217	.465**	.836**	1						
Nepeta	La	.255*	.349**	.881**	.890**	1					
micrantha	Rom	0.121	.529**	.769**	.858**	.808**	1				
	Sm	.368**	.336**	.850**	.889**	.929**	.784**	1			
	Lm	0.165	.279*	.790**	.778**	.882**	.736**	.850**	1		
	Rem	0.145	.255*	.545**	.683**	.605**	.588**	.611**	.583**	1	
	Tm	0.233	.331**	.757**	.857**	.834**	.767**	.853**	.810**	.928**	1
	He	1									
	Rl	0.015	1								
	Nl	.596**	0.182	1							
	Ns	.685**	.311**	.594**	1						
Eremopyum	La	.560**	.309**	.650**	.591**	1					
orientale	Rom	.489**	.360**	.614**	.604**	.623**	1				
	Sm	.703**	.308**	.798**	.765**	.762**	.772**	1			
	Lm	.525**	0.216	.842**	.550**	.812**	.737**	.850**	1		
	Rem	.667**	.342**	.625**	.884**	.699**	.638**	.860**	.667**	1	
	Tm	.663**	.317**	.821**	.763**	.817**	.829**	.970**	.925**	.873**	1

Notes.

He, height; Rl, root length; Nl, number of leaves; Ns, number of seeds; La, leaf area; Rom, root mass; Sm, stem mass; Lm, leaf mass; Rem, reproductive mass; Tm, total mass. N = 120.

*$P < 0.05$.

**$P < 0.01$.

found that increased nitrogen leaching in the rhizosphere under increased precipitation (*Huang et al., 2016*). For *E. distans*, increased nitrogen and precipitation plus nitrogen treatments significantly increased the height, leaf area, leaf number and seed number, which also supports the role played by the roots of *E. distans* in strong water uptake and soil fertility retention. Thus, roots probably determine the difference of plants in response to environmental changes. Future increased precipitation and nitrogen deposition are likely to promote the growth of fibrous root system species, but it have a negative impact on taproot system species.

Biomass is the primary manifestation of plant energy accumulation (*Eisenhauer & Scheu, 2008*; *Sherry et al., 2010*). A positive correlation between plant traits and biomass accumulation has been confirmed (*Lu et al., 2014*). In this study, the correlation analysis also revealed a positive correlation between plant traits and the total biomass accumulation of *N. micrantha* and *E. distans*, with the exception of the height of *E. distans*. The reason for the lack of correlation between the height and biomass accumulation is likely related to the growth characteristics of *E. distans*. We observed that plants of *E. distans* grow to a certain height (about 20 cm), and turn into growing branches (Y Chen, pers. obs., 2017), instead of increasing the height. Thus, the biomass accumulation of *E. distans* shows a nonsignificant correlation with the height. Our results also showed that the effect of N1 on
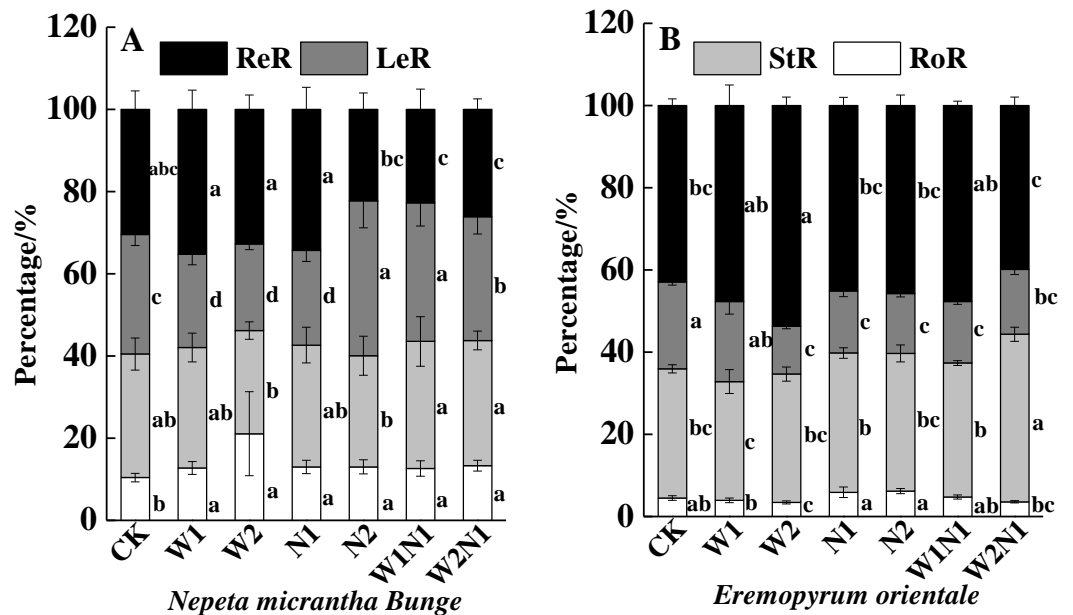
Figure 5 Effects of increased precipitation and nitrogen and precipitation plus nitrogen on biomass allocation (mean ± 1s.e) of *Nepeta micrantha* (A) and *Eremopyrum distans* (B). CK, control treatment; W1, increase 30% in precipitation; W2, increase 50% in precipitation; N1, increase 3 g nitrogen m^{-2} yr^{-1}; N2, increase 6 g nitrogen m^{-2} yr^{-1}; precipitation plus nitrogen: W1 + N1, W1N1; W2 + N1, W2N1. Different lowercase letters indicate significant differences among increased precipitation and nitrogen and precipitation plus nitrogen treatments.

the total biomass of *N. micrantha* is not significant, but N2 significantly increased the total biomass of *N. micrantha*. This is probably related to the nitrogen utilization percentage of *N. micrantha*. In the same study area, *Cui et al.*'s (*2017*) ^{15}N tracer experiment found that total nitrogen recovery percentage of herb was <10%, for one species, the nitrogen utilization percentage is much lower. Thus, we speculated that the amount of nitrogen (N1) was too less to be utilized by *N. micrantha*, and only when the amount of nitrogen (N2) reached a certain amount can promote plant growth. Therefore, our results indicate that future increased nitrogen deposition will not have a significant impact on plant growth of species levels in the short term, whereas this promotion will be more significant with enhancing nitrogen deposition.

The biomass allocation reflects the response of plant to the environment (*Sugiura, Kojima & Sakakibara, 2016*). With increased precipitation, the root and reproductive percentage of *N. micrantha* showed an increasing trend. The possible explanation is that plants allocated more biomass to the root to facilitate water and nutrient uptake and allocated more biomass to reproductive organs to maintain the population. Similar conclusions have been drawn about *Ceratocarpus arenarius* and *Erodium oxyrrhynchum* under drought stress (*Zhang, Sun & Tian, 2007*). By contrast, increased nitrogen improves the poor soil and provides nutrients for plant growth, hence, *N. micrantha* allocated more biomass to vegetative organs (stems and leaves), in order to maximize the light capture. For *E. distans*, increased
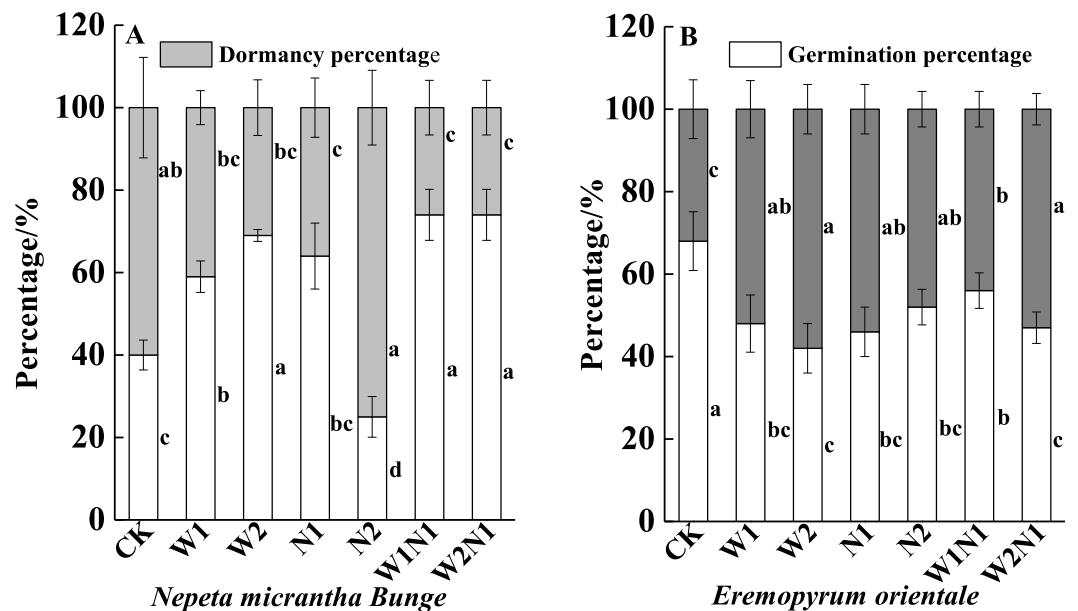
Figure 6 **Effects of increased precipitation and nitrogen and precipitation plus nitrogen on offspring (seeds)germination (mean ± 1s.e) of *Nepeta micrantha* (A) and *Eremopyrum distans* (B).** CK; W1, increase 30% in precipitation; W2, increase 50% in precipitation; N1, increase 3 g m^{-2} yr^{-1} in nitrogen; N2, increase 6 g m^{-2} yr^{-1} in nitrogen; precipitation plus nitrogen: W1N1, W1 + N1; W2N1, W2 + N1. Different lowercase letters indicate significant differences among increased precipitation and nitrogen and precipitation plus nitrogen treatments.

precipitation and nitrogen increased the total biomass accumulation, which is consistent with many species in the Gramineae, such as *Setarria viridis*, *Pennisetum centrasiaticum* (*Mao et al., 2016*), *Glyceria spiculosa* (*Chen et al., 2016*), and *Leymus chinensis* (*Yu, Yan & Jie, 2011*). Increased nitrogen reduced or eliminated the nitrogen limitation on the growth of *E. distans*, and it improved the light use efficiency, accelerated plant growth with sufficient precipitation, and then increased its dominance in the community (*Borer et al., 2014*; *Rajaniemi, 2002*). Therefore, in the context of climate change, increased nitrogen deposition is likely to promote plant growth, but different species showed a differential response to increased precipitation.

The seed stage is the most tolerant stage of life history to the environment, and dormancy is beneficial for allowing the seeds to germinate under suitable conditions (*Qu & Huang, 2005*). Previous research found that under appropriate environmental conditions, plants increased proportion of seeds remaining dormant but with high reproduction may prevent overcrowding during the following year (*Katja & Martina, 2010*; *Tielborger & Petru, 2010*). Our results showed that the number of *E. distans* seeds that remained dormant increased with increased precipitation and nitrogen. Thus, an increase in dormancy reduces not only the competition caused by siblings, but also the risk of population extinction via bethedging strategies (*Venable, 2007*), and this strategy has been a sensible practice throughout the course of evolution (*Evans et al., 2007*). However, we found that the number of *N. micrantha* seeds that remained dormant generally decreased with increased precipitation.

This finding is consistent with the conclusion that the maternal plants produced more non-dormant seeds when faced with environmental stress (*Huang et al., 2016*), and it provides a competitive advantage for the next generations. In addition, the decrease of W2N1 in the germination percentage of seeds produced by *E. distans* plants is more significant than W1N1. This is mainly related to increased precipitation improved the utilization percentage of nitrogen by herb (*Cui et al., 2017*), and showed an increase in the dormancy of offspring. Thus, the ability of plants to sense environmental changes can be passed on to the next generation by seed dormancy, which in turn affects population dynamics in the following year.

CONCLUSIONS

Ephemeral plants are a special group of plants that are extremely sensitive to environmental changes. Future increased precipitation and nitrogen deposition in the Gurbantunggut Desert may particularly affect the life history of ephemeral plants. *N. micrantha* and *E. distans* are two common ephemeral plants species in the study area. Most of the life history traits of these two species responded similarly to increased nitrogen and precipitation plus nitrogen but responded differently to increased precipitation. These differential responses are related primarily to species characteristics and the amount of precipitation and nitrogen in the experiment. In response to increased nitrogen and precipitation plus nitrogen, the *N. micrantha* and *E. distans* plants produced greater amounts of dormant seeds in conjunction high reproduction, which can also prevent overcrowding in the following year. However, the *N. micrantha* and *E. distans* plants produced more nondormant seeds in conjunction with increased precipitation, and these plants could occupy their habitat via the rapid seed germination in the future. Therefore, the differential responses of *N. micrantha* and *E. distans* to increased precipitation and nitrogen may affect their ecological niches in the community.

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The authors declare there are no competing interests.

Author Contributions

- Yanfeng Chen conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Lingwei Zhang and Xiang Shi performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, approved the final draft.
- Huiliang Liu and Daoyuan Zhang conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The raw measurements are provided in the Table S1 and Data S1.

Supplemental Information

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REFERENCES

Al-Solaimani SG, Alghabari F, Ihsan MZ, Fahad S. 2017. Water deficit irrigation and nitrogen response of Sudan grass under arid land drip irrigation conditions. *Irrigation and Drainage* **66**:365–376 DOI 10.1002/ird.2110.

Altenbach SB, Dupont FM, Kothari KM, Chan R, Johnson EL, Lieu D. 2003. Temperature, water and fertilizer influence the timing of key events during grain development in a US spring wheat. *Journal of Cereal Science* **37**:9–20 DOI 10.1006/jcrs.2002.0483.

Baez S, Fargione J, Moore DI, Collins SL, Gosz JR. 2007. Atmospheric nitrogen deposition in the northern Chihuahuan desert: temporal trends and potential consequences. *Journal of Arid Environments* **68**(4):640–651 DOI 10.1016/j.jaridenv.2006.06.011.

Bai YF, Wu JG, Xing Q, Pan QM, Huang JH, Yang DL, Han XG. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology* **89**:2140–2153 DOI 10.1890/07-0992.1.

Bardgett RD, Mommer L, De Vries FT. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* **29**(12):692–699 DOI 10.1016/j.tree.2014.10.006.

Barker DH, Vanier C, Naumburg E, Charlet TN, Nielsen KM, Newingham BA, Smith SD. 2006. Enhanced monsoon precipitation and nitrogen deposition affect leaf traits and photosynthesis differently in spring and summer in the desert shrub *Larrea tridentata*. *New Phytologist* **169**:799–808 DOI 10.1111/j.1469-8137.2006.01628.x.

Baskin CC, Baskin JM. 2014. *Seed: ecology, biogeography, and evolution of dormancy and germination*. San Diego: Elsevier/Academic Press.

Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Rödenbeck C, Arain MA, Baldocchi D, Bonan GB. 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* **329**:834–838 DOI 10.1126/science.1184984.

Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, Bustamante M, Cinderby S, Davidson E, Dentener F, Emmett B, Erisman JW, Fenn M, Gilliam F, Nordin A, Pardo L, De Vries W. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* **20**:30–59 DOI 10.1890/08-1140.1.

Borer ET, Seabloom EW, Gruner DS, Harpole WS, Hillebrand H, Lind EM, Adler PB, Alberti J, Anderson TM, Bakker JD. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**:517–520 DOI 10.1038/nature13144.

Cabaço S, Rui S. 2012. Seagrass reproductive effort as an ecological indicator of disturbance. *Ecological Indicators* **23**:116–122 DOI 10.1016/j.ecolind.2012.03.022.

Chen HM, Shi FX, Yang GS, Zhang XH, Mao R. 2016. Effects of nutrient addition on plant community composition and aboveground biomass in a marshy meadow in the Sanjiang Plain. *Chinese Journal of Ecology* **35**:1440–1446 DOI 10.13292/j.1000-4890.201606.010.

Cheng X, An S, Li B, Chen J, Lin G, Liu Y, Luo Y, Liu S. 2006. Summer rain pulse size and rainwater uptake by three dominant desert plants in a desertified grassland ecosystem in northwestern China. *Plant Ecology* **184**:1–12 DOI 10.1007/s11258-005-9047-6.

Cleland EE, Chiariello NR, Loarie SR, Mooney HA, Field CB. 2006. Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* **103**:13740–13744 DOI 10.1073/pnas.0600815103.

Cui XQ, Yue P, Gong YM, Li KH, Tan DY, Goulding K, Liu XJ. 2017. Impacts of water and nitrogen addition on nitrogen recovery in *Haloxylon ammodendron* dominated desert ecosystems. *Science of the Total Environment* **601**:1280–1288 DOI 10.1016/j.scitotenv.2017.05.202.

Diffenbaugh NS, Giorgi F, Pal JS. 2008. Climate change hotspots in the United States. *Geophysical Research Letters* **35**:375–402 DOI 10.1029/2008GL035075.

Ding J, Fan L, Li Y, Tang L. 2016. Biomass allocation and allometric relationships of six desert herbaceous plants in the Gurbantunggut Desert. *Journal of Desert Research* **36**:1323–1330.

Dube OP, Pickup G. 2001. Effects of rainfall variability and communal and semi-commercial grazing on land cover in southern African rangelands. *Climate Research* **17**:195–208 DOI 10.3354/cr017195.

Dunbabin V, Rengel Z, Diggle AJ. 2004. Simulating form and function of root systems: efficiency of nitrate uptake is dependent on root system architecture and the spatial and temporal variability of nitrate supply. *Functional Ecology* **18(2)**:204–211 DOI 10.1111/j.0269-8463.2004.00827.x.

Eisenhauer N, Scheu S. 2008. Invasibility of experimental grassland communities: the role of earthworms, plant functional group identity and seed size. *Oikos* **117**:1026–1036 DOI 10.1111/j.0030-1299.2008.16812.x.

Evans MEK, Ferriere R, Kane MJ, Venable DL. 2007. Bet hedging via seed banking in desert evening primroses (*Oenothera*, Onagraceae): demographic evidence from natural populations. *American Naturalist* **169**:184–194 DOI 10.1086/510599.

Eviner VT, Chapin FS. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology Evolution and Systematics* **34**:455–485 DOI 10.1146/annurev.ecolsys.34.011802.132342.

Frink CR, Waggoner PE, Ausubel JH. 1999. Nitrogen fertilizer: retrospect and prospect. *Proceedings of the National Academy of Sciences of the United States of America* **96**:1175–1180 DOI 10.1073/pnas.96.4.1175.

Fuertes-Mendizabal T, Setien I, Estavillo JM, Gonzalez-Moro MB. 2010. Late nitrogen fertilization affects carbohydrate mobilization in wheat. *Journal of Plant Nutrition and Soil Science* **173**:907–919 DOI 10.1002/jpln.200900262.

Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai ZC, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* **320**:889–892 DOI 10.1126/science.1136674.

Gebauer RL, Ehleringer JR. 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. *Ecology* **81**(**5**):1415–1424 DOI 10.2307/177218.

Griffin-Nolan RJ, Bushey JA, Carroll CJW, Challis A, Chieppa J, Garbowski M, Hoffman AM, Post AK, Slette IJ, Spitzer D. 2018. Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes. *Functional Ecology* **32**:1746–1756 DOI 10.1111/1365-2435.13135.

Hall SJ, Sponseller RA, Grimm NB, Huber D, Kaye JP, Clark C, Collins SL. 2011. Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. *Ecological Applications* **21**(**3**):640–660 DOI 10.1890/10-0758.1.

Han JJ, Li LH, Chu HS, Miao Y, Chen SP, Chen JQ. 2016. The effects of grazing and watering on ecosystem CO_2 fluxes vary by community phenology. *Environmental Research* **144**:64–71 DOI 10.1016/j.envres.2015.09.002.

Harpole WS, Potts DL, Suding KN. 2007. Ecosystem responses to water and nitrogen amendment in a California grassland. *Global Change Biology* **13**:2341–2348 DOI 10.1111/j.1365-2486.2007.01447.x.

Horn KJ, Nettles R, Clair SBS. 2015. Germination response to temperature and moisture to predict distributions of the invasive grass red brome and wildfire. *Biological Invasions* **17**(**6**):1849–1857 DOI 10.1007/s10530-015-0841-3.

Hsu JS, Powell J, Adler PB. 2012. Sensitivity of mean annual primary production to precipitation. *Global Change Biology* **18**:2246–2255 DOI 10.1111/j.1365-2486.2012.02687.x.

Huang G, Li CH, Li Y. 2018. Phenological responses to nitrogen and water addition are linked to plant growth patterns in a desert herbaceous community. *Ecology and Evolution* **8**:5139–5152 DOI 10.1002/ece3.4001.

Huang G, Su YG, Zhu L, Li Y. 2016. The role of spring ephemerals and soil microbes in soil nutrient retention in a temperate desert. *Plant and Soil* **406**:43–54 DOI 10.1007/s11104-016-2861-x.

Huang JJ, Zhang Q, Zhang S, Chen XH. 2017. Information entropy-based analysis of spatial and temporal variation in precipitation in Xinjiang. *Acta Ecologica Sinica* **37**:4444–4455.

Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* **141**:254–268 DOI 10.1007/s00442-004-1682-4.

Ji F, Ye W, Wei WS. 2000. Preliminary study on the formation causes of the fixed and semi-fixed dunes in Gurbantonggut Desert. *Arid Land Geography* **1**:32–36.

Jones M. 1985. *Modular demography and form in silver birch.* London: Academic Press.

Jordan N. 1996. Dynamics of weed populations. *Trends in Ecology & Evolution* **11(8)**:349–350.

Katja T, Martina P. 2010. An experimental test for effects of the maternal environment on delayed germination. *Journal of Ecology* **98**:1216–1223 DOI 10.1111/j.1365-2745.2010.01682.x.

Knapp AK, Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**:481–484 DOI 10.1126/science.291.5503.481.

Ladwig LM, Collins SL, Swann AL, Xia Y, Allen MF, Allen EB. 2012. Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *Oecologia* **169(1)**:177–185 DOI 10.1007/s00442-011-2173-z.

Li Y, Gu JL, Zhang P, Liu Y, Ma LY. 2010. Snow cover storage retrieval by remote sensing technology and variation analysis on the Junggar Basin. *Arid Land Geography* **33**:623–629.

Liu HF, Liu T, Han ZQ, Luo N, Liu ZC, Hao XR. 2018. Germination heterochrony in annual plants of Salsola L.: an effective survival strategy in changing environments. *Scientific Reports* **8**:6576 DOI 10.1038/s41598-018-23319-0.

Liu YX, Li X, Zhang Q, Guo YF, Gao G, Wang JP. 2010. Simulation of regional temperature and precipitation in the past 50 years and the next 30 years over China. *Quaternary International* **212**:57–63 DOI 10.1016/j.quaint.2009.01.007.

Liu X, Zhang Y, Han W, Tang A, Shen J, Cui Z, Vitousek P, Erisman JW, Goulding K, Christie P. 2013. Enhanced nitrogen deposition over China. *Nature* **494**:459–462 DOI 10.1038/nature11917.

Lloret F, Casanovas C, Penuelas J. 2010. Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. *Functional Ecology* **13**:210–216 DOI 10.1046/j.1365-2435.1999.00309.x.

Lu JJ, Tan DY, Baskin JM, Baskin CC. 2014. Germination season and watering regime, but not seed morph, affect life history traits in a cold desert diaspore-heteromorphic annual. *PLOS ONE* **9**:e102018 DOI 10.1371/journal.pone.0102018.

Lu JJ, Tan DY, Baskin CC, Baskin JM. 2016. Effects of germination season on life history traits and on transgenerational plasticity in seed dormancy in a cold desert annual. *Scientific Reports* **6**:25076 DOI 10.1038/srep25076.
Maberly SC. 2014. The fitness of the environments of air and water for photosynthesis, growth, reproduction and dispersal of photoautotrophs: an evolutionary and biogeochemical perspective. *Aquatic Botany* **118**:4–13 DOI 10.1016/j.aquabot.2014.06.014.

Mao W, Li Y, Sun D, Wang S. 2016. Aboveground biomass differentiations of different functional group species after nitrogen and snow addition altered community productivity of sandy grassland. *Journal of Desert Research* **36**:27–33.

McHugh TA, Morrissey EM, Mueller RC, Gallegos-Graves LV, Kuske CR, Reed SC. 2017. Bacterial, fungal, and plant communities exhibit no biomass or compositional response to two years of simulated nitrogen deposition in a semiarid grassland. *Environmental Microbiology* **19**:1600–1611 DOI 10.1111/1462-2920.13678.

Ogle K, Reynolds JF. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia* **141**:282–294 DOI 10.1007/s00442-004-1507-5.

Paz H, Pinedagarcía F, Pinzónpérez LF. 2015. Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia* **179**:551–561 DOI 10.1007/s00442-015-3359-6.

Qu X, Huang Z. 2005. The adaptive strategies of halophyte seed germination. *Acta Ecologica Sinica* **25**:2389–2398.

Rajaniemi TK. 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *Journal of Ecology* **90**:316–324 DOI 10.1046/j.1365-2745.2001.00662.x.

Shemtov S, Gutterman Y. 2003. Influence of water regime and photoperiod treatments on resource allocation and reproductive successes of two annuals occurring in the Negev Desert of Israel. *Journal of Arid Environments* **55**:123–142 DOI 10.1016/S0140-1963(02)00255-0.

Shen W, Reynolds JF, Hui D. 2010. Responses of dryland soil respiration and soil carbon pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature, precipitation, and atmospheric: a simulation analysis. *Global Change Biology* **15**:2274–2294 DOI 10.1111/j.1365-2486.2009.01857.x.

Sherry RA, Weng E, Arnone Iii JA, Johnson DW, Schimel DS, Verburg PS, Wallace LL, Luo Y. 2010. Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology* **14**:2923–2936 DOI 10.1111/j.1365-2486.2008.01703.x.

Sherry RA, Zhou XH, Gu SL, Arnone JA, Schimel DS, Verburg PS, Wallace LL, Luo YQ. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America* **104**:198–202 DOI 10.1073/pnas.0605642104.

Simkin SM, Allen EB, Bowman WD, Clark CM, Belnap J, Brooks ML, Cade BS, Collins SL, Geiser LH, Gilliam FS, Jovan SE, Pardo LH, Schulz BK, Stevens CJ, Suding KN, Throop HL, Waller DM. 2016. Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences of the United States of America* **113**:4086–4091 DOI 10.1073/pnas.1515241113.

Stocker TF, Qin D, Plattner GK, Alexander LV, Allen SK, Bindoff NL, Bréon FM, Church JA, Cubasch U, Emori S. 2013. Technical summary. In: Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. *Computational Geometry* **18**:95–123.

Sugiura D, Kojima M, Sakakibara H. 2016. Phytohormonal regulation of biomass allocation and morphological and physiological traits of leaves in response to environmental changes in *Polygonum cuspidatum. Frontiers in Plant Science* **7**:Article 1189 DOI 10.3389/fpls.2016.01189.

Tielborger K, Petru M. 2010. An experimental test for effects of the maternal environment on delayed germination. *Journal of Ecology* **98**:1216–1223 DOI 10.1111/j.1365-2745.2010.01682.x.

Venable DL. 2007. Bet hedging in a guild of desert annuals. *Ecology* **88**:1086–1090 DOI 10.1890/06-1495.

Verma V, Worland AJ, Sayers EJ, Fish L, Caligari PDS, Snape JW. 2005. Identification and characterization of quantitative trait loci related to lodging resistance and associated traits in bread wheat. *Plant Breeding* **124**:234–241 DOI 10.1111/j.1439-0523.2005.01070.x.

Wang B, Huang G, Ma J, Li Y. 2016a. Responses of nutrients resorption of five desert ephemeral plants to water and nitrogen additions. *Journal of Desert Research* **36**:415–422.

Wang X, Jiang J, Lei J, Zhang W, Qian Y. 2003. The distribution of ephemeral vegetation on the longitudinal dune surface and its stabilization significance in the Gurbantunggut Desert. *Acta Geographica Sinica* **58**:598–605.

Wang X, Jiang J, Lei J, Zhao C. 2004. Relationship between ephemeral plants distribution and soil moisture on longitudinal dune surface in Gurbantonggut desert. *Chinese Journal of Applied Ecology* **15**:556–560.

Wang J, Luo P, Yang H, Mou CX, Mo L. 2016b. Different responses of alpine plants to nitrogen addition: effects on plant-plant interactions. *Scientific Reports* **6**:38320 DOI 10.1038/srep38320.

Wang AB, Tan DY, Baskin CC, Baskin JM. 2010. Effect of seed position in spikelet on life history of *Eremopyrum distans* (Poaceae) from the cold desert of north-west China. *Annals of Botany* **106**:95–105 DOI 10.1093/aob/mcq089.

Wang J, Wang K. 2009. A review: the ecological function and forming mechanism of rhizosheath. *Grassland & Turf* **133**:88–92.

Wei S. 2015. Characteristics of chemical composition and deposition fluxes of atmospheric particles and reactive nitrogen in typical ecosystems of Xinjiang, China. PhD. Thesis, University of Chinese Academy of Sciences.

Xu W, Luo XS, Pan YP, Zhang L, Tang AH, Shen JL, Zhang Y, Li KH, Wu QH, Yang DW. 2015. Quantifying atmospheric nitrogen deposition through a nationwide monitoring network across China. *Atmospheric Chemistry & Physics Discussions* **15**:18365–18405 DOI 10.5194/acpd-15-18365-2015.

Xu XT, Liu HY, Wang W, Song ZL. 2018. Patterns and determinants of the response of plant biomass to addition of nitrogen in semi-arid and alpine grasslands of China. *Journal of Arid Environments* **153**:11–17 DOI 10.1016/j.jaridenv.2018.01.002.

Yu QI, Yan HY, Jie Z. 2011. Biomass and its allocation of four grassland species under different nitrogen levels. *Acta Ecologica Sinica* **38**:5121–5129.

Yuan SF, Tang HP. 2010. Patterns of ephemeral plant communities and their adaptations to temperature and precipitation regimes in Dzungaria Desert, Xinjiang. *Biodiversity Science* **18**:346–354 DOI 10.3724/SP.J.1003.2010.346.

Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, Field CB, Mooney HA. 2003. Grassland responses to three years of elevated temperature, CO(2), precipitation, and N deposition. *Ecological Monographs* **73**:585–604 DOI 10.1890/02-4053.

Zhang HZ, Khan A, Tan DKY, Luo HH. 2017. Rational water and nitrogen management improves root growth, increases yield and maintains water use efficiency of cotton under mulch drip irrigation. *Frontiers in Plant Science* **8**:Article 912 DOI 10.3389/fpls.2017.00912.

Zhang H, Wang XP, Zhang YF, Hu R, Pan YX, Chen N. 2015. Responses of plant growth of different life forms to rainfall amount changes in an arid desert area. *Chinese Journal of Ecology* **34**:1847–1853 DOI 10.13292/j.1000-4890.20150615.013.

Zhang T, Sun Y, Tian CY. 2007. Ecological and biological differences between spring and autumn plants of two desert ephemerals. *Journal of Plant Ecology* **31**:1174–1180 DOI 10.17521/cjpe.2007.0146.

Zheng YR, Xie ZX, Yu Y, Jiang LH, Shimizu H, Rimmington GM. 2005. Effects of burial in sand and water supply regime on seedling emergence of six species. *Annals of Botany* **95**:1237–1245 DOI 10.1093/aob/mci138.

Zhou BJ, Zhou HF, Dai Q. 2009. Experimental study of the snow evaporation in desert and oases of Junggar Basin, Xinjiang. *Journal of Glaciology & Geocryology* **31**:843–849.

Zhou XB, Zhang YM, Ji XH, Downing A, Serpe M. 2011. Combined effects of nitrogen deposition and water stress on growth and physiological responses of two annual desert plants in northwestern China. *Environmental and Experimental Botany* **74**:1–8 DOI 10.1016/j.envexpbot.2010.12.005.