Direct and indirect effects of precipitation change and nutrients addition on desert steppe productivity in Inner Mongolia, northern China

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Abstract

Background and Aims Global changes (precipitation changes and nutrient deposition) profoundly impact structure and function of steppe ecosystem. However, it is unclear the mechanism by which multiple limiting resources affect plant aboveground net primary productivity (ANPP) in desert steppe.

Methods We conducted a field experiment manipulating both precipitation (3 levels: ambient and ±50% precipitation) and nutrients addition (3 levels: ambient; nitrogen (N) addition; N/phosphorus (P)/potassium (K) addition) in a factorial design. We focused on the effects of these treatments on species diversity (species richness, Shannon index, abundance), ANPP, plant functional traits, and soil properties. We used structural equation model (SEM) to evaluate the...
direct and indirect effects of precipitation amount and nutrient addition on ANPP through affecting species diversity and functional traits.

**Results** Increasing precipitation increased species diversity and ANPP. NPK addition and increased 50% precipitation significantly increased ANPP over all other treatment combinations. Drought (-50%) reduced plant height and leaf dry matter content (LDMC), but increased leaf nitrogen content (LNC). Species richness, abundance, height and LDMC were positively correlated with ANPP, while specific leaf area (SLA) and LNC were negatively correlated with ANPP. SEM suggested that precipitation amount indirectly affected ANPP through its effect on abundance and SLA, while nutrient addition indirectly affected ANPP only through its effect on abundance.

**Conclusion** In desert steppe, the interaction of precipitation and nutrient addition had a significant positive effect on ANPP, which was mainly mediated by species diversity and functional traits. Our results highlight the importance of species diversity and functional traits in driving short-term responses of ANPP to environmental factors in desert steppe ecosystems.

**Keywords** Multiple limiting resources · aboveground net primary productivity · Species diversity · community-level functional traits · Structural equation model

Human activities and climate change have greatly affected global precipitation patterns and biogeochemical cycles, including the nitrogen (N), phosphorus (P), and potassium (K) cycles. These global change drivers (especially precipitation and N deposition) have significantly impacted plant productivity, species diversity, functional traits and soil properties of steppe ecosystem (Chen et al. 2013; Hooper and Johnson 1999). In particular, arid and semi-arid steppes may be particularly susceptible to changes in soil nutrient (Avolio et al. 2014; Fay et al. 2015), besides being frequently limited by precipitation (Luo et al. 2019). It is crucial to study the effects of precipitation and nutrient addition on the structure and function of desert steppe ecosystem, which can provide theoretical basis for dynamic prediction and management of arid and semi-arid steppes under global change. However, there is still a lack of research on the responses of plant and soil characteristics, and especially the mechanisms affecting productivity under different resource limitation alleviation in desert steppe.

Aboveground net primary productivity (ANPP) is a key basic indicator to measure production function of arid and semi-arid steppes (Foley 1994; Gower et al. 1999), and it is mainly controlled by precipitation in arid and semi-arid ecosystems (Lu et al. 2018b; Wilcox et al. 2016). There is important evidence that extreme precipitation events (both droughts and extreme extra-precipitation) are occurring more frequently in arid and semi-arid areas of northern China (Kim et al. 2020; Luo et al. 2019; Naumann et al. 2018). Many studies have shown that steppe ANPP is positively correlated with precipitation (Bin et al. 2014; DeMalach et al. 2017). However, in barren steppes (those where both available nutrients content to plants in the soil and the vegetation coverage are low), low baseline nutrient levels in soils cannot support high productivity when water limitation is alleviated (Gao et al. 2013; Knapp et al. 2017). Further work is needed to explore the interaction of precipitation and nutrient input on the productivity of steppe ecosystems. Furthermore, the accumulation of reactive N anthropogenically altered may lead to the scarcity and limitation of P and K in soil, altering plant community composition and ANPP in arid and semi-arid steppe ecosystems (Cleland and Harpole 2010a; Fowler et al. 2013; Galloway et al. 2008). Phosphorus (P) and K are important nutrient elements that affect the energy metabolism and resistance of plants (Albornoz et al. 2020; Vitousek et al. 2010). Previous studies have shown that N availability was generally limited by water and available P content in soil (Elser et al. 2007). The synergistic interactions between multiple limiting resources has been widely reported in steppe ecosystem (Harpole et al. 2011). One of the most common synergies is co-limitation (i.e., a simultaneous response to combined additions of two or more factors, or an independent response to each of them, Marleau et al. 2015). For example, a meta-analysis of fertilization experiments in arid and semi-arid ecosystems found that ANPP was co-limited by both water and N, namely ANPP was significantly higher when water and nitrogen were added together than when water or N were added alone (Hooper and Johnson 1999). In addition, serial limitation (i.e.,
a synergistic response to a second resource occurs unless a primary resource has also been added first) is another type of synergy, which emphasizes the order of action of different limiting resources (Cardinale et al. 2009; Harpole et al. 2011). However, there is few studies on how multiple resources synergistically affect ANPP in desert steppe. This study attempted to further explore the mechanisms and pathways of the effects of various resources on ANPP in desert steppe through the interaction experiment of water and multiple nutrient addition.

Species diversity reflects community vegetation characteristics and distribution dynamics, and is an important determinant affecting steppe ecosystem function (Hooper et al. 2005). Species planted and weeded experiments showed that species diversity was positively correlated with ANPP (Tilman et al. 1997). The diversity hypothesis explains this by proposing that greater species diversity provides more functional strategies and complementary resource use to increase ANPP (Diaz and Cabido 2001). The relationship between species diversity and ANPP under multiple nutrient limitations has also been a hot topic of discussion among ecologists (Grace et al. 2014; Harpole et al. 2017; Pither et al. 2016). Most studies suggested that resource enhancement reduces species diversity but increased ANPP (Isbell et al. 2013; Siddique et al. 2010; Soons et al. 2017; Suding et al. 2005). But some evidence showed that nutrients addition increased species diversity in the resource-poor steppe communities (Bai et al. 2010). Further studies are needed on the effect of species diversity on productivity under multiple resource-limited changes in resource-poor desert steppe.

Both species diversity and plant functional traits are increasingly being important parameters in the structural equation model (SEM) construction of ANPP and limiting resources change (Forrestel et al. 2017; Ladwig et al. 2012; Lavorel and Garnier 2002). Community weighted-means (CWM) of function traits are the adaptation characteristic of internal physiology and external form formed by plants in response to environmental change (Butterfield and Suding 2013; Ma et al. 2019). Under limited resource changes, different plants exhibit different functional strategies that change community composition and ANPP (Cleland and Harpole 2010b). In addition, the mass ratio hypothesis provided the basis for the influence mechanism of CWM of functional traits on ANPP, that is, the community function overwhelmingly determined by the functional traits of dominant species with higher biomass in the community (Grime 1998). Most scholars deemed that light acquisition traits (such as plant height and specific leaf area (SLA)) enhanced plant light acquisition ability to effect steppe community ANPP with precipitation and N addition (Zhan et al. 2019; Zhang et al. 2020). Nutrient acquisition traits, such as leaf nitrogen content (LNC), increased with drought and N application (Lu et al. 2018a). The change of the proportion of high LNC plants in community can further change plant community structure and soil N content, thus affecting ANPP (Craine et al. 2002). However, it remains unclear the pathway and mechanism of ANPP changes driven by functional traits under multiple limiting resource changes in desert steppe.

The Urat desert steppe is located in a marginal zone of the semi-arid and arid area of northwest Inner Mongolia in China and is a xerophytic steppe ecosystem transiting from steppe to desert (Luo et al. 2020; Zhang et al. 2019). This desert steppe ecosystem is very fragile due to climate fluctuations and a barren habitat (Luo et al. 2018). Previous studies in desert steppes have reported that ANPP is associated with inter-annual and N addition interactions, while species richness is only affected by inter-annual rainfall changes and has no significant response to N addition (Ladwig et al. 2012). Previous studies in the Urat steppe mainly focused on the response of the steppe ecosystem to precipitation changes (Luo et al. 2018). Compared with grassland, the N content of plant canopy in the Urat desert steppe was less sensitive to drought (Luo et al. 2019). The carbon sequestration capacity of the desert steppe ecosystem enhanced by increased precipitation (Zhang et al. 2019). Little is known the effects of water and multiple nutrients coupling on the structure and function of plant community in the desert steppe.

In this study, we asked the following questions: (1) How do species diversity, functional traits and soil properties respond to precipitation manipulation and nutrient addition in desert steppe? (2) Which indicators of vegetation and soil systems can drive variation in ANPP?
Materials and methods

Site description

The experimental site is located in the central part of Urad Rear Banner, Inner Mongolia, China (41°25′ N, 106°58′ E, 1650 m a.s.l.) (Du et al. 2019). This area has a continental arid climate with mean annual temperature of 5.3 °C and mean annual precipitation of 142 mm (falling mainly in July and August, accounting for about 70% of total precipitation). Over the past 38 years, extreme precipitation events (the annual precipitation is more than 231 mm (150% of the mean annual precipitation) or less than 71 mm (50% of the mean annual precipitation)) have occurred 18.4% of the time in the area (Fig. S1). The vegetation in this region is mainly desert shrub lands and desert steppes (Zhang et al. 2019). The soil is mainly grey brown desert soil and brown calcium brown soil according to the Chinese soil taxonomy system (Yang et al. 2007). The sampling site is placed in the *Stipa glareosa* community of the Urad Desert Steppe Research Station of Chinese Academy of Sciences. The *Stipa glareosa* community is dominated by perennial species including *Stipa glareosa*, *Allium polyrhizum* and *Peganum harmala*. Several subordinate plant species in the community include *Allium mongolicum*, *Corispermum hyssopifolium*, *Salsola collina*, *Bassia dasyphylla*, *Asparagus gobicus* and *Artemisia frigida*.

Experimental design

We designed the experiment in homogeneous ~1000 m² vegetation patch in 2018. Within this patch we manipulated two drivers of global change, (1) precipitation and (2) nutrient deposition. Precipitation treatments included an extreme drought treatment (precipitation decreased by 50% (-50%)), an ambient precipitation treatment (W0) and a water addition treatment (precipitation increased by 50% (+50%)). The annual precipitation in 2019 was 207 mm, the three levels precipitation were 103.5 mm (-50%), 207 mm (W0) and 310.5 mm (+50%) respectively. The nutrient treatment consisted of 3 levels, a no-nutrients addition (N0), a 10·g·m⁻²·yr⁻¹ N addition (+N) (it is a rate that overcomes local N limitation and most steppe systems without being toxic) and a treatment with N/P/K additions (+NPK) (N, P and K were added 10 g·m⁻²·yr⁻¹, respectively). The experiment followed a factorial complete randomized block design with two factors (precipitation amount and nutrient addition). Six block respectively consisted of 54 experimental plots (6 m × 6 m). Between each plot, a 2 m buffer strip was set to avoid interference among plots (Zhan et al. 2019).

We monitored rainfall during the growing season through a weather station set up in the experimental station in 2019. Based on such actual rainfall data, the amount of ambient precipitation was calculated on each plot per week. We added groundwater equal to 50% of the ambient precipitation amount using sprinkling cans in increased-precipitation treatment plot every week from April to August. Similarly, the decreased-precipitation treatment consisted of reducing precipitation 50% with respect to ambient precipitation by using a strip-grooved flashing board rain-shelter arranged at equal intervals at the top of the canopy (Fig. S2) (Yue et al. 2019). The board panels were made of high-light transmittance polycarbonate, which allows penetration of nearly 90% effective light radiation. Each plot was separated from each other with a metal partition (1 m deep) covered with plastic film to reduce lateral water flows. We applied fertilizer at the beginning of May each year (Borer et al. 2014). Fertilizer was added as coated urea for N (pure N content of 44%), heavy calcium superphosphate for P (P₂O₅ content 40%, including 17% pure P), and potassium sulfate for K (K₂O content 50%, pure K content of 40%).

Sampling and measurement

During peak biomass in early August 2019, we measured plant species richness in one 100 cm × 100 cm quadrat randomly positioned on each plot. The vegetative stand height of each plant species within each quadrat was measured with a tape. After these measurements, above-ground biomass on each sampling quadrat was harvested and sorted by species. Harvested material was oven-dried at 65°C for 48 h to a constant weight and weighed separately per plant species (Zhao et al. 2016).

Mature leaves of dominant species (those which represented over 90% of the total cumulative plant cover per plot) were collected for determination of leaf functional traits (Cornelissen et al. 2003; Luo et al. 2019). The collected leaves were soaked in deionized water at 4°C for 6 h to obtain rehydrated...
leaves (Perez-Harguindeguy et al. 2013). Then, the
surface water was blotted dry before scanning the
leaves. These were first SLA (the one-sided area of
a fresh leaf divided by its oven-dry mass) measured
by scanning fully unfolded fresh leaves on a scanner
(Epson perfection v330 photo, Japan) and the scanned
area then calculated with WinFOLIA software
(Regent Instruments 2016b Pro, Canada). Secondly,
leaf dry matter content (LDMC, the ration between
leaf dry weight and leaf saturated fresh weight) was
also determined. Leaf thickness (LT) was measured
with a vernier caliper (DL91150, China). The car-on and N contents of leaves (LCC and LNC) were
determined with an elemental analyzer (Costech ECS
4010, Italy).

After removing surface debris, three randomly
selected soil cores (0–10 cm depth) were collected
within each plot using a soil auger (3 cm-diameter).
The three cores were evenly pooled, litter and pebbles
were removed; and the pooled sample was divided
into two parts (Zuo et al. 2016). The first part was air-
dried and sieved (pore diameter 2 mm) and used for
measuring soil pH and electrical conductivity (EC)
(measured in a 1:5 soil–water supernatant mix with
a probe) (Multiline F/SET-3, Germany). Soil C and
N contents were assayed in this soil sample part too
by elemental analysis (Zuo et al. 2016). The other
soil sample part was used to quantify gravimetric soil
moisture content (Luo et al. 2018). Soil bulk density
was obtained by drying additional soil samples col-
cected with a ring knife (a 100 cm³) in an oven at
105°C for 48 h.

Statistical analysis

We analyzed vegetation characteristics (species rich-
ness, Shannon index, abundance, ANPP), plant func-
tional traits (height, SLA, LDMC, LNC, LCC, LT),
and soil properties (pH, EC, soil moisture content,
soil bulk density, soil C and N contents) of the desert
steppe community under different water and nutri-
tent treatments. We calculated the Shannon–Wiener
diversity index (H) as: \( H = - \sum N_i \ln N_i \), where \( N_i \)
is the relative ecological importance value of species
(i.e., (relative height + relative cover + relative bio-
mass)/3) (Luo et al. 2019). Weighted-mean values of
community-level functional traits (CWM) were cal-
culated using the relative biomass of species as the
weighting factor (Leps et al. 2011, Lu et al. 2018a).

Simple correlation analysis was used to study the
relationship between ANPP, species diversity, plant
functional traits and soil properties. To investigate the
influence paths of precipitation amount and nutrient
addition on ANPP, we constructed an initial structural
equation model (SEM) based on regression regres-
sis and previous experience (Fig. S3). In the initial
conceptual model, precipitation amount and nutrient
addition were treated as exogenous variables (pre-
cipitation amount are represented by 1, 2 and 3 as
-50%, W0 and +50%, respectively; nutrient addition
are represented by 0, 1 and 3 as N0, +N and +NPK
respectively). Species diversity (Species richness,
Abundance) and plant functional traits (CWM.height,
CWM.LDMC, CWM.SLA, CWM.LNC) were con-
sidered as endogenous variables. ANPP was regarded
as a response variable. By removing non-significant
pathways (\( p > 0.05 \)) and related variables, we finally
obtained a model with the lowest AIC value, Chi-
square test (\( p > 0.05 \)), root mean square error of
approximation (RMSEA < 0.05) and goodness-of-fit
index (GFI > 0.95) (Zuo et al. 2016).

A mixed-effect model was used to analyze the
response of each variable to treatment, in which pre-
cipitation amount and nutrient addition were fixed
factors and block was a random factor. Community
traits differences between water and nutrient treat-
ments were compared by using two—way ANOVAs,
with Duncan’s test performing multiple compari-
sions when ANOVA tests were considered significant
(\( p < 0.05 \)). The functional diversity were calculated
with FDiversity software (Casanoves et al. 2011).
SPSS22 and AMOS25.0 were used for ANOVA and
SEM, respectively. SigmaPlot12.5 software and the
basic Trendline package in R were used for drawing.
All data are presented as mean ± 1 SE (\( n = 6 \)).

Results

Species diversity had a significant response to precip-
itation amount (\( p < 0.05 \)), but not to nutrient addition
(\( p > 0.05 \), Table 1). Species richness, abundance and
Shannon diversity index were significantly increased
under the treatment of increased 50% precipita-
tion (P+50%), especially with NPK addition (Table 2,
Fig. 1a-c). The interaction between precipitation and
nutrient addition had a marginally positive effect on
the Shannon diversity index (\( p = 0.077 \), Table 1).
Specifically, under water addition condition, there were significant differences in Shannon diversity index under different nutrient addition treatments ($p < 0.05$, Fig. 1b).

Higher precipitation increased standing biomass overall ($p < 0.001$, Table 1, Fig. 1d). The ANPP under ambient ($P_{W0}$) and $P_{+50\%}$ increased by 70.7% and 255.6% in comparison to the treatment of decreased 50% ($P_{-50\%}$) respectively (Table 2). The ANPP under NPK addition was significantly higher than that of ambient nutrients ($N0$) and nitrogen addition ($p < 0.01$, Tables 1 and 2). Precipitation amount and nutrient addition significantly interacted to affect ANPP ($p < 0.05$, Table 1), with positive effects of NPK addition occurring under $P_{+50\%}$ (Fig. 1d). This resulted mainly because of the strong positive response of ANPP to NPK addition, but only under $P_{+50\%}$ (Fig. 1d); whereas the response in the other precipitation treatments was null or without a clear pattern. Compared with the interaction of $P_{W0}$ and $N0$, the increment of ANPP under the interaction of $P_{+50\%}$ and NPK addition (71.2 g·m$^{-2}$) is higher than the sum of increment (37.1 g·m$^{-2}$) under the interaction of $P_{+50\%}$ and $N0$ (28.4 g·m$^{-2}$), and the interaction of $P_{W0}$ and NPK addition (8.7 g·m$^{-2}$).

Precipitation amount significantly affected the CWM of height, LDMMC, LCC, and LNC ($p < 0.01$, Table 1). In this way, compared with $P_{W0}$, CWM of height, LDMMC, and LCC significantly decreased, under $P_{+50\%}$; but CWM of LNC significantly increased under $P_{-50\%}$ (Table 2, Fig. 2a-e-f). Compared with $N0$, CWM of LNC significantly increased with $N$ and NPK additions (Tables 1 and 2, Fig. 2f). The CWM of SLA and LT had no significant response to precipitation amount and nutrient addition ($p > 0.05$, Table 1).

Soil pH and moisture content had significant responses to precipitation amount ($p < 0.01$, Table 1). Soil pH was increased significantly under $P_{+50\%}$. On the other hand, soil moisture content significantly decreased under $P_{-50\%}$ (Table 2, Fig. 3a-c). Addition of NPK significantly reduced soil pH and enhanced soil EC (Table 2, Fig. 3a-b). None of the treatments did have an effect on soil bulk density, C and N contents ($p > 0.05$, Table 1, Fig. 3d-f).

Species richness, abundance, CWM of height and LDMMC were positively correlated with ANPP, but CWM of SLA and LNC were negatively correlated with ANPP ($p < 0.05$, Fig. 4). No significant correlation was found between soil properties and ANPP (Fig. S4). Our structural equation model (SEM) ($\chi^2 = 0.367$, d. f. = 3, $p = 0.947$, RMSEA = 0.000, GFI = 0.997) fitted the variance best and explained 70% of the variance in ANPP (Fig. 5). The SEM showed that both precipitation amount and nutrient addition had direct and indirect effects on ANPP. Specifically, nutrient addition indirectly affected ANPP through a weak positive effect on abundance. Accordingly, increased precipitation indirectly positively affected ANPP by increasing abundance and regulating SLA (Table 3, Fig. 5).

**Discussion**

We used an experiment manipulating precipitation and nutrient availability to understand the effects of these global change factors on plant community structure, function and soil properties in the desert steppe. We also aimed to explore how precipitation
Table 2: Community vegetation characteristics and soil physical and chemical properties among different precipitation or nutrient treatments (Mean ± SE)

|                      | Precipitation       | Nutrient       |
|----------------------|---------------------|----------------|
|                      | -50%                | W0             | + 50% | N0   | + N  | + NPK |
| Species richness     | 7.39 ± 0.43b        | 7.72 ± 0.36b   | 9.28 ± 0.4a | 8.28 ± 0.43 | 7.67 ± 0.44 | 8.44 ± 0.45 |
| Shannon diversity    | 1.81 ± 0.06b        | 1.79 ± 0.04b   | 1.97 ± 0.04a | 1.86 ± 0.05 | 1.82 ± 0.06 | 1.89 ± 0.05 |
| Abundance            | 60.56 ± 3.39b       | 73.72 ± 5.86b  | 103.78 ± 9.86a | 70.28 ± 6 | 79.61 ± 7.28 | 88.17 ± 10.11 |
| ANPP                 | 18.22 ± 2.29c       | 31.1 ± 2.98b   | 64.79 ± 8.26a | 30 ± 5.7b | 33.22 ± 3.69b | 50.89 ± 9.46a |
| CWM.height           | 8.87 ± 0.45b        | 11.11 ± 0.45a  | 11.76 ± 0.57a | 10.23 ± 0.67 | 10.49 ± 0.59 | 11.02 ± 0.41 |
| CWM.LDMC             | 234.23 ± 7.74b      | 321.73 ± 18.85a | 306.52 ± 16.47a | 298.34 ± 18.96 | 297.06 ± 19.51 | 267.08 ± 12.92 |
| CWM.SLA              | 13.78 ± 0.43        | 13.04 ± 0.46   | 12.45 ± 0.6   | 13.04 ± 0.58 | 12.88 ± 0.38 | 13.35 ± 0.57 |
| CWM.LT               | 0.72 ± 0.03         | 0.63 ± 0.05    | 0.63 ± 0.03   | 0.63 ± 0.02 | 0.67 ± 0.05 | 0.69 ± 0.03 |
| CWM.LCC              | 402.81 ± 3.65c      | 426.94 ± 4.12a | 415.46 ± 3.13b | 417.08 ± 4.17 | 415.14 ± 5.25 | 412.98 ± 3.44 |
| CWM.LNC              | 33.84 ± 0.89a       | 29.57 ± 1.12b  | 28.44 ± 0.92b | 27.9 ± 0.99b | 31.37 ± 1.23a | 32.57 ± 0.82a |
| Soil pH              | 8.81 ± 0.06b        | 8.83 ± 0.05b   | 9 ± 0.04a     | 9.01 ± 0.03a | 8.94 ± 0.03a | 8.68 ± 0.06b |
| Soil moisture content| 3.76 ± 0.32b        | 5.34 ± 0.39a   | 5.27 ± 0.31a  | 4.94 ± 0.33 | 4.66 ± 0.44 | 4.77 ± 0.38 |
| Soil bulk density    | 158.77 ± 2.23       | 161.21 ± 1.92  | 159.82 ± 2.64 | 158.48 ± 2.58 | 162.71 ± 1.68 | 158.61 ± 2.38 |
| Soil carbon content  | 6.69 ± 0.33         | 6.71 ± 0.41    | 6.38 ± 0.29   | 6.81 ± 0.33 | 6.66 ± 0.33 | 6.3 ± 0.37 |
| Soil nitrogen content| 0.43 ± 0.02         | 0.47 ± 0.06    | 0.37 ± 0.01   | 0.39 ± 0.01 | 0.42 ± 0.03 | 0.46 ± 0.06 |

CWM, community weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LT, leaf thickness; LCC, leaf carbon content; LNC, leaf nitrogen content; EC: electrical conductivity. Different lowercase letters indicate significant differences among precipitation change or nutrient addition treatments at \( p < 0.05 \) level.

Fig. 1: Response of community vegetation characteristics (species richness (a), Shannon diversity (b), abundance (c), and ANPP (d)) to precipitation change and nutrient addition. Water treatments: W0: ambient precipitation; +50%: increased precipitation by 50%; -50%: decreased precipitation by 50%. Nutrient treatments: N0: 0 g·m\(^{-2}\)·yr\(^{-1}\); +N: N 10 g·m\(^{-2}\)·yr\(^{-1}\); +NPK: N/P/K each for 10 g·m\(^{-2}\)·yr\(^{-1}\). ANPP, aboveground net primary productivity. Lowercase letters indicate the difference between different water treatments under the same nutrient addition. An asterisk (*) indicates significant differences between different nutrient addition treatment under same water condition (\( p < 0.05 \)). Error bars ± 1SE.
and nutrient availability affect ANPP, both directly or indirectly through their effect on species diversity, plant functional traits and soil properties. Species diversity (species richness, Shannon diversity index, abundance) increased under water addition (Table 2). Most studies shown that species diversity was positively correlated with precipitation (Sternberg et al. 1999; White et al. 2014; Yang et al. 2011), but decreased with the addition of multiple limiting resources (Harpole et al. 2016; Harpole et al. 2017). However, we observed that nutrient addition had no effect on species diversity neither on its own nor through its interaction with precipitation (Table 2). But species diversity with the treatment of NPK addition, under P\textsubscript{+50\%} was significantly higher with respect to that under ambient precipitation (Fig. 1). In the Urat desert steppe, light resources are abundant and the surface vegetation cover is low so that competition for light resources among plants is low (DeMalach and Kadmon 2017). Therefore, the higher plant diversity observed might result from more niches provided by higher water availability once nutrient constraints were removed (Lu et al. 2018b). Our results also verify the physiological tolerance hypothesis, which suggests that benign environments with abundant water and solar energy support more species and permit a wider range of functional strategies (Spasojevic et al. 2014).

The ANPP is synergistically affected by water and nutrient in the Urat desert steppe. Furthermore, this synergy may be serial limitation rather than co-limitation. As shown in our results, under the three nutrient levels, ANPP under P\textsubscript{+50\%} was significantly higher than that under P\textsubscript{-50\%}, but added NPK showed a significant positive effect on ANPP only under P\textsubscript{+50\%} (Table 2, Fig. 1). Moreover, the ANPP increment

![Fig. 2 Response of community weighted mean of functional traits (CWM height (a), CWM.LDMC (b), CWM.LCC (c), CWM.LT (d), CWM.LCC (e), and CWM.LNC (f)) to precipitation change and nutrient addition. Water treatments: W0: ambient precipitation; +50\%: increased precipitation by 50\%; -50\%: decreased precipitation by 50\%. Nutrient treatments: N0: 0 g·m\textsuperscript{-2}·yr\textsuperscript{-1}; +N: N 10 g·m\textsuperscript{-2}·yr\textsuperscript{-1}; +NPK: N/P/K each for g·m\textsuperscript{-2}·yr\textsuperscript{-1}. CWM, community weighted mean; LDMC, leaf dry matter content; LCC, leaf carbon content; LNC, leaf nitrogen content; SLA, specific leaf area; LT, leaf thickness. Lowercase letters indicate the difference between different water treatments under the treatment of same nutrient addition. ^ indicates significant differences between different nutrient addition treatment under same water condition (0.05 < p < 0.1). Error bars ±1SE.](image-url)
under the interaction of P+50% and NPK addition was higher than the sum of increment under the two separate treatments (Fig. 1). That is to say, the addition of water and NPK are interactive and super-additive effect on ANPP, but order-dependent in this case. Moreover, the relief of water stress enabled NPK addition to exert the enhancement effect on ANPP (Kuchenbuch et al. 1986; Liu et al. 2018; Yang et al. 2008). The effect of NPK addition on ANPP was dramatically more significant than that of single N addition. This may be due to the lack of phosphorus or potassium in the soil in this area.

Decreased precipitation reduced community plant height, LDMC and LCC. This suggests that drought significantly affects the light acquisition ability and dry matter accumulation of plant communities in desert steppe (Ma et al. 2019; Wilson et al. 1999). But LNC was diluted by increased precipitation, as also verified by a higher LNC when precipitation was reduced (Luo et al. 2020). However, SLA has no obvious response to water and nutrient addition, a result which differs from a previous result in an alpine steppe where N enrichment increased SLA (Zhan et al. 2019). Our previous studies may explain this difference. With the increase of precipitation, biomass of *Allium polyrhizum* increased while SLA significantly decreased; and *Stipa glareosa* adopted a relatively conservative strategy to cope with short-term environmental changes (Hu et al. 2020). Trade-off strategies for biomass and SLA of dominant species may be why CWM of SLA remains stable under short-term habitat changes.

Increased precipitation somehow buffered the effects of nutrient addition on soil pH and EC (Fig. 3). In this way, addition of NPK significantly reduced soil pH and increased EC under ambient

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**Fig. 3** Response of community soil properties (soil pH (a), soil EC (b), soil water content (c), soil bulk density (d), soil carbon content (e), and soil nitrogen content (f)) to precipitation change and nutrient addition. Water treatments: W0: ambient precipitation; +50%: increased precipitation by 50%; -50%: decreased precipitation by 50%. Nutrient treatments: N0: 0 g·m⁻²·yr⁻¹; +N: N 10 g·m⁻²·yr⁻¹; +NPK: N/P/K each for g·m⁻²·yr⁻¹. Soil EC: soil electrical conductivity. Lowercase letters indicate the difference between different water treatments under the treatment of same nutrient addition. ^, *, ** and *** respectively indicate the difference significant levels at 0.05 < p < 0.1, p < 0.05, p < 0.01 and p < 0.001 among different nutrient treatments under the same water condition. Error bars ± 1SE
Simple linear regression analyses between ANPP (aboveground net primary production) and species richness, abundance, CWM.height, CWM.LDMC, CWM.SLA and CWM.LNC. Regression coefficients ($R^2$) and $p$ values are given for simple linear model regressions of community vegetation characteristics and community weighted mean values of functional traits (CWM) by ANPP. LDMC, leaf dry matter content; SLA, specific leaf area; LNC, leaf nitrogen content. Indicators with insignificant linear relationship with ANPP are not listed, and the specific data can be seen in Fig. S4.

![Fig. 4](image_url)

**Table 3** Direct, indirect and total effects on above-ground net primary productivity (ANPP) on standardized values of statistically significant SEM paths ($p < 0.05$). Direction of relationship indicated by + (positive relationship) or – (negative relationship).

| Predictor | Pathway to ANPP | Effect |
|-----------|-----------------|--------|
| Precipitation | Direct | 0.385 |
| | Indirect | 0.264 |
| | Total | 0.649 |
| | Direct | 0.252 |
| Nutrient | Indirect | 0.079 |
| | Total | 0.329 |
| Abundance | Direct | 0.362 |
| | Indirect | NS |
| | Total | 0.362 |
| CWM.SLA | Direct | -0.292 |
| | Indirect | NS |
| | Total | -0.292 |

NS, no significant relationships
and P-50%, in comparison to P+50%. This indicated that higher precipitation could enhance exchange ability of soil basic cations thus diluted the acidifying influence of nutrients on pH (Cai et al. 2017). The effect on EC can be explained as a result of higher precipitation leaching salts in the 0–10 cm soil profile (Akther et al. 2021). Nitrogen (N) addition mediated the effect of drought on soil moisture content reduction, and decreased plants’ drought resistance (Yu et al. 2019). However, the soil C and N contents and soil bulk density did not respond significantly to all treatments. It may be because these three soil properties generally have slow dynamic changes and our manipulation was short-term.

Aboveground net primary productivity (ANPP) is comprehensive embodiment of the structure and function of the steppe ecosystem. Our study showed a positive correlation between species diversity (species richness and abundance) and ANPP under multiple resource-limited changes in desert steppe, confirming the diversity hypothesis (Mokany et al. 2008). But species richness was not selected into SEM, which was different from previous studies on sandy grassland (Zuo et al. 2016). However, both increased precipitation and nutrient addition indirectly increased ANPP by increasing abundance. These results suggested that plant communities in Urat desert steppe mediated the effects of short-term habitat change on ANPP mainly through species relative abundance shift rather than species migration (Albert et al. 2010; Luo et al. 2021). In addition, our SEM highlighted that precipitation, not nutrient addition, positively and indirectly affected ANPP through its negative effects on CWM of SLA. These results indicated the selective effect of community functional traits on precipitation as well as the potential advantage of CWM of SLA in Urat desert steppe mediating precipitation change and ANPP (Loreau and Hector 2001). The dominant plants (e.g., Allium polyrhizum) in Urat desert steppe adopt the growth strategy of rapidly acquiring and utilizing resources under P+50%; low SLA of new leaves is conducive to preventing excessive water loss and improving photosynthetic capacity of leaves (Luo et al. 2019). Altered precipitation affected ANPP by regulating SLA and biomass proportion of the dominant plants, supporting mass ratio hypothesis (Grime 1998; Mokany et al. 2008). The reason why soil properties were not selected into the SEM may be related to the short term in our experiment.

Conclusion

This study demonstrates how precipitation amount and nutrient addition affect species diversity, community-level functional traits, ANPP and their relationship in desert steppe. Our results suggest ANPP responds strongly to the interaction between increased precipitation and NPK addition. Both increased precipitation and nutrient addition not only have direct positive effects on ANPP, but also indirectly increase ANPP by increasing abundance. Community-level SLA mediates the effect of altered precipitation on ANPP. Longer term field observations are needed to more definitively determine how changes in limiting resources induce community composition and functional traits to affect productivity in desert steppe. Our study provides a theoretical basis for predicting the response of vegetation structure and function of desert steppe to multiple global change factors. It is critical to understand the influence mechanism of precipitation and soil nutrients changes on productivity for the management of arid grassland ecosystems.

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Author contributions

X.Z. and X.G. designed experiments; X.G., X.L., and Y.H. conducted the experiments and analyzed the data; X.G. wrote the manuscript; P.Y., M.C., and Q.Y. revised the manuscript. All authors have read and agreed to the published version of the manuscript.

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Declarations

Conflicts of interest

The authors declare no conflict of interest.
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