Legacy Effects of Nitrogen Deposition and Increased Precipitation on Plant Productivity in a Semi-Arid Grassland

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Abstract

Nitrogen (N) deposition and increased precipitation induced by anthropogenic activities were widely reported to promote plant productivity in terrestrial ecosystems. However, few studies have explored the effects of historical resource supplement on plant communities although N deposition was predicted to decrease in the near future and the directional change of precipitation would shift among years. Here, we examined the legacy effects of N deposition and increased precipitation on plant productivity in a semi-arid steppe after cessation of a 13-year N and water addition experiment. 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 effect of N and water addition on productivity were stronger in a wet year (i.e., 2019) than an extremely drought year (i.e., 2018). Although N and water availability decreased rapidly, the independently positive effects of historical N and water input persisted after 2 years of cessation largely due to the stable community composition. The increased plant stature of dominant functional groups largely contributed to the increased current productivity after the historical N and water addition. Together, these findings will facilitate the projection of the primary productivity and carbon cycling under the scenarios of predicted reduce in N deposition and changeable precipitation.

1 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 attracted increasing attention under the ongoing global climate change (IPCC 2013; Zhang et al. 2007). Worldwide increased nitrogen (N) deposition and precipitation in temperate regions over the past century (Chapin et al. 2011; Fowler et al. 2013) have enhanced plant productivity of most terrestrial ecosystems (Song et al. 2019; Stevens et al. 2015). Recently, N deposition rate has declined in Europe and Northern America (Du 2016; Engardt et al. 2017) and tended to stabilization 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 is becoming more frequent (IPCC 2013; Min et al. 2011) and increased precipitation would not be continuous at regional scales (Peters et al. 2012; Scheffer et al. 2001). However, once intense N deposition and precipitation cease, how historical N and water input alter the ecosystem functions remains largely unknown, especially in arid and semi-arid grasslands co-limited by water and N availability.

Increasing soil N and water availability induced by high N deposition and precipitation would promote plant growth (DeMalach et al. 2017) through stimulating plant photosynthesis (Liang et al. 2020) and providing both reactant and environment to most biochemical processes (Zhang et al. 2007). It has been reported that positive effects of N and water input on plant productivity would decrease over time after treatment cessation (Sala et al. 2012; Shi et al. 2014) because of the decline in N (O'Sullivan et al. 2011) and water availability (Zhao et al. 2017). However, Hrevušová et al. (2009) reported a persisting legacy N effect on plant productivity even N availability recovered after 15-year cessation of fertilization. Similarly, lag response of plant productivity to changes of water availability varied from 2 months to even 10 years (Sala et al. 2012; Wiegand et al. 2004; Yahdjian and Sala 2006). The magnitude and duration of historical N and water effects varied between different ecosystems and the underlying mechanism are still unclear. In addition, N and water input contributed to an independently additive increase of plant annual net primary productivity (ANPP) in semi-arid grassland (Lü et al. 2018; Xu et al. 2018). Although considerable efforts have been devoted to 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 how historical increase in N interact with precipitation would affect the plant productivity under the scenarios of decreasing N deposition along with changeable precipitation regimes in the future (IPCC 2013). Moreover, 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, Lü et al. (2018) found that plant productivity was more sensitive to water input in dry year but equally sensitive to both N and water resources in wet year. Consequently, legacy effect of resource addition on plant growth showed significant inter-annual variation (Hrevušová et al. 2009). 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.

The large variation of community productivity in grasslands in response to N and water resource could also be attributed to the differential responses of different plant functional groups and species (DeMalach et al. 2017; Lü et al. 2018). Species with different life forms and functional traits usually have different N and water acquiring and use strategies (Craine 2009). For example, aboveground productivity of two dominant annual grasses increased in combined N and water addition treatment while forbs showed no response to either N or water input in a California grassland (Harpole et al. 2007). With regard to functional traits, tall grasses usually benefit more from N enrichment (Yang et al. 2011a) because of their high advantage in light competition in N-rich environment (DeMalach and Kadmon 2017). The enhancing stature of plant community by N and water addition would then increase plant productivity (Xu et al. 2018). Additionally, increasing dominance of shallow-rooted species was reported after water addition due to greater increase of soil moisture in topsoil (Nippert and Knapp 2007; Yang et al. 2011a). Therefore, changes in key functional traits and species turnover of plant community would contribute to variation of plant productivity (Chalcraft et al. 2004; Moles et al. 2009) and could in turn regulate N and water acquiring and using strategies of plant community. However, how historical N deposition and increased precipitation interactively affect plant productivity through soil characteristics and plant functional groups remains largely untested.

Here, 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. We hypothesized that 1) positive N and water effects on community-level plant productivity would decline after cessation of treatment due to a fast decline of soil N and water availability; 2) legacy effect of historical N input on productivity would be weaker in dry year while water input can strengthen historical N effect even in dry years; 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.

2 Materials And Methods

2.1 Site description and experimental design

This experiment is 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 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 heat wave 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 (WRB 2015). This temperate steppe is dominated by two grasses *Agropyron cristatum* and *Stipa krylovii* and one forb *Artemisia frigida* before nitrogen and water addition.

Our experiment is part of a long-term fertilizer and water addition experiment (Xu et al. 2017) designed to investigate the effects of increased N deposition and precipitation on grassland ecosystem. 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 sub-plots. Specifically, a total of 180 mm of additional water (*i.e.*, a 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 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 were ceased in the other half (Fig.S2).

2.2 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. 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 (Lü et al. 2018) (Table S1). We calculated the community weighted mean stature (CWM_{stature}) as:

$$CWM_{stature} = \sum p_i \times stature_i \quad (1)$$

where p_i is 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 using in-growth core approach (Xu et al. 2017). Briefly, two 8-cm soil cores were excavated to 40 cm depth and separated in to 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).

2.3 Soil sampling and measurement

Soil moisture was monitored biweekly from May to September in each ceasing-treatment plot. Briefly, two cores of topsoil (0-10cm) were taken randomly and then weighed before and after oven-dried at 105°C for 24 h. Soil moisture was defined as weight loss in per gram of dry soil. To measure soil inorganic nitrogen, five cores of topsoil (0-10cm) 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

inorganic nitrogen was extracted using 2 M KCl solution from each fresh soil sample at 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).

2.4 Statistical analysis

The Kolmogorov-Smirnov test and Levene's test were performed to ensure the normality of data and homogeneity of variances, respectively. We used a liner 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. A Duncan's multiple range test was conducted for detecting the differences of aboveground productivity among different treatments in each year ($P < 0.05$). We used liner 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.*, relative abundance of six dominant species) on aboveground productivity at 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 (R package: Vegan).

3 Results

Before the cessation of treatments, nitrogen addition significantly increased soil total inorganic nitrogen (TIN) content by 57.2% and water addition increased soil moisture by 56.1%, respectively (Table 1). After 2-year cessation of N addition, soil TIN decreased to only 8.1% higher than that in control plots (Table 1). The legacy effect of water addition on soil moisture varied in different years and disappeared in the hot year 2018 (Table 1, $P = 0.08$). Nitrogen addition increased soil moisture in 2017 and the positive effect remained significant in 2018 and 2019 (Table S2). Both N and water addition increased stature of plant community in 2017 (Table 1), with N addition mainly through enhancing stature of all functional groups (*i.e.*, intra-group variations) while water addition through promoting abundance of tall grasses (*i.e.*, group turnover, Fig. S3). However, positive effects of N addition declined after the treatments ceased because advantage in stature of tall grasses could hardly persist, especially in treatments with historical water addition (Fig. S3). In contrast, water addition continuously enhanced stature of plant community in both 2018 and 2019. Both N and water addition increased BNPP in topsoil in 2017, while enhanced BNPP was only occurred in combined N and water addition treatment in 2019 after treatments ceased (Table 1).

Table 1
Effects of (historical) nitrogen addition (N) and water addition (W) on soil characteristics, plant stature and shallow BNPP.

Year	Treatment	TIN (mg kg ⁻¹)	Moisture (%)	CWM _{stature} (cm)	BNPP _{0-10 cm} (g m ⁻² yr ⁻¹)
2017	Control	13.07 ± 0.50 b	7.58 ± 0.35 d	15.66 ± 1.32 c	23.36 ± 7.05 b
	+ N	23.15 ± 1.81 a	9.08 ± 0.30 c	21.28 ± 0.46 bc	88.20 ± 16.01 ab
	+ W	12.27 ± 0.84 b	11.83 ± 0.24 b	25.45 ± 2.43 b	127.85 ± 37.31 a
	+ NW	19.86 ± 1.02 a	12.80 ± 0.30 a	31.55 ± 2.74 a	132.19 ± 38.45 a
2018	Control	17.03 ± 0.66 b	7.88 ± 0.68 b	10.90 ± 1.35 b	18.44 ± 8.53 a
	+ N	21.85 ± 1.47 a	9.90 ± 0.63 ab	15.60 ± 1.08 ab	32.86 ± 11.42 a
	+ W	17.84 ± 1.82 b	9.32 ± 0.83 ab	20.12 ± 1.26 a	33.07 ± 5.23 a
	+ NW	19.76 ± 1.87 a	11.65 ± 0.86 a	20.71 ± 2.59 a	32.97 ± 10.03 a
2019	Control	12.69 ± 1.44 ab	7.42 ± 0.25 d	16.57 ± 2.06 b	28.48 ± 6.94 b
	+ N	13.76 ± 1.31 a	8.89 ± 0.33 c	25.43 ± 1.38 ab	46.85 ± 10.55 b
	+ W	9.96 ± 0.34 b	9.47 ± 0.16 b	34.48 ± 4.14 a	55.16 ± 8.44 b
	+ NW	13.05 ± 1.17 ab	10.34 ± 0.22 a	33.94 ± 5.01 a	113.62 ± 20.61 a
Results were presented as mean ± 1 standard error. Different lowercase letters indicate significant differences among different treatments at the level in each year of $P < 0.05$. TIN: total inorganic nitrogen; CWM _{stature} : community weighted mean stature; BNPP: belowground net primary 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 suggested by 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 N and water addition decreased to 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). However, the additive increase of N and water addition was not detected after 2-year cessation of treatment (by 56.3%, Fig. 1c). Positive correlation between soil TIN and productivity was not detected while effects of increasing moisture and shallow BNPP on productivity were still significant (Fig. 1).

No matter before and after the treatments were ceased, neither N nor water addition significantly affected forb productivity (Fig. 2) although forb stature was significantly increased (Fig. S3), because both N and water addition decreased forb abundance in the three sampling years (Fig. S4). In contrast, water addition significantly increased tall grasses productivity by 142%, 101% and 136% in the three years by increasing the relative abundance of tall grasses (Fig. 2a). In addition, N addition also enhanced tall grasses productivity through increasing their stature (Fig. S3). 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, whereas increased with stature of individuals (*i.e.*, intra-group variation) in N addition plots (Fig. S5). In addition to plant traits, increasing relative abundance of tall grasses was positively correlated with productivity across the three sampling years in enhanced precipitation plots, whereas productivity in N deposition treatment increased with increasing relative abundance of short grasses (Fig. S6).

Plant productivity showed interspecific differential responses to enhanced precipitation and nitrogen before and after treatments ceased (Fig. 3). Water addition significantly increased productivity of *Leymus chinensis* in 2017 and the positive effects declined in 2018 and 2019 (Fig. 3). 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 the legacy effects of N addition on community productivity (Fig. 1). *Agropyron cristatum* and *Setaria viridis* productivity only increased under combination of N and water addition plots, and the positive effects vanished after cessation of resources addition (Fig. 3).

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

Year	Source	Community	Functional groups			Species					
			Tall grasses	Short grasses	Forbs	<i>Leymus chinensis</i>	<i>Agropyron cristatum</i>	<i>Setaria viridis</i>	<i>Carex korshinskyi</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	5.92*	0.82	18.16***	1.50	0.33	16.54***	2.10	24.53***	20.42***	7.24*
	W	3.95^	17.02***	21.57***	2.60	6.02*	1.91	2.66	21.45***	0.09	0.23
	N*W	1.24	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
Statistical significance is represented as: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ^, $0.05 < p < 0.1$, respectively											

Partial RDA showed that variations in aboveground productivity at community level were well explained by soil properties (68.2%), following by functional traits (50.1%) and community composition (31.0%) in 2017 (Fig. 4a). However, pure effects of all the three components were insignificant due to their strong correlations. After cessation of N and water addition, the explanation of soil properties and functional traits decreased, especially in hot 2018 (Fig. 4b, 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).

4 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 recovery largely depended on natural precipitation and temperature in 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 recovery of soil N availability and moisture.

Partially different from our first hypothesis, historical N addition increased productivity of plant community after two years of treatment ceased 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 TIN in historical N addition plots in our study suggested that the high N demand of plant for growth consumed the historical accumulation of excess N input (Bai et al. 2010). However, effect size of historical N input was declining with the continuous decrease of soil TIN (Fig. 1). In addition, long-term N input showed long-lasting positive effects on plant cover and litter mass after cessation (Table S3), subsequently decreasing soil evaporation and increased soil moisture in this semi-arid area, 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 effects of N and water input on plant productivity (Lü et al. 2018; Yang et al. 2011a). Our study showed strong inter-annual variations in legacy effects of N and water addition on plant community aboveground productivity due to the extreme heat wave event in 2018 (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 higher water availability can promote N effect on plant productivity (DeMalach et al. 2017). Effect of water input on productivity was proven to be greater in dry years (Knapp 1984; Lü et al. 2018), so we expected a stronger legacy effect of water addition on productivity with higher water limitation caused by increased evaporation in hot 2018. However, plant community with historical long-term water input was even more sensitive to hot and dry condition (Fig. 1). Weaker effects of water addition on productivity in hotter year after cessation than before was not terribly surprising, but the decline of effect size (by 48.4% as compared with 2017 before cessation), even reached the control value, was impressive. One possible reason is that decline in relative abundance of taprooted forbs (Fig. S4), 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). Therefore, the community with these successful species in the competition under adequate water supply tended to be sensitive to drought stress after cessation of water addition in our study. 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 (Craine et al. 2012). As a result, compared with the stable community maintaining productivity (Fig. 1) by regulating multifunctions (Jentsch et al. 2011), the community changed by 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 N and water addition revived with adequate precipitation in the second year of cessation. In all, our results strongly suggested that legacy effects of long-term N and 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 positive correlation with community productivity after 13-year N and water amendment, but the relationship disappeared rapidly after cessation in hot 2018 (Fig. 1). By disentangling the variation of $CWM_{stature}$ into the changes in stature of each functional group and the species turnover under N and water addition according to mass ratio hypothesis (Lepš et al. 2011; Spasojevic and Suding 2012), we found that N-induced increase in community stature was mainly derived from positive N effects on stature of all three functional groups (*i.e.* intra-group variation), rather than through changing the abundance of taller plants as suggested by Yang et al. (2011a). 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. S5). Therefore, one important reason for lower N legacy effect on productivity in the hotter 2018 was lower intra-group variation of stature than other years, which was attributed to lower N effect size on height of grasses (Fig. S3). Different from N addition, water input enhanced plant stature and productivity at community level via increasing both the relative abundance of tall grasses (*i.e.*, species turnover, Fig. S4 and S5) and height of short grasses and forbs (*i.e.*, intra-group variation). After the cessation of water addition, the positive effect of species turnover on community productivity did not change 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 the 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 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). Dominant species showed differential responses (Fig. 3) due to 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. 4d). 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 of community productivity by N and water addition (Fig. 1). This result suggested the disadvantage of species co-limited by multiple resources in competition of the limited resource (*i.e.*, decreasing N availability here), and they could hardly co-exist with other species limited by N alone after cessation of N and water addition according to the competitive exclusion theory (Dutta et al. 2014; Hardin 1960). Moreover, 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.

5 Conclusions

Long-term N and water addition has positive legacy effects on community aboveground productivity in the studied temperate steppe. However, the legacy effects declined after 2-year cessation of treatments, and such decreasing effects would largely depend on inter-annual climate changes. Independent effects of historical N and water input on community productivity declined in the hot and dry year (*i.e.*, 2018) because of 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 have several implications for modeling the primary productivity and carbon cycling under the scenarios of predicted reduce in N deposition and changeable precipitation regimes. First, N- and water- induced shifts in species composition would increase the community vulnerability in response to environmental changes (e.g., high temperature, drought stress) once the exogenous resources input ceased. Second, 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 deposition and increased precipitation. Third, our study also indicates that different species, even belong to the same function group, would show divergent responses after cessation of N and water addition, where productivity of species limited by more resources may decrease faster. Our study also suggests the complications in predicting recovery of community productivity from long-term resource addition due to the extreme climatic events and longer observation is needed for more accurate projection.

Declarations

Author contributions

Z.X. and Y.J. conceived the project. Y.M., T.L. and H.L. performed nitrogen and water addition, plant community survey, soil sampling and analyses every year. T.L. and Y.M. performed statistical analyses and graphs. Y.M. and T.L. prepared the manuscript with suggestions from all the co-authors.

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Data availability statement

Data sets can be obtained from the corresponding author.

Conflict of interest

The authors declare that they have no conflict of interest.

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Figures

Figure 1

Effect of nitrogen (N) and water addition (W) on 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, total inorganic nitrogen (TIN), community weighted mean stature (CWM_{stature}) and shallow BNPP in different year. 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 95% confidence interval of the linear regression.

Figure 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 ($\pm$ 1 standard error) for each treatment. Different lowercase letters above bars indicate significant differences among different treatments at the level of $P < 0.05$.

Figure 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 $P < 0.05$.

Figure 4

Variation partitioning analyses to partition 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) and after (2018b and 2019c) cessation of N and water addition. The numbers in corresponding circles indicated contribution (R², %) of each component to plant productivity and the colored numbers indicated the simple effects of corresponding components. A conceptual diagram (d) illustrating the legacy effects of N and water addition on aboveground productivity at community level through soil properties, functional traits and community composition.

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