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REGULAR ARTICLE

Intraspecific variation drives community-level stoichiometric responses to nitrogen and water enrichment in a temperate steppe

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Abstract
Aims The responses of functional structures in plant communities to global change drivers is predicted to be driven by both species turnover and intraspecific trait variability (ITV). However, the relative importance of those two drivers is not well-known, which retards our ability to predict the functional changes of plant community under global change scenarios. We hypothesized that ITV rather than species turnover would drive the nutritional responses of plant community at the initial stage after nitrogen and water enrichment.
Methods We measured community weighted means (CWM) and non-weighted means (CM) of foliar N and P concentrations and N:P ratio in a temperate steppe after two years factorial N and water addition. Species composition and nutrition traits of each species were recorded in each plot.
Results The impacts of N addition on community level nutrition traits were highly dependent on water conditions, as indicated by significant interactive effects between N and water addition. Nitrogen addition significantly increased CWM of foliar N, but only under ambient water condition. Water addition decreased CWM of foliar P and increased that of N:P. Consistent with our hypothesis, communities responded to both N and water addition after two years treatments mainly through ITV.
Conclusions Our results highlight the importance of ITV in driving short-term responses of community functional composition to the increases of nitrogen and water availability in the temperate steppe. The existence of interactive effects of N and water addition would make it more difficult to predict the impacts of N deposition on plant-mediated biogeochemical cycling under the scenarios of precipitation regime changes than previously assumed.

Keywords Ecological stoichiometry · Interspecific and intraspecific variation · Leaf chemical traits · Nitrogen deposition · Plant community structure · Plant functional traits · Precipitation regime

Introduction

Global change drivers have significant consequences on ecosystem functioning through altering functional structure of plant community (Lavorel and Garnier 2002). Environmental changes in response to global change

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drivers would select or filter species, even individuals, based on the plasticity of their functional traits. Plant functional traits are increasingly used to assess the impacts of global change drivers on plant communities (Jung et al. 2014; Suding et al. 2008). The changes of community mean trait values in response to global change drivers are driven by a hierarchical system of ecological forces at different scales, including phenotypic plasticity and adaptive evolution at intra-specific level and species turnover at inter-specific level (Ackerly 2003). While most previous works have addressed the importance of inter-specific variation in driving community-level functional changes, more and more evidence showed that the role of intraspecific trait variability (ITV) should not be neglected (Albert et al. 2011; Bolnick et al. 2011; Jung et al. 2014), especially when the impacts of short-term perturbations on community functional structure being considered (Volf et al. 2016).

The relative contribution of intra- and inter-specific trait variation to the changes in community mean trait values in response to global change drivers have implications for the resistance of plant communities to those changes (Albert et al. 2011; Violle et al. 2012). Higher relative importance of intra-specific variation implies higher adaptation ability of plant species and contributes to higher resistance. In contrast, higher relative importance of inter-specific variation indicates greater species turnover and thus implies lower resistance of plant communities to environmental changes (Kichenin et al. 2013). Moreover, the implications of the relative contributions of ITV to community-level mean trait values would vary depending on which one of those two types of community trait values being considered, that is, non-weighted (CM) and weighted community trait means (CWM) (Volf et al. 2016; Zuo et al. 2017). The changes of CM are driven by species presence and absence, and the variations of CWM are driven by the variations of dominant species. In the case of CM, a higher relative contribution of ITV indicates greater resistance of plant community composition to such changes (Mason et al. 2012), whereas in the case of CWM, that would imply greater resistance of both community composition and the relative abundance of dominant species (Violle et al. 2007). Consequently, comparing the responses of CM and CWM to the same treatments would help understand the role of subdominant and dominant species.

Nutrient concentrations and ratios are important functional traits, with implications for plant growth, trophic interactions and plant-soil feedbacks (Austin and Zanne 2015; Cornelissen et al. 2003; Hobbie 2015). Moreover, the relative extent of ITV for plant nutritional traits is much greater than that of commonly-measured morphological traits, including leaf area, thickness, and specific leaf area (Siefert et al. 2015). While many studies have shown that nutrient concentrations and stoichiometric ratios at species-level are sensitive to global change drivers, such as nitrogen deposition and alteration of precipitation regime (Henry et al. 2006; Lü et al. 2012; Sardans and Penuelas 2012), the changes of nutritional traits at community-level have seldom been addressed. The changes at community-level would not mirror that at species-level due to the following reasons. First, global change drivers would change plant community composition and structure. Our previous results showed that the community composition and relative biomass of plant species were sharply changed by N deposition in a temperate steppe of northern China (Zhang et al. 2015). Second, plant nutritional traits vary greatly among different species. For instance, foliar N:P ratios ranged from 14 to 42 for six species in the Cedar Creek Natural History Area of Minnesota (Novotny et al. 2007). Thus, any changes in community composition would have implications for the changes of community-level nutritional traits.

Furthermore, the direction and magnitude of the responses of plant nutritional traits to the increases of N and water availability are generally species-specific (Lü et al. 2012), which makes it even more difficult to predict nutritional changes at community-level. There is new evidence showing that directional changes of community-level functional composition in response to environmental changes can be resulted from idiosyncratic changes from a few species in the community (Katabuchi et al. 2017). Our previous results showed that N addition increased foliar N:P ratios in four grasses but had no impacts on that of *Agropyron cristatum* in the temperate steppe (Lü et al. 2012). Similarly, in the calcareous and acidic grasslands of Great Britain, Morecroft et al. (1994) reported that the responses of nutritional traits (N and P concentrations, N:P ratio) for nine plant species varied greatly along a N input gradient after three years treatments. Out of those nine species, three species showed positive responses in foliar N and other species showed no response to N input. At the same time, foliar P concentration in eight out of those nine species showed neutral response and only one species showed significantly negative response (Morecroft et al. 1994). The availability and uptake capacity of P is considered as important factors modulating the response of plants to N deposition (Blanes et al. 2012; Menge and Field 2007). Moreover, previous studies reported that the impacts of N deposition on species-level nutritional traits are dependent on the status of soil water availability (Henry et al. 2006; Lü et al. 2012). We still don't know whether such an interactive effect of N and water addition on species-level nutritional traits occurs at plant community-level or not.

Here, we focus on plant nutritional traits including N and P concentrations and N:P ratios, all of which are important for biomass production and trophic interactions. We would like to disentangle the relative contributions of species turnover and ITV in the nutritional trait responses of the temperate steppe community to N and water addition. We hypothesized that N and water addition would interact to affect community mean values of nutritional traits following the case at species-level. In a previous work, we found that N and water addition interacted to affect foliar C:N:P ratios for the dominant species (Lü et al. 2012). Further, we hypothesized that shifts in nutritional composition after short-term (two years) treatments would be mainly driven by ITV rather than species turnover. Empirical and theoretical evidence shows that ecosystem responses to global change drivers will follow a temporally hierarchical way with rapid physiological responses at individual-level initially and then with reordering of species at community-level (Smith et al. 2009).

Materials and methods

Study site

The study site is a temperate steppe ecosystem near the Inner Mongolia Grassland Research Station, China (43°38 N, 116°42 E). The mean of annual temperature is 0.9 °C and mean of annual precipitation is 355 mm. The plant community are dominated by *Stipa grandis*, *Achnatherum sibiricum*, *Agropyron cristatum*, *Cleistogenes squarrosa*, and *Potentilla bifurca*. The ecosystem has been fenced since 1999 to exclude grazing by large animals. Soil is classified as chestnut soil following Chinese Soil Taxonomy and corresponds to Calcis-orthic Aridisol in the US Soil Taxonomy.

Experimental design and sampling

The experiment was established in 2007 in a factorial design with four treatments (C, control; +N, N addition; +W, water addition; +NW, both N and water addition). Each treatment was replicated for five times, with 20 plots in total (each measuring 4 m × 4 m). Nitrogen as urea in dry form was added twice each year with an annual rate of 17.5 g N m^{-2} $yr.^{-1}$, the amount which has been suggested for alleviating N limitation in the grassland of this region. The plots with water addition were sprinkled with 10 mm tap water per week from May to September each year, with totally 180 mm water being added each growing season.

In mid-Aug of 2008, aboveground biomass of plant communities were sampled by clipping all vascular plants in a 1 m × 1 m quadrat in each plot. Each species from each plot were separated into leaves and stems. All the samples were oven-dried at 65 °C for 48 h and then weighed. We used species composition characterized by the dry biomass of each individual species. Leaf samples were ground with a ball mill. Plant N concentrations were analyzed with a PE-2400 CHN analyzer (Perkin-Elmer, Foster City, USA) and P concentrations were determined by persulfate oxidation followed by colorimetric analysis. Mass ratios of N:P were used here to facilitate comparisons with other related studies.

Data calculation and analysis

Community trait means for N and P concentrations and N:P ratios were calculated as CWM and CM on each plot basis. While CM was calculated by the arithmetic average of all species in each plot, the CWM was calculated by using species relative biomass as a weighting factor in accordance with Leps et al. (2011). Thus, both changes of species identities and their relative abundances were considered for CWM, whereas only species identities being considered for CM. For each trait and plot, we first calculated 'specific' community mean trait value by considering species-specific trait measured in that plot, which included the effects of species turnover and ITV. The 'fixed' community mean trait for each plot was calculated using species trait values averaged across all plots in the experiment, which included the effects of only species turnover. After that, 'intraspecific' community average was quantified as the difference between 'specific' and 'fixed' community mean trait values. This method was used for CWM and CM separately. To disentangle the relative contributions of species turnover and ITV to both CWM and CM, the method proposed by Leps et al. (2011) was used, which is based on the decomposition of the total sum of squares (SSspecific) of the community level trait variation related to treatments (N and water addition in this study) into 'fixed' (SSfixed), 'instraspecific' (SSintra) and 'covariation' (SScov) effects, in that SSspecific = SSfixed + SSintra + SScov.

Bray–Curtis dissimilarity distance (BC) between each set of plots were computed using relative biomass data. Based on the BC matrix, we carried out a non-metric multi-dimensional scaling analysis (NMDS), yielding a visual representation of the similarities across different treatments. The NMDS analysis was performed in the R software package using 'Adonis' function the vegan package (R Core Team, 2013).

The impacts of N addition and water addition on CWM and CM values of examined leaf nutrition traits and on the community mass of N and P were analyzed by two-way ANOVAs with SPSS 17.0 (SPSS Inc., Chicago, USA).

Results

Nitrogen addition significantly increased foliar N for both CWM and CM (Table 1, Fig. 1a), but being largely dependent on water addition as indicated by significant N × W interaction (Table 1). Foliar N showed larger responses to N addition under ambient water condition than that under water addition condition (Fig. 1a). Water addition had no significant impacts on foliar N for both CWM and CM (Table 1). Water addition significantly decreased CWM of foliar P, whereas N addition did not affect foliar P (Table 1; Fig. 1b). The main and interactive effects of N and water addition on CM of foliar P were all marginally significant (Table 1). While N addition had no impacts on foliar N:P, water addition significantly increased the CWM and CM of foliar N:P (Table 1; Fig. 1c), but only under ambient N condition as indicated by the significant N × W interaction (marginally significant for CWM). Nitrogen addition significantly enhanced community mass of N and P (Table 1). Water addition significantly increased community N mass but had no impact on community P mass (Table 1).

The community composition for plots across all the four treatments were largely overlapped in the NMDS ordination (Fig. S1), indicating no differences in plant community composition among those treatments. Plots within the treatment of combined N and water addition grouped more closely with each other in the NMDS ordination than the control plots (Fig. S1).

The total variation of all the examined leaf chemical traits were mainly driven by ITV, with the relative contribution of species turnover being minor (Fig. 2). While ITV accounted for 76%, 97%, and 30% of the total variation in foliar N, P, and N:P, respectively (Fig. 2), the contribution of species turnover was 9%, 0%, and 1%. The variability in foliar N can be well explained by the experimental treatments (especially by N addition), with the unexplained variability (Res.) being low (Fig. 2a). In contrast, the variations in foliar P and N:P cannot be well explained by treatments (Fig. 2c, f), with ~60% of the variation being unexplained.

While the use of CWM and CM did not alter the results for foliar N and P, it did modulate the outcome for foliar N:P (Fig. 2). For CWM of foliar N:P, a positive covariation between species turnover and IVT drove its variability (Fig. 2e). In contrast, IVT drove the variability of CM of foliar N:P (Fig. 2f).

Table 1 *p* values for each trait indicating the effects of N addition (+N) and water addition (+W) on the community weighted trait mean values based on relative biomass (CWM) and the community non-weighted trait mean based only on species presence or absence (CM), and on community mass of N and P

Source	N concentration		P concentration		N:P		N mass	P mass
	CWM	CM	CWM	CM	CWM	CM		
+N	<0.001	0.004	0.166	0.058	0.913	0.660	0.01	0.011
+W	0.605	0.926	0.019	0.069	0.018	0.037	0.006	0.57
N × W	0.002	0.003	0.148	0.092	0.056	0.012	0.082	0.473

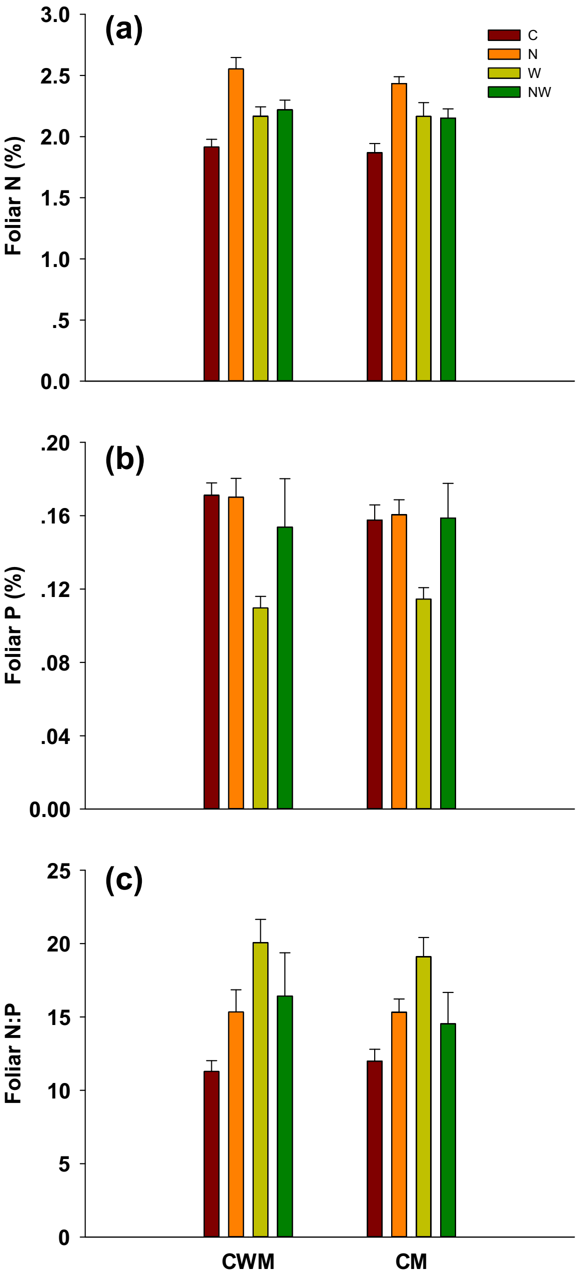

Fig. 1 The effects of N addition and water addition on foliar N (**a**), foliar P (**c**), and N:P (**e**) using the community weighted trait mean (CWM) based on dry biomass and non-weighted trait mean (CM) based on presence/absence

Discussion

The main aim of our study was to assess the relative contribution of species turnover and ITV to the responses of community nutritional trait to N and water enrichment which are projected to happen in the near future in the temperate steppe of northern China (Galloway et al. 2004; Sun and Ding 2010). Our results showed that N enrichment would enhance N status of plant community but in ambient water conditions. Moreover, water addition decreased community P concentration and with the potential to shift the nutrient limitation status of plant growth from N-limitation to P-limitation. Importantly, we got robust evidence that such functional changes of plant community were mainly driven by ITV. Our results highlight the importance of ITV instead of species turnover in driving chemical traits of plant community in response to global change drivers, at least in the initial stage.

For both CM and CWM, N addition significantly increased community N status, implying convergent responses of dominant and subdominant species to N enrichment in this ecosystem. Our previous results showed that N addition substantially increased foliar N concentrations in five dominant species, which constituting 75% of aboveground biomass in this ecosystem (Lü et al. 2012). Together with our new findings, those results suggest that the impacts of N addition on plant N status are consistent across different biological organization levels. However, N addition showed no significant impacts on P concentration and N:P ratio at the community level. It has been proposed that N enrichment would shift nutrient limitation status from N-limitation to P-limitation, with lower foliar P concentration and higher N:P ratio being expected (Sardans et al. 2017; Vitousek et al. 2010). Our findings did not support such expectation. In this experiment, N addition showed no significant effects of the concentrations of plant available P in soils (Lü et al. 2012), which would have direct consequence on plant P status. Interestingly, we found no impacts of N enrichment on plant community N:P ratio, even under the background of enhanced N status and unchanged P status in response to N inputs. Our results indicates that plant P status and N:P ratio are not as sensitive as N status to short-term N enrichment in the semiarid grassland.

In contrast, water addition significantly decreased community P status and had no impacts on community N status. We propose that such phenomenon was resulted from the balance between the changes of soil nutrient availability and plant growth in response to water addition in this ecosystem. Water addition significantly stimulated primary productivity in this ecosystem (Lü et al. 2014), implying a substantial enhancement of nutrient uptake at community level. The

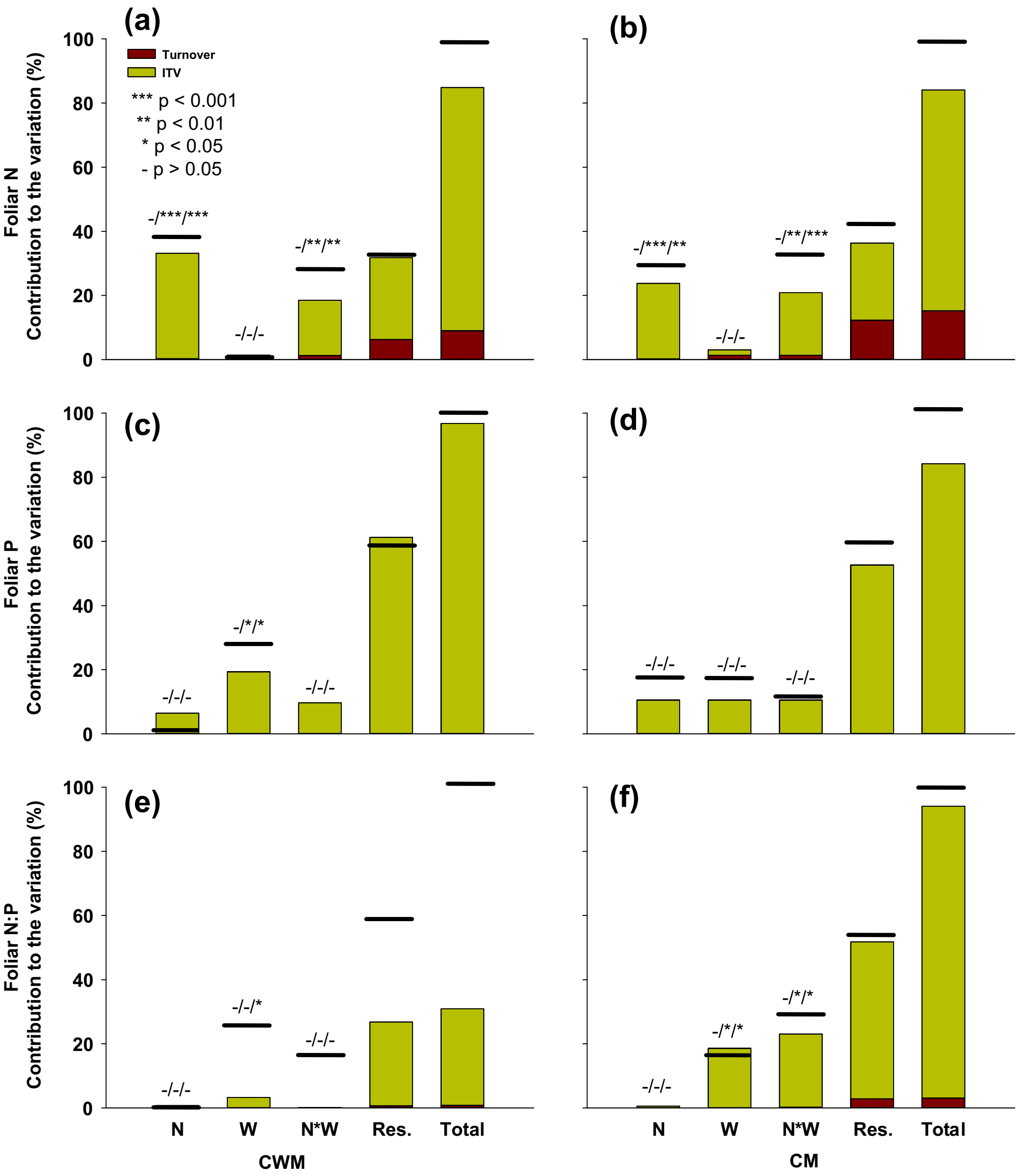

Fig. 2 Decomposition of changes in foliar N (**a**, **b**), foliar P (**c**, **d**), and N:P (**e**, **f**) using the community weighted trait mean (CWM) based on dry biomass and non-weighted trait mean (CM) based on presence/absence. Black bars denote total variation. The space between the top of the column and the bar corresponds to the effects of covariation; the covariation is positive when the bar is above the column and negative when the bar crosses the column. The positioning of an * within the −/−/− graphic represents significance of the turnover/intraspecific variation/total, respectively

responses of N and P availability to water addition were different, however, with positive response of soil inorganic N concentration and neutral response of plant available P to water addition in this ecosystem (Lü et al. 2012). Consequently, P in plants would be diluted by the rapid growth following water enrichment. Water addition significantly increased N:P ratio at community level, suggesting that plant growth following water enrichment tend to be more limited by P availability in the semiarid grassland. Recently, Ren et al. (2017) highlighted the role of N-limitation in driving primary production following long-term increased precipitation in a nearby grassland ecosystem. With stoichiometric evidence, our results suggest that P-limitation for plant growth following water enrichment also deserves much attention.

Partly consistent with our first hypothesis, we found significantly interactive effects of N and water addition on community N status and N:P ratio. Such interactive effects of N and water addition on plant nutrition and stoichiometric ratio also existed at species level as shown by our previous results (Lü et al. 2012). For both CWM and CM, N addition substantially increased plant N concentration under ambient water conditions, but showed no effect under water enriched conditions. We suspect that the positive effects of N addition on plant N was diluted by the water-stimulated growth under water enriched conditions. For N:P ratio, water addition had a significantly positive effects under ambient N conditions but with no effects under N enriched conditions. While there is mounting evidence for the significant consequences of N deposition on plant nutrition traits, our results highlight the role of water availability in modulating the impacts of N enrichment on nutrient concentrations and stoichiometry in plants. Given the projected variation of precipitation regime and thus water availability in most terrestrial ecosystems (IPCC 2013), the changes of plant stoichiometry under the scenarios of increasing N deposition would be more difficult to be projected than previously assumed.

Our second hypothesis was supported by the robust evidence that the community-level responses of plant nutritional traits, including plant N and P concentrations and N:P stoichiometric ratio, to N and water enrichment at the initial stage of treatments were dominantly driven by ITV instead of species turnover. The minor role of species turnover in driving community functional composition is understandable given the short-term treatments of N and water addition in this experiment. We found no evidence for significant variation of plant community composition across different treatments in this experiment as indicated by the results of NMDS analysis (Fig. S1). In a mesic meadow of Czech, Volf et al. (2016) reported that short-term management treatments induced changes of community functional composition of plant morphological traits (specific leaf area and height) mainly through ITV. Our results here suggest that ITV also plays important role in driving the responses of functional composition of plant chemical traits to N and water enrichment, at least in the initial stage. The higher relative contribution of ITV may contribute to the resistance of plant community to N and water enrichment, and thus lead to slower species turnover. Those results highlight the importance of ITV in modulating the changes of functional composition in response to environmental changes.

The use of CWM vs. CM influenced the outcome for the responses of community N:P ratio with no impacts on the responses of nutrient concentrations. Using CM highly increased the contribution of ITV to the variation of community N:P ratio, indicating that intra-specific variation for N:P was more significant for sub-dominant species than dominant ones under N and water enrichment. The higher contribution of ITV under the usage of CM was especially obvious for the changes of N:P ratio caused by water addition (Fig. 2e, f). Such differences indicate that water addition may affect sub-dominant species by inducing alteration in stoichiometric ratios instead of modifying their relative biomass. Recently, Mariotte et al. (2017) showed that N:P ratio was more flexible for sub-dominant species than the dominant species, which substantially contributed to the resistance of sub-dominant species to drought perturbation in a semi-natural grassland of Australia. Together, those results indicate that sub-dominant species would play an important role in driving the resistance of plant community to environmental perturbations due to their higher intraspecific variation in stoichiometric traits.

As an important driver in ecosystem nutrient cycling, the role of plants would not only depend on the concentrations of nutrients within their tissues but also on their mass. Our previous results showed that water addition significantly enhanced but N addition had no significant impacts on aboveground biomass in this community (Lü et al. 2014). Here, we found that N addition increased CWM of foliar N but had no effect on that of foliar P and that water addition had not impact on CWM of foliar N but decreased that of foliar P. Although we found that both N addition and water addition significantly enhanced community N mass, the underlying pathways were different. Nitrogen addition enhanced community N mass mainly through its positive effects on plant N concentrations, whereas water addition enhanced community N mass mainly through the increases of community biomass. The positive impacts of water addition on community biomass but negative impacts on plant P concentrations resulted in no impact of water addition on community P mass. Together, those results indicate that it is important to consider the responses of community biomass when we discuss the role of plant in biogeochemical cycling under the global change scenarios.

Conclusions

Community-level nutritional traits of the temperate steppe are sensitive to the shifts of N and water availability. The projected occurrence of increasing N deposition and precipitation in this region would have great consequences on ecosystem functioning due to the nutritional changes of plant communities. The significantly interactive effects of N and water addition on community nutritional traits imply that it would be more difficult to predict the nutritional changes of plant community due to co-occurrence of several global change drivers. For all nutritional traits studied here, ITV dominated the contribution to the community-level changes in response to N and water enrichment, presenting new evidence for the importance of ITV in driving community functional composition changes in response to short-term environmental perturbations. Such flexibility of nutritional traits at intra-specific level shows the adaptation of plant species to N and water inputs and may contribute to the resistance of community composition to such perturbations.

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