



Legacy effects of nitrogen deposition and increased precipitation on plant productivity in a semi-arid grassland

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Received: 15 November 2021 / Accepted: 11 June 2022
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Abstract

Purpose Nitrogen (N) deposition and increased precipitation were widely reported to promote plant productivity in terrestrial ecosystems. However, few studies have explored the effects of historical resource supplements on plant communities (legacy effects).

Methods Based on a field experiment, we examined the legacy effects of N deposition and increased precipitation on plant productivity in a semi-arid steppe after the cessation of 13-year N and water addition.

Results We found historical N and water addition generally had positive effects on plant productivity even after the treatments were ceased. However, such legacy effects showed strong inter-annual variation, and the positive effects of historical N and water addition on

productivity were stronger in a wet year (i.e., 2019) than in an extreme drought year (i.e., 2018). Although N availability decreased rapidly, the positive effect of historical N input persisted after 2 years of cessation largely due to the maintenance of the enhanced community plant stature ($CWM_{stature}$) through the increased stature of all functional groups. Moreover, the dominance of tall grasses persisted in water added plots largely contributed to the increased productivity after the historical N and water addition.

Conclusions Our study highlights the importance of plant traits and community compositions in regulating the short-term legacy effects of historical N and water input on community productivity. The positive N and water legacy effects on productivity would both last for long given the substantially changed species compositions. Long-term observation is needed for further validation of these legacy effects because of their great year-to-year variability.

Responsible Editor: Wen-Hao Zhang.

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Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11104-022-05550-x>.

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Keywords Legacy effects · Nitrogen and water addition · Plant biomass · Plant functional group · Plant traits · Semi-arid grassland

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Introduction

The exploration of resource limitation on plant productivity is one of the most classical themes in ecology (Harpole et al. 2011; Lü et al. 2018), which has gained increasing attention under the ongoing global climate change (IPCC 2013; Zhang et al. 2007). Worldwide increased nitrogen (N) deposition and altered precipitation regimes over the past century (IPCC 2014; Fowler et al. 2013) have been reported to affect plant productivity by regulating nitrogen and water resources availability in most terrestrial ecosystems (Song et al. 2019; Stevens et al. 2015). Recently, the N deposition rate has declined in Europe and Northern America (Du 2016; Engardt et al. 2017) and tended to stabilize in China (Yu et al. 2019) with the increasingly effective controls of NO_x emissions and fertilizer application. Meanwhile, global extreme precipitation and drought events are becoming more frequent (IPCC 2013; Min et al. 2011). The prediction about alternating sequences of wet and dry years at the regional scale indicates that the directional precipitation changes, such as the increased precipitation in the north of China would not be continuous (Peters et al. 2012; Scheffer et al. 2001). However, once intense N deposition and precipitation cease, how historical N and water input will alter the ecosystem functions remains largely unknown, especially in arid and semi-arid grasslands co-limited by water and N availability.

Long-term N deposition or intense precipitation may cause over-saturated N and adequate water in soil (Bai et al. 2010; Zhao et al. 2017). The accumulated N and transferred water in the soil can then alleviate limitations to plant growth and maintain plant productivity even if the N and water enrichment ceases (Hrevušová et al. 2009; Wiegand et al. 2004). However, the magnitude and duration of the effects of historical resource change (hereafter “legacy effect”) largely varied among studies (Power and Alessi 1971; Pallett et al. 2016), and the underlying mechanisms are still unclear. One previous study has reported a rapid decline in biomass production after nitrogen applications ceased in grassland in England (Pallett et al. 2016). However, an experiment in shortgrass steppe suggested the legacy effect of 4-year nitrogen addition on productivity remains significant following 20 years of recovery (Vinton and Burke 1995).

The dynamics of N availability after ceasing could be an important determinant of the legacy effect. For example, empirical studies showed fading effects of historical low-level N input on plant productivity with decreasing N availability over time after treatment cessation (Stevens et al. 2012; Hu et al. 2020). Nevertheless, Hrevušová et al. (2009) reported a persisting legacy N effect on plant productivity even if N availability recovered to the level prior to N input after a 15-year cessation of fertilization in an alluvial grassland ecosystem. Similarly, the lag response of plant productivity to changes in water availability varied from 2 months to even 10 years (Sala et al. 2012; Wiegand et al. 2004; Yahdjian and Sala 2006). Therefore, the attenuated legacy effects of N and water addition on productivity might not uniquely result from the decreasing soil available resources.

The legacy of N and water input on community productivity in grasslands could also be subject to the changed functional traits under historical N and water changes (DeMalach et al. 2017; Lü et al. 2018). For example, tall plant stature under N and water enrichment enhanced the advantage in light competition (DeMalach and Kadmon 2017; Yang et al. 2011a), and in turn promoted community productivity (Xu et al. 2018). Nevertheless, stature incurs costs as continuing maintenance of stems and disadvantages in the transport of N and water to the height (Falster and Westoby 2003). Both advantages and the costs of height could be continuous after N and water input cease, increasing the uncertainty of legacy effects on community productivity. Moreover, N and water input increased plant root distribution within topsoil in semiarid grasslands, which helps plants grab resources from soil and consequently benefits plant productivity (Yang et al. 2011a; Xu et al. 2017). However, with the potentially decreasing available resource in topsoil after treatment cessation, whether current roots distribution affects plant nutrient uptake and then productivity is still unclear. In addition to the control of functional traits, changing species composition under N and water input also play essential roles in regulating plant productivity (Chalcraft et al. 2004; Moles et al. 2009), because communities composed of species with different life forms and functional traits usually have different N and water acquiring and use strategies (Craine 2009). For example, long-term N and water addition could increase the

dominance of tall and shallow-root grasses (Xu et al. 2018) but decrease the proportion of tap-root forbs or N-fixed legumes in semi-arid grasslands (Nippert and Knapp 2007; Yang et al. 2011a). Compared with soil characteristics and plant traits, species and functional composition are usually more stable and would change slowly after the cessation of resource input given the lack of the seed bank for those disappeared species (Stevens 2016). As a result, the legacy N and water effects on community productivity would be largely driven by the adaptive strategies of these species to the decreasing resources after cessation. However, our knowledge of how plant species turnover regulates productivity after the cessation of N deposition and increased precipitation remains limited.

In addition, previous studies suggested that N and water input contributed to an additive increase in plant net primary productivity (NPP) in semi-arid grassland (Lü et al. 2018; Xu et al. 2018). Although there have been some experiments studying legacy effects of N deposition (Schmitz et al. 2019; Stevens 2016) and increased precipitation (Yahdjian and Sala 2006) on plant community, little is known about the interaction of historical water and N addition after the cessation of resources amendment in grassland. Moreover, the effects of N and water inputs were largely driven by inter-annual climate events such as extreme precipitation and warming (Hutchison and Henry 2010; Lim et al. 2015). For example, Hrevušová et al. (2009) found the legacy effect of resource addition on plant growth showed significant inter-annual variation. Additionally, long-term water addition makes the community dominated by species adapted to sufficient water conditions (Xu et al. 2017), which would flourish in wet years and decrease in dry years after treatment ceased. Thus, the interaction between N and water availability in regulating plant productivity and the association with temporal variation in precipitation may propose a great challenge to the projection of future dynamics of semi-arid ecosystems under recovery from elevated N deposition and precipitation.

Here, to test the legacy effects of N and water addition on plant community, we investigated the aboveground productivity at plant community, functional group and species levels before and after the cessation of a 13-year N and water addition experiment in a semi-arid grassland. Our previous studies in this long-term N and water manipulation experiment

suggested that N and water input increased soil N and water availability, enhanced the stature of the plant community (Xu et al. 2018) and the shallow-root biomass (Xu et al. 2017). Long-term N and water addition also increased the dominance of shallow-root grasses but decreased the proportion of tap-root forbs (Xu et al. 2017), and further promote aboveground productivity (Xu et al. 2018). We hypothesized that (1) positive N and water effects on community-level plant productivity would decline after cessation of addition due to a fast decline of soil N and water availability; (2) legacy effects of historical N and water input on productivity would vary with annual precipitation, these legacy effects would be stronger in the wet year and weaker in the dry year; (3) productivity of species with greater heights and shallow roots (i.e. tall grasses) would decrease first when N and water inputs ceased because they are more sensitive to N and water input, especially for those species simultaneously co-limited by N and water input.

Materials and methods

Site description and experimental design

This experiment was conducted in a temperate steppe fenced since 2001 at the Duolun Restoration Ecology Station in Inner Mongolia, China (42° 02' N, 116° 17' E, 1324 m a.s.l.). The long-term mean annual air temperature of this site is 2.1 °C and the mean annual precipitation is 379 mm (Xu et al. 2018). The mean daily temperature was 18.36 °C while the total precipitation was 255.7 mm during the growing season of 2017–2019 (Fig. S1). This grassland experienced a global extreme heatwave event in 2018 (Bastos et al. 2020), which potentially led to extreme summer drought for plants co-occurred with the increased temperature and solar radiation (Fig. S1). The soil is classified as Haplic Kastanozems according to the Food and Agriculture Organization classification system (IUSS Working Group WRB 2015). Dominant plant species in this study include four grasses *Agropyron cristatum*, *Leymus chinensis*, *Carex korshinskyi* and *Stipa krylovii* and two forbs *Artemisia frigida* and *Potentilla bifurca*.

Our experiment is part of a long-term fertilizer and water addition experiment designed to

investigate the effects of increased N deposition and precipitation on the grassland ecosystem (Xu et al. 2017). The experiment was established in 2005 following a split-plot design with seven blocks. Each block was set up with two water treatments (ambient precipitation and ambient precipitation plus water addition) in the main plots and two levels of N addition randomly assigned in 8 × 8 m subplots. Specifically, a total of 180 mm of additional water (i.e., half of mean annual precipitation) was sprinkled with 15 mm of groundwater weekly from June to August. Nitrogen was added as urea in dry form at two levels: 0 and 10 g N m⁻² yr⁻¹ with half applied in early May and the other half in late June. Both N and water addition were conducted in the growing season from 2005 to 2017. In May 2018 (i.e., after 13 years of treatments), we divided each sub-plot into two halves by a 1-m buffer zone. One half of the plot continued the treatments of N and water addition, and all treatments ceased in the other half (Fig. S2).

Plant community survey and estimation of shallow root growth

In May 2005, a permanent quadrat of 1 m × 1 m was established in each plot. All the permanent quadrats were left in the half of ceased treatment of N and water addition when dividing each plot. We measured the abundance and stature of each plant species in each quadrat from 2017 to 2019. The stature of each plant species was determined as the average height of three randomly picked individuals. Aboveground productivity was sampled by clipping all plant species to soil surface within a randomly selected 0.15 m × 2 m strip in each subplot outside the permanent quadrat when productivity reached the peak in late August. The clipped plants were oven-dried at 65 °C for 48 h and weighed for each species. All the plant species were classified into three functional groups including tall grasses, short grasses and forbs based on their growth form and stature (Lü et al. 2018) (Table S1). We calculated the community weighted mean stature (CWM_{stature}) as:

$$\text{CWM}_{\text{stature}} = \sum p_i \times \text{stature}_i \quad (1)$$

where p_i is the relative density of species i in the plant community and stature_i is the stature of species i . To clarify the relative importance of intra-group variation of plant stature and changes in community composition in driving community-level stature and productivity, we disentangled the variation of CWM_{stature} into the changes in stature of each functional group and the group turnover (Lepš et al. 2011) before and after treatment cessation.

We estimated the root growth in topsoil (0–10 cm layer) using in-growth core approach (Xu et al. 2017). Briefly, two 8-cm soil cores were excavated to 40 cm depth and separated into three layers (i.e., 0–10 cm, 10–20 cm and 20–40 cm) in early May. The sampled soils were passed through a 2-mm sieve to remove all roots and then refilled to corresponding layers. In late August, roots were collected from three layers of the previous two soil cores using a 6-cm diameter sampler. Roots were rinsed with deionized water, oven-dried at 65 °C and weighted to determine belowground net primary productivity (BNPP). Shallow root growth was estimated using BNPP in topsoil (i.e., 0–10 cm layer).

Soil sampling and measurement

Soil moisture was monitored biweekly from May to September in each ceasing-treatment plot. Briefly, two cores of topsoil (0–10 cm) were taken randomly and then weighed before and after oven-dried at 105 °C for 24 h. Soil moisture was defined as weight loss per gram of dry soil. To measure soil nitrogen availability, five cores of topsoil (0–10 cm) were taken randomly from each ceasing-treatment plot and then mixed thoroughly in late August from 2017 to 2019. Soil samples were then passed a 2-mm sieve to remove rocks and plant residuals and then stored at 4 °C. Soil extractable inorganic nitrogen (SIN: sum of ammonium and nitrate concentration) was extracted using 2 M KCl solution from each fresh soil sample at a soil to solution ratio of 1:10 (w / v), and then determined using a continuous-flow ion auto-analyzer (Scalar SANplus segmented flow analyzer, the Netherlands).

Statistical analysis

We used a linear mixed-effects model to test the effects of N and water addition on aboveground productivity at community, functional group and species levels. Nitrogen, water addition and their interactions were designated as fixed effects with blocks and interaction between water addition and blocks as random effects for the split-plot design. The Kolmogorov-Smirnov test and Levene's test were performed to ensure the normality of data and homogeneity of variances, respectively. The data were tested for outliers using the box-plot analysis. A Duncan's multiple range test was conducted for detecting the differences in aboveground productivity among different treatments each year ($P < 0.05$). We used linear regression analysis to test the correlations of plant productivity with soil N availability, moisture, plant stature and shallow BNPP. To further analyze the relative importance of soil properties (N and water availability), functional traits (plant stature and shallow BNPP) and community composition (i.e., the relative abundance of six dominant species) on aboveground productivity at the community level before (2017) and after (2018 and 2019) cessation of N and water addition, we conducted partial redundancy analyses (RDA) and partition the contribution (R^2 , %) of each component using variation partitioning in the "Vegan" package (Oksanen et al. 2020). Data analyses were performed using the R statistical software v4.1.1 (R Core Team 2021). Additionally, structural equation modelings were conducted to depict

the direct and indirect pathways of legacy effect on community productivity. An *a priori* model (Fig. S3) was established by assuming that plant productivity could be directly affected by soil resource availability (N and water availability), or indirectly by plant functional traits (stature and BNPP), and community composition (relative abundance of tall grass). The piecewise SEMs were finally established with Amos 24.0 (Amos Development Co., Greene, Maine, USA) using the maximum likelihood estimation method. Data were fitted to the model using the maximum likelihood estimation method, and χ^2 test ($P > 0.05$) was used to evaluate the adequacy of the models.

Results

Legacy effects of historical N and water addition on soil properties and plant traits

Before the cessation of treatments, nitrogen addition significantly increased soil extractable inorganic nitrogen (SIN) content by 57.2% and water addition increased soil moisture by 56.1%, respectively (Table 1). After the 2-year cessation of N addition, soil SIN decreased and showed no significant difference from that in control plots (Table 1). The legacy effect of water addition alone on soil moisture varied in different years and disappeared in the hot year 2018 ($P = 0.08$), while combined N and water addition enhanced soil water availability by 47.8% and 39.4% after treatment ceased in 2018 and 2019,

Table 1 Effects of (historical) nitrogen addition (N) and water addition (W) on soil characteristics, plant stature and shallow BNPP. Results were presented as mean $\pm$ 1 standard error. Different lowercase letters indicate significant differences among different treatments at the level in each year of $P < 0.05$. SIN: soil extractable inorganic nitrogen; CWM_{stature}: community weighted mean stature; BNPP: belowground net primary productivity

Year	Treatment	SIN (mg kg ⁻¹)	Moisture (%)	CWM _{stature} (cm)	BNPP _{0-10 cm} (g m ⁻² yr ⁻¹)
2017	Control	13.07 $\pm$ 0.50 b	7.58 $\pm$ 0.35 d	15.66 $\pm$ 1.32 c	23.36 $\pm$ 7.05 b
	+ N	23.15 $\pm$ 1.81 a	9.08 $\pm$ 0.30 c	21.28 $\pm$ 0.46 bc	88.20 $\pm$ 16.01 ab
	+ W	12.27 $\pm$ 0.84 b	11.83 $\pm$ 0.24 b	25.45 $\pm$ 2.43 b	127.85 $\pm$ 37.31 a
	+ NW	19.86 $\pm$ 1.02 a	12.80 $\pm$ 0.30 a	31.55 $\pm$ 2.74 a	132.19 $\pm$ 38.45 a
2018	Control	17.03 $\pm$ 0.66 b	7.88 $\pm$ 0.68 b	10.90 $\pm$ 1.35 b	18.44 $\pm$ 8.53 a
	+ N	21.85 $\pm$ 1.47 a	9.90 $\pm$ 0.63 ab	15.60 $\pm$ 1.08 ab	32.86 $\pm$ 11.42 a
	+ W	17.84 $\pm$ 1.82 b	9.32 $\pm$ 0.83 ab	20.12 $\pm$ 1.26 a	33.07 $\pm$ 5.23 a
	+ NW	19.76 $\pm$ 1.87 a	11.65 $\pm$ 0.86 a	20.71 $\pm$ 2.59 a	32.97 $\pm$ 10.03 a
2019	Control	12.69 $\pm$ 1.44 ab	7.42 $\pm$ 0.25 d	16.57 $\pm$ 2.06 b	28.48 $\pm$ 6.94 b
	+ N	13.76 $\pm$ 1.31 a	8.89 $\pm$ 0.33 c	25.43 $\pm$ 1.38 ab	46.85 $\pm$ 10.55 b
	+ W	9.96 $\pm$ 0.34 b	9.47 $\pm$ 0.16 b	34.48 $\pm$ 4.14 a	55.16 $\pm$ 8.44 b
	+ NW	13.05 $\pm$ 1.17 ab	10.34 $\pm$ 0.22 a	33.94 $\pm$ 5.01 a	113.62 $\pm$ 20.61 a

respectively (Table 1). Linear mixed-effect model showed that nitrogen addition increased soil moisture in 2017 ($P < 0.001$), and the positive N effect on soil moisture remained significant in 2018 and 2019 (Table S2, $P = 0.03$ and $P < 0.001$, respectively). Both N and water addition increased the stature of plant community in 2017 (Table S2, $P = 0.002$ and $P < 0.001$, respectively), with N addition mainly through enhancing the stature of all functional groups (i.e., intra-group variations, Fig. S4d and e), while water addition through promoting both the intra-group stature and the abundance of tall grasses (i.e., group turnover, Fig. S4e). However, the positive effects of N addition declined after the treatments ceased because the advantage in stature of tall grasses could hardly persist, especially in treatments with historical water addition (Fig. S4a). In contrast, water addition continuously enhanced the stature of plant community in both 2018 and 2019. Both N and water addition increased BNPP in topsoil in 2017, while enhanced BNPP only occurred in combined N and water addition treatment in 2019 after treatments ceased (Table 1).

Legacy effects of historical N and water addition on aboveground community productivity

Overall, both N and water addition increased aboveground productivity of plant community (by 52.6% and 57.7%, respectively) and an additive increase was observed in 2017 (by 87.1%, Fig. 1a). Increasing soil N availability and moisture by N addition significantly enhanced aboveground productivity before treatments ceased, as their positive correlations under both ambient and increased precipitation (Fig. 1d and g). In addition, plant stature and shallow BNPP also positively correlated with plant productivity (Fig. 1j and m). Legacy effects of N and water addition on plant productivity showed an inter-annual variation. In 2018, independent effects of historical N and water addition decreased to the control level while the additive increase persisted (Fig. 1b). In 2019, N and water addition alone enhanced aboveground productivity (by 54.3% and 49.3%, respectively, Fig. 1c). The productivity in combined historical N and water addition plots, however, was not significantly higher than that in either N or water addition alone treatment (Fig. 1c), suggesting the additive increase of N and water addition disappeared after the 2-year cessation

of treatment. A positive correlation between soil SIN and productivity was not detected while the effects of increasing moisture and shallow BNPP on productivity were still significant (Fig. 1f and o).

Legacy effects of historical N and water addition on productivity at functional group and species levels

No matter before and after the treatments ceased, neither N nor water addition significantly affected forb productivity (Fig. 2c). In contrast, water addition significantly increased tall grasses productivity by 142%, 101% and 136% in the three years (Fig. 2a) by increasing the relative abundance of tall grasses (Fig. S5b). In addition, N addition also enhanced tall grass productivity by increasing their stature (Fig. S4a). Nitrogen and water addition interacted to affect short grasses productivity, with positive N effects (260%, 127% and 179% higher than control) only occurring under ambient water treatment (Fig. 2b). Aboveground productivity of plant community increased with CWM-fixed stature (i.e., variation from species turnover) in enhanced precipitation plots (Fig. S6a, d, and g), whereas it increased with the stature of individuals (i.e., intra-group variation) in N addition plots (Fig. S6b, e, and h). In addition to plant traits, productivity was also positively correlated with the increased relative abundance of tall grasses across the three sampling years in enhanced precipitation plots. In contrast, productivity in N deposition treatment increased with the increased relative abundance of short grasses (Fig. S7).

Plant productivity showed interspecific differential responses to enhanced precipitation and nitrogen before and after treatments ceased (Fig. 3). Water addition significantly increased the productivity of *Leymus chinensis* in 2017 and the positive effects declined in 2018 and 2019 (Fig. 3a). Nitrogen addition increased *Carex korshinskyi* and *Potentilla bifurca* but decreased *Artemisia frigida* productivity in 2017 (Table 2). The legacy effects of N addition on these species were significant in 2018 and 2019, contributing to the legacy effects of N addition on community productivity (Fig. 1). *Agropyron cristatum* and *Setaria viridis* productivity only increased under the combination of N and water addition, and the positive effects vanished after the cessation of resources addition (Fig. 3b and c).

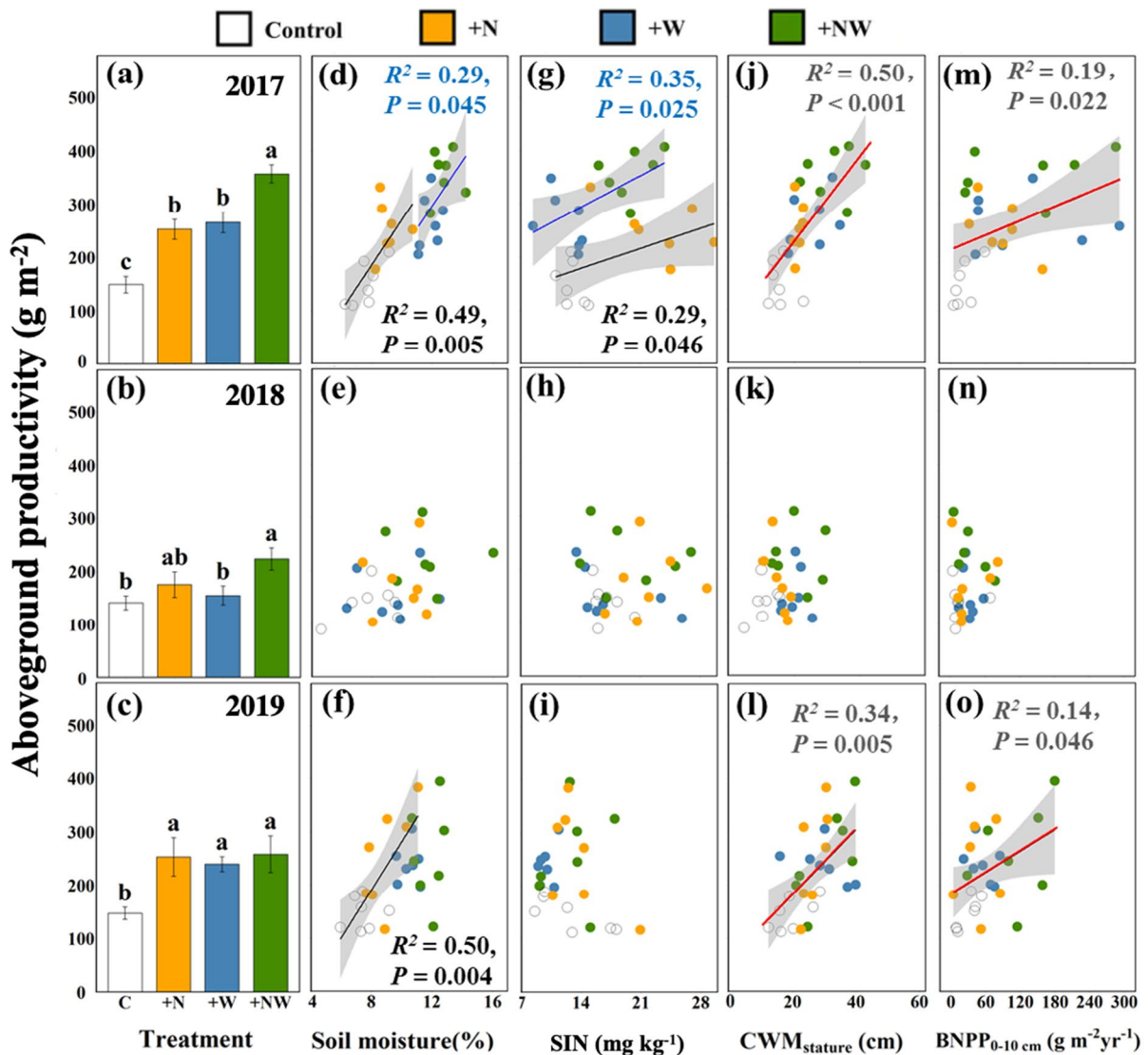


Fig. 1 Effect of nitrogen (N) and water addition (W) on aboveground community productivity before (a, 2017) and after (b–c, 2018–2019) the cessation of treatments. We also showed the correlations of productivity with soil moisture, soil extractable inorganic nitrogen (SIN), community weighted mean stature (CWM_{stature}) and shallow BNPP in different years. Bar indicates the mean value (± 1 standard error) for each treatment. Points in the same color indicate the value for

each treatment. Different lowercase letters above bars indicate significant differences among different treatments at the level of $P < 0.05$. Black and blue lines indicate significant correlations within ambient and enhanced precipitation treatments, respectively, while red lines indicate significant correlations within all treatments. The gray area represents the 95% confidence interval of the linear regression

The underlying mechanisms of historical N and water effects on aboveground productivity

Partial RDA showed that variations in aboveground productivity at the community level were well explained by soil properties (68.2%), followed by

functional traits (50.1%) and community composition (31.0%) in 2017 (Fig. 4a). However, the pure effects of all three components were insignificant due to their strong correlations. After the cessation of N and water addition, the explanation of soil properties and functional traits decreased, especially in hot 2018 (Fig. 4b

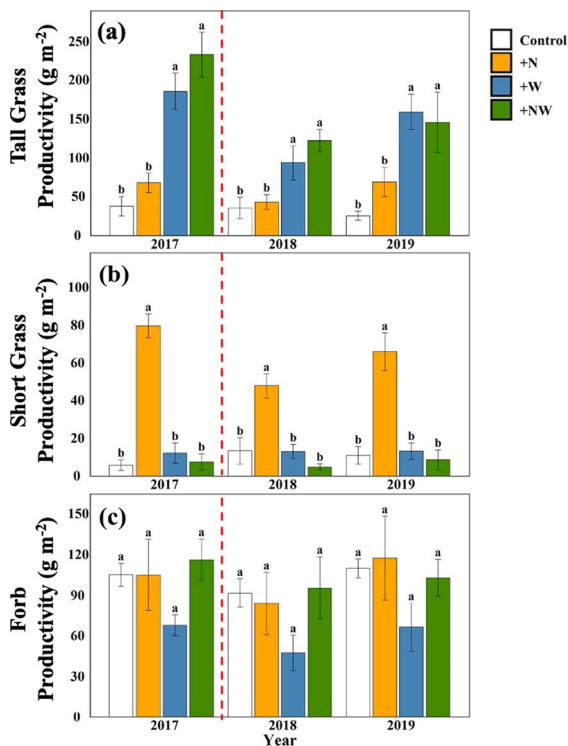


Fig. 2 Effects of N and water addition on plant productivity before and after ceasing treatments at functional group level (**a**, tall grasses; **b**, short grasses; **c**, forb). Bar indicates the mean value (± 1 standard error) for each treatment. Different lower-case letters above bars indicate significant differences among different treatments within each year at the level of $P < 0.05$. Red dash lines indicate the cessation of N and water addition

and **c**). In contrast, contributions of plant community composition variations to aboveground productivity did not change in both 2018 and 2019 (36.3% and 35.9%, respectively).

In addition, structural equation modelings showed that long-term N and water input increased aboveground productivity indirectly through increasing soil N and water availability as well as via enhancing the stature of the community in 2017 (Fig. 4d). Specifically, water addition increased CWMs by enhancing both stature of each functional group (through the ITV pathway) and the proportion of tall grass, while N addition increased CWMs by only promoting the stature of all functional groups. These pathways were largely weakened after the cessation of N and water addition. In hot 2018, historical N addition directly increased plant productivity while the indirect pathways via resource availability or the stature were not

significant (Fig. 4e). After 2 years of cessation, historical N and water addition still showed a positive effect on the plant productivity via increasing soil moisture (Fig. 4f). Historical N and water addition increased the community stature via enhancing the relative abundance of tall grass and the ITV pathway, respectively, which in turn increased community productivity.

Discussion

Understanding how plant productivity changes from historical high N and water input is of great importance under the global scenarios of reducing atmospheric N deposition and precipitation (IPCC 2013; Yu et al. 2019), especially in semi-arid grasslands where plant growth is co-limited by N and water availability (DeMalach et al. 2017; Lü et al. 2018; Xu et al. 2018). By determining the responses of aboveground productivity after cessation of a 13-year N and water addition experiment, we found that both independently and interactively positive effects of N and water addition on productivity declined after the cessation of treatments, but the magnitude of the legacy effects largely depended on natural precipitation and temperature in the growing season. Our study also differs from most of the previous work on legacy effects of global change on ecosystems by considering the roles of both plant key functional traits and community composition in the changes of productivity with the expected fast decline in soil N availability and moisture.

Partially different from our first hypothesis, positive effects of historical N addition on productivity of plant community persisted after two years of treatment ceased (Table 2) although positive effects on soil N availability significantly decreased (Table 1). In one similar temperate grassland, soil inorganic N decreased to control values in a short time after cessation of N addition (Hu et al. 2020), while other studies reported that recovery of N availability took longer time from long-term N input in grasslands (O'Sullivan et al. 2011; Stevens et al. 2012). High plant productivity under decreasing soil N availability in historical N addition plots in our study suggested that the high N demand of plants for growth consumed the historical accumulation of excess N input (Bai et al. 2010). In addition, long-term N input

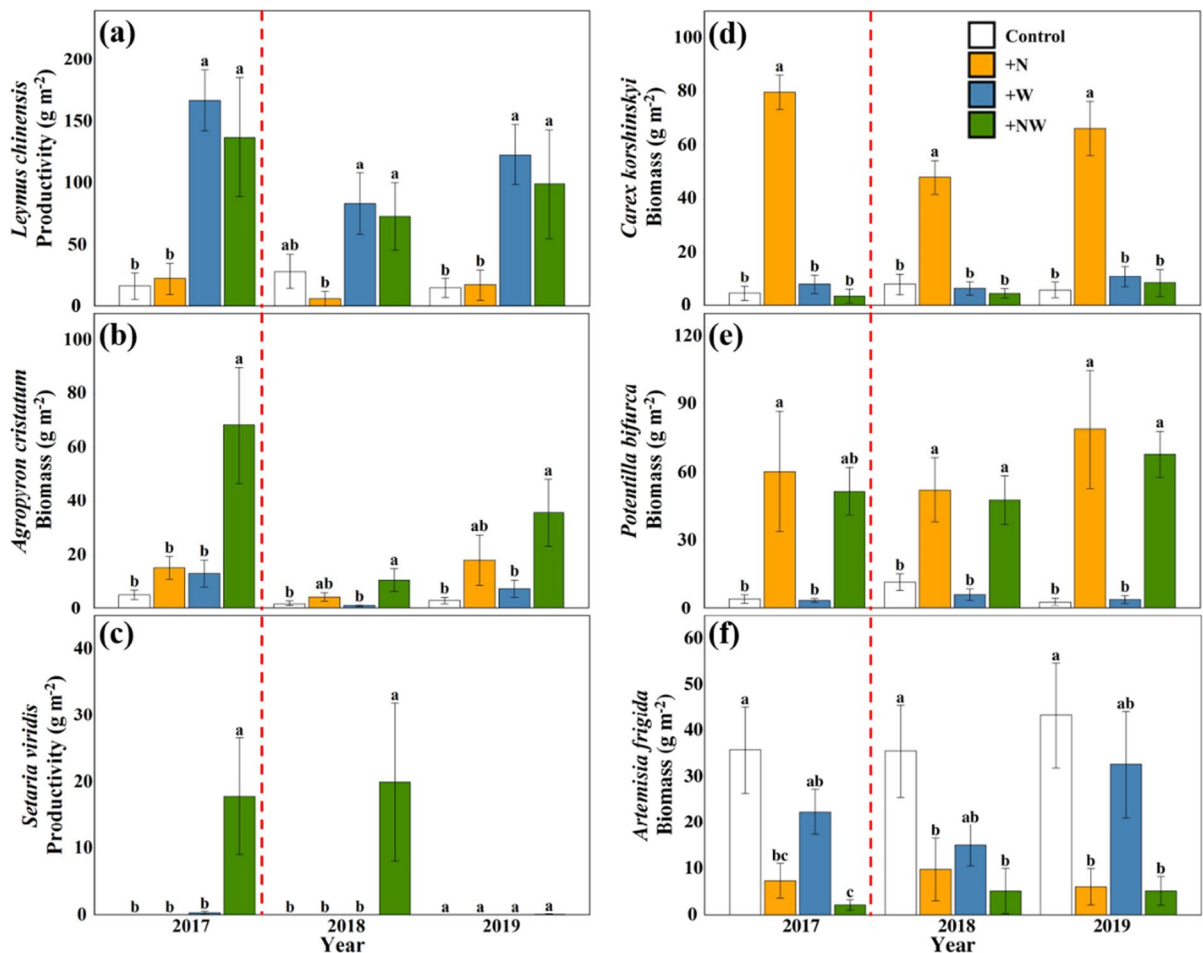


Fig. 3 Effects of N and water addition on plant productivity before and after ceasing treatments at species level. Bar indicates the mean value (± 1 standard error) for each treatment.

Different lowercase letters above bars indicate significant differences among different treatments at the level of $P < 0.05$. Red dash lines indicate the cessation of N and water addition

showed long-lasting positive effects on plant cover and litter mass after cessation ($P < 0.05$, Table S2), subsequently decreasing soil evaporation and increasing soil moisture in this semi-arid area (Fig. S8), which could possibly extend the advantage for plant productivity. In this semi-arid grassland, inter-annual water change is one of the most important factors in regulating the effects of water input on plant productivity, the low soil water availability in dry years may attenuate the effect of nitrogen on productivity (Lü et al. 2014). Therefore the weaker and non-significant legacy effect of N input alone on aboveground productivity in 2018 may be due to the extreme heatwave event in (about 2 °C difference in air temperature between the two years, Fig. S1), which could cause

strong drought stress (Bastos et al. 2020). This year-to-year fluctuations of legacy effects of N addition on plant productivity with annual climatic conditions have been reported across different types of grasslands (Hao et al. 2018; Hrevušová et al. 2009) and also suggested that further studies with longer duration are needed.

Different from the soil N accumulation in the historical N addition plots, the advantage in water availability usually disappeared quickly through leaching or evapotranspiration after water addition ceased in semi-arid grassland (Zhao et al. 2017). Therefore, the legacy effect of water addition on productivity depends mainly on the historical water-induced change in species composition and the adaptability

Table 2 Results of mixed effect model with (historical) nitrogen addition (N) and water addition (W) as fixed factor and block as random factors on aboveground productivity at plant community, functional group, and species levels

Year	Source	Community	Functional groups			Species					
			Tall grasses	Short grasses	Forbs	<i>Leymus chinensis</i>	<i>Agropyron cris- tatum</i>	<i>Setaria viridis</i>	<i>Carex korshin- skyi</i>	<i>Potentilla bifurca</i>	<i>Artemisia frigida</i>
2017	N	82.43***	4.32^	62.17***	2.55	0.03	31.32***	4.64*	55.07***	25.86***	9.11**
	W	106.36***	70.97***	56.29***	0.76	9.18**	35.96***	4.99*	52.64***	1.86	3.02
	N*W	0.33	0.22	80.37***	2.62	0.16	17.38***	4.65*	72.39***	1.60	0.11
	Block	10.84***	0.12	0.19	0.00	0.98	0.20	0.00	0.01	0.00	0.08
2018	N	14.69***	1.59	8.15**	2.88	0.03	10.87**	3.25^	27.38***	18.84***	5.10 *
	W	5.32*	22.69***	21.98***	1.90	2.03	2.71	3.27^	31.56***	0.37	4.36^
	N*W	1.64	0.54	21.38***	5.52*	0.17	6.40*	3.25^	26.92***	0.01	0.48
	Block	6.04*	0.00	0.27	8.62**	0.00	0.00	0.00	0.59	0.00	4.61*
2019	N	7.12*	0.82	18.16***	1.50	0.33	16.54***	2.10	24.53***	20.42***	7.24*
	W	4.40*	17.02***	21.57***	2.60	6.02*	1.91	2.66	21.45***	0.09	0.23
	N*W	3.50^	0.41	25.29***	0.66	0.20	0.05	2.53	28.82***	0.18	0.00
	Block	0.00	0.00	0.01	0.00	0.00	1.09	0.00	0.04	0.00	0.00

F-values were shown for N and W and Chi-Square values were shown for block

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

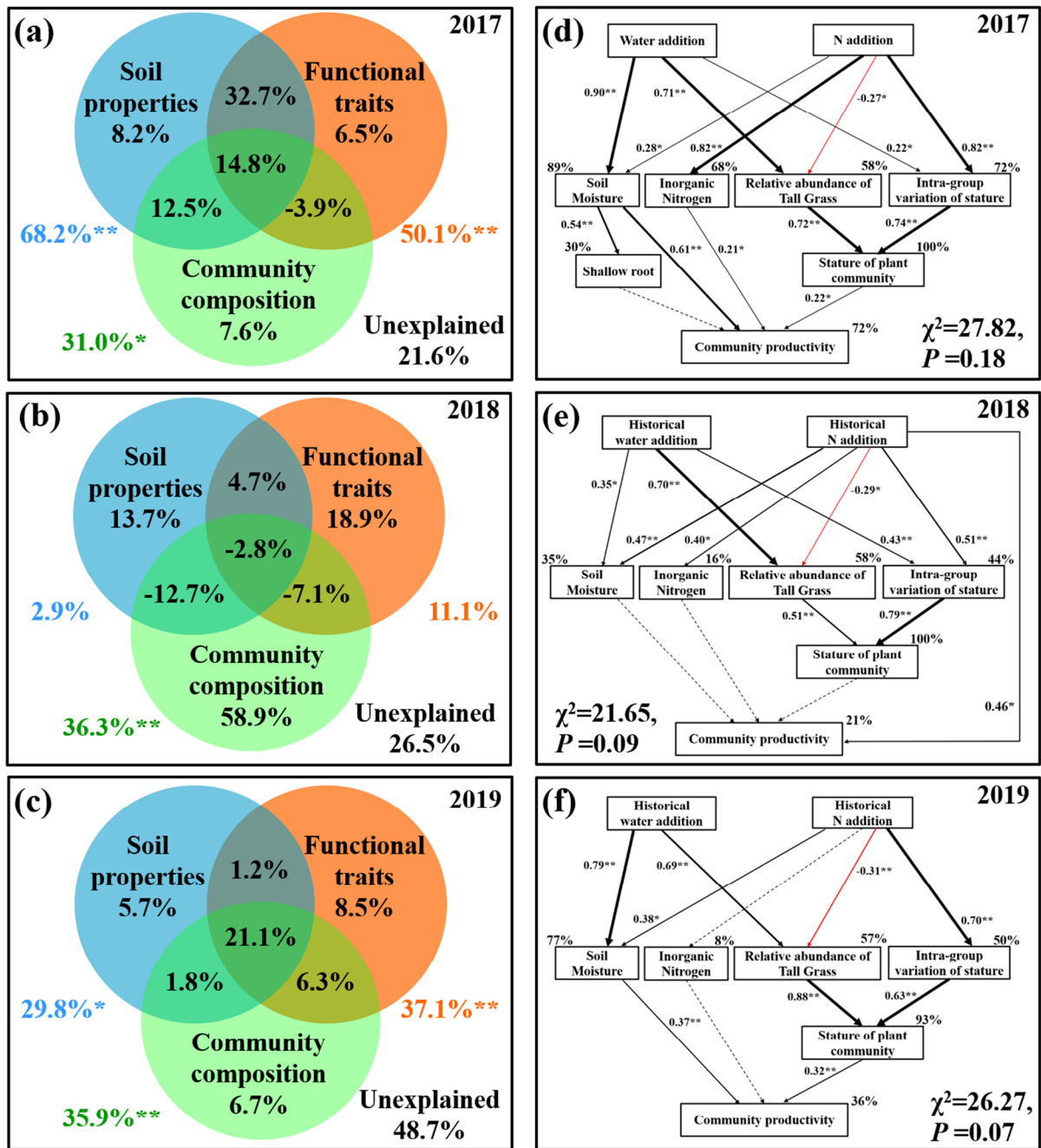


Fig. 4 Variation partitioning analyses (left) and structural equation modelings (SEM, right) to partition and depict the effects of soil properties (N and water availability), functional traits (plant stature and shallow BNPP) and community composition on aboveground productivity at community level before (2017a, d) and after (2018b,e and 2019c,f) cessation of N and water addition. The numbers in corresponding circles indicated contribution (R^2 , %) of each component to plant pro-

ductivity and the colored numbers indicated the simple effects of corresponding components (a-c). Black and red solid arrows in (d)-(f) panels indicate significant (* $p < 0.05$, ** $p < 0.01$) positive and negative pathways, respectively, and dashed arrows indicate insignificant pathways. Numbers along the arrows are standardized path coefficients, and the proportion of variance explained (R^2) appears alongside response variables in the model

of dominant species to the hydrothermal conditions in the current year. Consistent with our second hypothesis, the legacy effect of historical water input alone on productivity was stronger in wet 2019 and weaker in dry 2018. The effect size of water addition decreased by 48.4% in the hot 2018 as compared with 2017 before cessation. One possible reason is that decline in the relative abundance of taprooted forbs (Fig. S5b), in accordance with several previous studies (Xu et al. 2017; Yang et al. 2011a), suppressed the water-acquiring ability of the community from deep soil (Nippert and Knapp 2007). We also found historical water addition in our study reduced the percentage of BNPP by 34.0% and 20.9% in 10–20 cm and 20–40 cm layers, respectively (unpublished data). Shallow-root species (mainly tall grass in our study, e.g., *L. chinensis*) generally have a greater competitive advantage in communities with adequate water supply, but these species are vulnerable to drought stress after the cessation of water addition in our study. Moreover, the high relative abundance of tall grass in historical watered plots may aggravate the stress of the plant growth in dry and hot years, because stature incurs costs as continuing maintenance of stems and disadvantages in the transport of water to height (Falster and Westoby 2003). Another explanation was that long-term water addition decreased the functional diversity of the plant community (Xu et al. 2018), which is important for plant physiological drought tolerance and maintaining productivity (Craine et al. 2012; Jentsch et al. 2011). As a result, the plant community with low functional diversity under long-term water addition became more sensitive to water deficiency caused by the increased temperature and evaporation. Moreover, the advantages of communities under long-term water addition revived with adequate precipitation in the second year of cessation. In all, our results strongly suggested that legacy effects of long-term water addition on plant productivity have a large environmental dependency.

Key functional traits of plant community play important roles in increasing productivity by water and N addition in this semi-arid grassland (Xu et al. 2018). Stature is one of the most crucial components of a plant species' ecological strategy, since it determines a plant's ability for light competition, and then carbon gain and biomass accumulation (Falster and Westoby 2003). The CWM of stature showed a positive correlation with community

productivity with 13-year N and water amendment, but the relationship disappeared rapidly after cessation in hot 2018 (Fig. 1). According to the mass ratio hypothesis (Lepš et al. 2011; Spasojevic and Suding 2012), disentangling the variation of $CWM_{stature}$ can help us identify the roles of “intra-functional group stature variability (ITV)” and the “group turnover” in regulating the community productivity under historical N and water addition. In our study, N-induced increase in community stature was mainly derived from positive N effects on the stature of all three functional groups (i.e. intra-group variation, Fig. 4d), rather than through changing the abundance of taller plants. An increase in stature of all the three functional groups in N addition plots contributed to enhanced productivity as suggested by the positive correlation between productivity and intra-group variation of stature across three years (Fig. S6). Therefore, one important reason for the lower N legacy effect on productivity in the hotter 2018 was the lower intra-group variation of stature than in other years, which was attributed to the lower N effect size on the height of grasses (Fig. S4a). Different from N addition, water input enhanced plant stature and productivity at the community level by increasing both the relative abundance of tall grasses (i.e., species turnover, Fig. S4d) and the height of short grasses and forbs (i.e., intra-group variation). After the 2-year cessation of water addition, the positive effect of species turnover on community productivity did not change (Fig. 4f) while the correlation between intra-group variation and productivity decoupled. This result was in line with Moles et al. (2009), who suggested the importance of water availability in determining plant height at global scale, especially in arid regions. Moreover, simultaneously increasing $CWM_{fixed_stature}$ and intra-group variation contributed to the additive stimulation of productivity in combined N and water addition plots after 13-year treatments. However, this additive increase declined after cessation and disappeared in 2019 because the height advantage derived from intra-group variation faded away, especially for the dominant tall grasses, and led to a decrease in productivity of tall grasses (Fig. 2a). Consequently, our study emphasized that although both species turnover and intra-group variation of plant stature contribute to the increase of community productivity, changes in the intra-group

variation are more important in the recovery of plant productivity from long-term N and water addition and are more sensitive to environmental changes.

Changes in inter-specific relationships induced by N and water input can also regulate the response of plant community in semiarid regions (Xu et al. 2014; Yang et al. 2011b). Differential responses of dominant species to legacy N and water (Fig. S5a) supported our third hypothesis. One possible reason is their intrinsic sensitivity to increased resource availability (Yang et al. 2011a) and variations in soil microenvironment (e.g., soil pH) under N and water addition (Bowman et al. 2008; Cai et al. 2017), contributing to variations in productivity of functional groups and plant community (Fig. 4). Unlike the functional traits, species composition showed a good explanation for productivity across the three years (Fig. 4c). Accordingly, we could find some clues to the puzzle of how specific responses mediate N and water legacy effects on productivity. Interestingly, we found independent increases in productivity of one species by N or water input could be hardly reversed after two years of cessation. For example, positive effects of N addition on *C. korshinskyi* and *P. bifurca*, and positive effects of water addition on *L. chinensis* showed no difference between 2017 and 2019. Consequently, we can still observe significant increases in community productivity under historical N and water addition alone. In contrast, for species co-limited by N and water availability (i.e., biomass responded only to combined N and water addition), such as *A. cristatum* and *Setaria viridis*, the simultaneous increases by both N and water input declined rapidly, contributing to the disappearance of additive increase in community productivity by N and water addition (Fig. 1). This result indicated that species co-limited by multiple resources are apparently less competitive than those limited by N or water resources alone after the cessation of N and water amendment. As a result, these co-limited species (e.g., *A. cristatum* and *Setaria viridis*) could hardly co-exist with other species due to their competitive disadvantage (Dutta et al. 2014; Hardin 1960). Moreover, the inter-specific difference in response to cessation of multiple resources addition was also reported by Liu et al. (2020), where the biomass of graminoids co-limited by nitrogen and phosphorus decreased first after cessation of treatments.

Conclusions

Long-term N and water addition had persistent legacy effects on community aboveground productivity in the studied temperate steppe. However, the strength of N legacy effect declined with decreasing N available after the 2-year cessation of treatments, and the effect size of historical N and water addition varied with inter-annual climate conditions. The independent effect of historical N and water input on community productivity was weaker in the hot and dry year (i.e., 2018) because of the high dominance of shallow-rooted grasses which were sensitive to drought stress. The additive effects of N and water addition on community productivity disappeared after 2 years of cessation due to the decrease in stature of tall grasses and the decline of species simultaneously co-limited by N and water availability. Our results highlight the importance of plant functional traits (e.g., plant stature), especially the intra-group variation, in regulating the response of plant community aboveground productivity to historical N accumulation. So, we predict that the positive N and water legacy effects on productivity would last for long given the substantially changed species composition under long-term resources input in our experiment, while such legacy effects on productivity may largely depend on inter-annual climatic conditions. Our study also suggests the complexity in predicting recovery of community productivity from long-term resource addition due to the extreme climate events, and long-term observation is needed for more accurate projection on plant community dynamics.

Acknowledgements We thank the Duolun Restoration Ecology Research Station for permission to access to the study site. This work was financially supported by the Major Science and Technology Projects of Inner Mongolia Autonomous Region (2020ZD0009), the National Natural Science Foundation of China (32060284), the Inner Mongolia Science Fund for Distinguished Young Scholars (2019JQ04), the West Light Foundation of the Chinese Academy of Sciences (2020ZY0027), and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA23080402).

Author contributions Z.X. and Y.J. conceived the project. Y.N.M., T.L. and H.L. performed nitrogen and water addition, plant community survey, soil sampling and analyses every year. T.L. and Y.N.M. performed statistical analyses and graphs. Y.N.M. and T.L. prepared the manuscript with suggestions from all the co-authors. Z.W. and S.P.L. contributed to the interpretation and discussion of the results.

Data availability Data sets can be obtained from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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