RESEARCH ARTICLE

Growing season temperature and precipitation affect nutrient resorption in herbaceous species through a foliar stoichiometric control strategy

**Xiaowei Liu · Youqi Wang · Wenhui Fu ·
Zhiyou Yuan · Qiang Yu · Changhui Peng ·
Sally E. Koerner · Liang Guo**

Abstract

Aims Foliar nutrient resorption is a critical process for considerations of ecosystem nutrient cycles. Previous studies have described the independent effects of climatic factors, plant and soil nutrient status on nutrient resorption. However, little is known about the comprehensive effects of these factors on nutrient resorption, especially based on observations in *situ*.

Methods In a semi-arid grassland of the Loess Plateau, China, we conducted an eight-year field survey and sampled leaves and soils separately in 2013, 2016, and 2020. We explored interannual variation in foliar nutrient resorption efficiency (NuRE, including nitrogen and phosphorus resorption efficiency, i.e.,

NRE and PRE) and the driving factors in graminoids and forbs.

Results The NuRE in graminoids varied significantly, but in forbs varied insignificantly among years, indicating a more flexible nutrient resorption strategy in graminoids. Further, climatic variables showed stronger effects on NuRE than soil nutrients. Specifically, growing-season temperature and precipitation controlled NuRE of graminoids and forbs by regulating green leaf N:P ratio ([N:P]g), while soil nutrients did not affect NuRE. The regulation of [N:P]g on NuRE was explained by foliar stoichiometric control in which N and P were resorbed proportionally with [N:P]g. Meanwhile, the positive relationships between NRE and PRE and between NRE:PRE and [N:P]g confirmed stoichiometric control on NuRE.

X. Liu · W. Fu
College of Grassland Agriculture, Northwest A&F University, Yangling 712100, China

Y. Wang
School of Ecology and Environment, Ningxia University, Yinchuan 750021, China

Z. Yuan · Q. Yu · L. Guo (✉)
State Key Laboratory of Soil Erosion and Dryland Farming On the Loess Plateau, Northwest A&F University, Yangling 712100, China
e-mail: guoliang2014@nwafu.edu.cn

Z. Yuan · Q. Yu · L. Guo
Institute of Soil and Water Conservation, Chinese Academy of Science and Ministry of Water Resource, Yangling 712100, China

C. Peng
School of Geographic Sciences, Hunan Normal University, Changsha 410081, China

C. Peng
Institute of Environmental Sciences, University of Quebec at Montreal, Montreal H3C3P8, Canada

S. E. Koerner
Department of Biology, University of North Carolina Greensboro, Greensboro 27402, USA

Conclusion Our findings suggested that growing season hydro-thermal factors affected the interannual variations of NuRE through a foliar stoichiometric control strategy. Meanwhile, more NuRE plasticity and positive responses to climatic factors in graminoids (the dominant group here) could explain their dominance in this grassland.

Keywords Nutrient resorption · Nitrogen-phosphorus ratio · Precipitation · Temperature · Semi-grassland

Introduction

Nitrogen (N) and phosphorus (P) are limiting resources that significantly affect plant growth and ecosystem function in terrestrial ecosystems worldwide (Reich and Oleksyn 2004; Vitousek et al. 2010; Wang et al. 2020). Nutrient resorption during the senescence of plant organs is a critical nutrient preservation strategy (Eckstein et al. 1999; Kobe et al. 2005; Drenovsky et al. 2019; Zhang et al. 2022). Previous studies of perennial plants found that more than 60% of N and P were resorbed during leaf senescence (Vergutz et al. 2012). Nutrient resorption enables plants to reuse nutrients directly and reduces their dependence on soil nutrient supplies (Aerts 1996; Ratnam et al. 2008; Freschet et al. 2010), thus altering plant growth, reproduction, and competitive ability and subsequently affecting ecosystem services and functions (Kobe et al. 2005; Yuan et al. 2005; Zhang et al. 2022). Characterizing variations in N and P resorption efficiency (NRE and PRE, i.e., the percentage of N and P resorbed before leaf senescence, respectively), as well as the abiotic and biotic regulators underlying the variations, are therefore essential to understanding plant nutrient resorption patterns and nutrient cycling in terrestrial ecosystems, especially in nutrient-poor regions (Brant and Chen 2015; Xu et al. 2021).

Due to variations among plant species in life-history traits, size, and water or nutrient use strategies, plant functional groups and functional traits are likely important biotic drivers of intra- and interspecific variations in nutrient resorption (Bertiller et al. 2006; Li et al. 2010; Vergutz et al. 2012). Previous studies showed distinct nutrient resorption efficiencies (NuRE, including NRE and PRE) between different

herbaceous functional groups, with a higher (Wang et al. 2018; He et al. 2020) or lower value (Yuan et al. 2005) in graminoids than forbs. Similarly, the relationship between NuRE and foliar morphology is also controversial. For example, some studies have found a positive correlation between specific leaf area (i.e., leaf area per unit dry mass) and NuRE (Xu et al. 2021). However, other studies have proposed that specific leaf area was not, but leaf dry matter content (i.e., leaf dry mass per fresh mass) was negatively related to NuRE (Zhang et al. 2015a; Wang et al. 2017). Moreover, studies reported that NRE was strongly related to leaf thickness, but PRE was not (Zhang et al. 2015a, b). In addition to the above, the impacts of foliar nutrient and its stoichiometry on NuRE have been reported widely, which then developed three control strategies, including nutrient concentration control, nutrient limitation control, and stoichiometry control (Ratnam et al. 2008; Reed et al. 2012; Han et al. 2013; Chen et al. 2021). In detail, the nutrient concentrations control strategy believes that NuRE depends on the original nutrient concentrations in green leaves (Chen et al. 2021). In other words, the NuRE of a certain nutrient is low when that nutrient is already abundant in the green leaves and vice versa (Kobe et al. 2005; Ratnam et al. 2008; Chen et al. 2021). Thus, the negative correlation between NuRE and green-leaf nutrient concentration will be observed when nutrient concentration control occurs. The nutrient limitation control strategy suggests plants will more strongly resorb the nutrient that limits their growth (Chen et al. 2021). Green leaf N:P ratio ([N:P]g) is widely used to describe the relative limitation of N and P on plant growth (Zhao et al. 2017). A lower [N:P]g (i.e., N limitation) means plants will show a higher NRE, while a higher [N:P]g (i.e., P limitation) means plants will deliver a higher PRE. These imply that [N:P]g will negatively correlate to NRE but positively relate to PRE if plants are regulated by nutrient limitation control (Sorrell et al. 2011; Chen et al. 2021). Furthermore, the stoichiometric control strategy argues that plants resorb nutrients with a proportion paralleled to [N:P]g. Consequently, the positive relationships between NRE and PRE and between NRE:PRE and [N:P]g can be considered stoichiometric control (Güsewell 2005; Lü et al. 2016; Chen et al. 2021). However, to date, which control strategy dominates plant NuRE remains unclear and challenging (Chen et al. 2021). Therefore, it is necessary to

explore further the effects of plant functional groups, foliar morphology, and leaf nutrient status on NuRE.

Temperature and precipitation are the main abiotic factors affecting soil moisture, which regulates plant growth and nutrient resorption (Ordoñez et al. 2009; Brant and Chen 2015; Yuan et al. 2017). Studies focused on woody species found that NRE decreases with increasing mean annual temperature (MAT) and mean annual precipitation (MAP) (Tang et al. 2013; Yan et al. 2018; Xu et al. 2021), while PRE is related to MAT and MAP positively (Yuan and Chen 2009) or negatively (Vergutz et al. 2012; Yan et al. 2018). For herbaceous species, a positive relationship between NuRE and MAT exists in forbs, and a negative relationship in graminoids. However, NuRE in both graminoids and forbs is negatively related to MAP (Wang et al. 2018). Additionally, the responses of NuRE to MAP were highly variable along precipitation gradients (Veldhuis et al. 2016; Zhao et al. 2017). Meanwhile, several studies focused on the effects of interannual climate variability on NuRE found that NRE reduced with temperature (Du et al. 2021), while both NRE and PRE increased or initially decreased and then increased with precipitation (Du et al. 2021; Liu et al. 2023). Overall, climatic effects on plant NuRE were still controversial and showed the life-form-specificity. Meanwhile, existing studies paid more attention to woody plants rather than herbaceous species (Du et al. 2020), and how local plants respond to interannual climate variability is largely unknown. Consequently, more exploration performed in grasslands will help clarify how climatic factors affect nutrient resorption across ecosystems.

In addition to climatic effects on plant NuRE, the relative availability of soil nutrient elements can also shift plant stoichiometry (Tully et al. 2013; Wang et al. 2018) and thus regulate nutrient resorption (Reed et al. 2012; Wang et al. 2014; See et al. 2015). In some studies, increased soil N and P availability due to fertilization decreased NRE and PRE (Mayor et al. 2014; Zhang et al. 2015b; Li et al. 2016). Nevertheless, other reports suggested that different levels of N and P additions affect plant NuRE with positive (Li et al. 2016; Zong et al. 2018) or insignificant effects (Chen et al. 2015; Yang 2018). In the previous meta-analysis, NRE and PRE in woody species were negatively related to soil total N (TN), available N (AN), total P (TP), and available P (AP), respectively (Reed et al. 2012; Yan et al. 2018; Xu et al. 2021).

However, the NREs of deciduous and evergreen trees were positively correlated with TN in a few individual studies (Tang et al. 2013). For herbaceous species, NRE and PRE decreased with increasing TN and TP, respectively (Wang et al. 2018). Additionally, studies focused on the effects of interannual variations in soil nutrients on NuRE showed NRE negatively correlated to AN and PRE positively related to AP (Liu et al. 2023); however, both them insignificantly related to TN and TP (Du et al. 2021; Liu et al. 2023). These findings suggest that much uncertainty remains about how soil nutrients affect plant nutrient resorption.

We performed a long-term field survey in *situ* to improve our understanding of the patterns and regulations of foliar NuRE in a semi-arid grassland on the Loess Plateau, China. We aimed to explore the interannual variation of foliar NuRE among the selected three years in two herbaceous functional groups and the key factors and mechanisms driving this variation. As previously mentioned, compared with forbs, graminoids generally showed higher NuRE (Aerts 1996; Wang et al. 2018; He et al. 2020), and possess higher phenotypic plasticity in climate change impact relevant traits (Van-Sundert et al. 2021). Therefore, we hypothesized that: i) Foliar NuRE would be greater in graminoids than in forbs, and graminoids will have a higher plasticity response to climate change than forbs; ii) Climatic variables controlled foliar NuRE indirectly via the regulation of plant traits and soil nutrients.

Materials and methods

Study site

Our study was carried out at the Yunwushan National Nature Reserve (36°10′–36°17′N, 106°21′–106°27′E, 1800–2100 m a.s.l.), which is located in the typical steppe (fenced since 1982) in the Loess Plateau, China. This region experiences a semi-arid temperate climate. Mean annual temperature (MAT) during 1982–2020 was 7.5℃ with an interannual fluctuation from 5.8℃ to 9.2℃. Mean annual precipitation (MAP) was 450 mm, which ranged from 282 to 710 mm, and mainly fell in the growing season (April–August, more than 70% of total MAP). The vegetation represents typical steppe and includes graminoid species (e.g., *Stipa bungeana*, *Spectrunculus grandis*,

and *Stipa przewalskyi*) and some forb species (e.g., *Thymus mongolicus*, *Artemisia sacrorum*, and *Potentilla acaulis*) (Cheng et al. 2014). According to the Chinese soil taxonomic system, soil type is montane gray-cinnamon soils (Wei et al. 2015).

Experimental design and sampling

An eight-year (2013–2020) field survey was employed to collect data on nutrient resorption, with plant and soil sampling occurring in 2013, 2016, and 2020. The survey focused on two main functional groups (i.e., graminoids and forbs), including four perennial graminoid species (*Agropyron cristatum*, *Leymus secalinus*, *Stipa grandis*, and *Stipa przewalskyi*) and six perennial forb species (*Artemisia sacrorum*, *Chrysanthemum lavandulifolium*, *Heteropappus altaicus*, *Leontopodium leontopodioides*, *Potentilla bifurca*, and *Thymus mongolicus*), which together covered up more than 90% of the community biomass.

In late August 2013, three 50 m×50 m plots separated by more than 20 m were established in a fenced grassland area to initiate the study. The same plant and soil sampling methods were used in all three years (i.e., 2013, 2016, and 2020). Three 5 m×5 m subplots were randomly situated at 10 m intervals for sampling within each plot. In each subplot, 20 shoots were selected (and numbered) for each graminoid species and five individuals for each forb species (Lü and Han 2010). Next, two fully expanded leaves of the same size from each graminoid individual and six leaves from each forb individual were selected and marked. In late August, a single marked, green graminoid leaf and three leaves per forb were sampled in all subplots. The remaining leaves (numbered in late August) were sampled at the end of October when they had senesced (Lü and Han 2010). In total, in each plot, 60 leaves per graminoid species (i.e., 20 shoots×1 leaf×3 subplots) and 45 leaves per forb species (i.e., 5 individuals×3 leaves×3 subplots) were sampled for both green and senesced leaves. Leaves for each species from the same plot were combined and transported immediately to the laboratory for later analysis.

Soil samples were also collected in the surveyed years. In detail, soil samples were taken from three randomly selected sampling points in each subplot using a soil auger (4 cm diameter, 10 cm depth) in late August. Soil cores from the same plot were then mixed into a single, composite soil sample. Each composite soil sample was passed through a 2 mm sieve to remove plant debris, roots, and stones and divided into two parts. One was air-dried for later analysis of soil total organic carbon (TOC) and available phosphorus (AP), and the other was stored at 4 °C for quantification of available nitrogen (AN). In addition, from 2013–2020, daily air temperatures and precipitation were obtained from a local weather station, situated only 0.9 km from the surveyed area. Annual temperature and precipitation were defined as yearly averages for the 365 days preceding the last sample date for a given year (i.e., running from the previous November to the current October), while the growing season was taken as April to August of the current year.

Assays of foliar functional traits and soil nutrients

Green leaf thickness (LT) was measured using a thickness gauge micrometer in the laboratory, and the measurements were taken at three locations along each leaf. The mass of each fresh green leaf was also measured. The green leaf area was determined by scanning fresh, flattened leaves using the Image J software. Next, all green leaves were oven-dried at 60 °C to a constant weight. Specific leaf area (SLA) was calculated as the leaf area per dry mass. Leaf dry matter content (LDMC) was calculated as the mass ratio of dried to fresh leaves (Cornelissen et al. 2003). Similarly, senesced leaves were also oven-dried and then weighed. All oven-dried leaves were finely ground using a grinding mill and passed through a 40-mesh sieve prior to subsequent analyses. For each plant sample, green and senesced leaf N concentrations (i.e., Ng and Ns) were measured on a Kjeldahl apparatus (Kjeltec 8400, FOSS, Hillerød, Denmark) after extraction by sulfuric acid from 0.10 g leaf sample (Zhu et al. 2020). Additionally, for leaf P concentrations (green and senesced leaf P concentrations, i.e., Pg and Ps), a 0.10 g leaf sample was used to measure it using the molybdate/ascorbic acid method after H_2SO_4-$HClO_4$ digestion (Li et al. 2021).

Soil TOC was analyzed using the dichromate oxidation method. In detail, 0.50 g soil was digested using $K_2Cr_2O_7$ and H_2SO_4 and titrated by $FeSO_4$ (Guan et al. 2016). Soil AN (the sum of ammonium and nitrate) were measured by a continuous-flow

auto-analyzer (Alpkem, OI Analytical, USA) after extraction with 2 M KCl at a soil: KCl ratio of 1:5 from 10 g soil (Zhang et al. 2018). The AP (Olsen-P) was determined using the Olsen method described by Cui et al. (2018). Briefly, 2.50 g soil sample, 50 ml NaHCO$_3$, and moderate active carbon were mixed and shaken for 30 min at 25 °C, filtered, then 10 ml filtrate was added with 5 ml Molybdenum antimony reagent and diluted with water to 25 ml. The solution was measured by an ultraviolet spectrophotometer at 700 nm.

Calculation of nutrient resorption efficiency
NRE and PRE were calculated using the following equations (Vergutz et al. 2012; Du et al. 2020):

$$NRE(\%) = [(N_g - N_s \times MLCF)/N_g] \times 100$$

$$PRE(\%) = [(P_g - P_s \times MLCF)/P_g] \times 100$$

where N_g and P_g are the N and P concentrations in green leaves, respectively; N_s and P_s are the N and P concentrations in senesced leaves, respectively; and MLCF, the leaf mass loss correction factor, is used to account for leaf mass lost during the senescence period (Wang et al. 2020). The values of MLCF were 0.713 and 0.640 for graminoids and forbs, respectively (Vergutz et al. 2012; Du et al. 2020).

Statistical analysis

All data of each plant variable were grouped by graminoids and forbs separately, and the two-way ANOVA was performed to examine how leaf functional traits, leaf NuRE, and soil nutrients varied among study years and functional groups. The arithmetic mean was considered as the overall effects of each variable at the functional group level. The post hoc test was performed using least significant difference (LSD) multiple comparison tests ($P < 0.05$) implemented in the R package "agricolae".

Based on the data grouped by functional groups, the relationships among climatic factors (mean annual and growing season temperature and precipitation), leaf functional traits, soil nutrients, and nutrient resorption were explored separately by partial correlation with "species" as the control factor, visualized using the R packages "corrplot" and "ggcorrplot". Additionally, based on the arithmetic mean of each plant variable at the functional

group level (i.e., one data point per functional group in each plot in each year), the pairwise correlations among leaf functional traits and Mantel tests between NuRE and leaf functional traits were explored using the R package "linkET" (Sunagawa et al. 2015).

Piecewise structural equation model (piecewiseSEM, the component model was the linear mixed effect model with "species" as a random factor) was used to determine the direct and indirect effects of climate, leaf functional traits, and soil nutrients on NuRE. First, an overall model was outlined using a priori knowledge of possible interactions with all hypothesized effects (see Fig. S1a). Next, potential variables were screened based on partial correlation and a Mantel test. A backward stepwise elimination process based on Fisher's C statistic and a Shipley test was then used to select plausible models and to evaluate possible missing paths (Fig. S1b-f). The final models represent the best-fit models (Fisher's $P > 0.05$) among possible models generated by the SEM analysis (Lefcheck 2016; Domeignoz-Horta et al. 2020). Finally, a linear mixed effect model with "species" as a random factor was used to detect the relationships between NuRE and foliar nutrients and between NuRE and foliar nutrients ratio by the R package "nlme". All statistical analyses were performed in R 4.0.3 (https://www.r-project.org).

Results

Inter-annual variation in climatic and edaphic factors

Comparing annual or growing season mean climate values from 2013–2020, differences among the three study years were observed (Fig. 1a, c). Roughly, the year 2013 was defined as a warm-wet year, 2016 as a warm-dry year, and 2020 as a cold-dry year. Moreover, the relatively obvious differences in temperature and precipitation among the three years were also detected on a monthly scale (Fig. 1b, d). In contrast, TOC, AN, and AP did not vary significantly among years (Fig. S2).

Variations in foliar functional traits and nutrient resorption efficiency

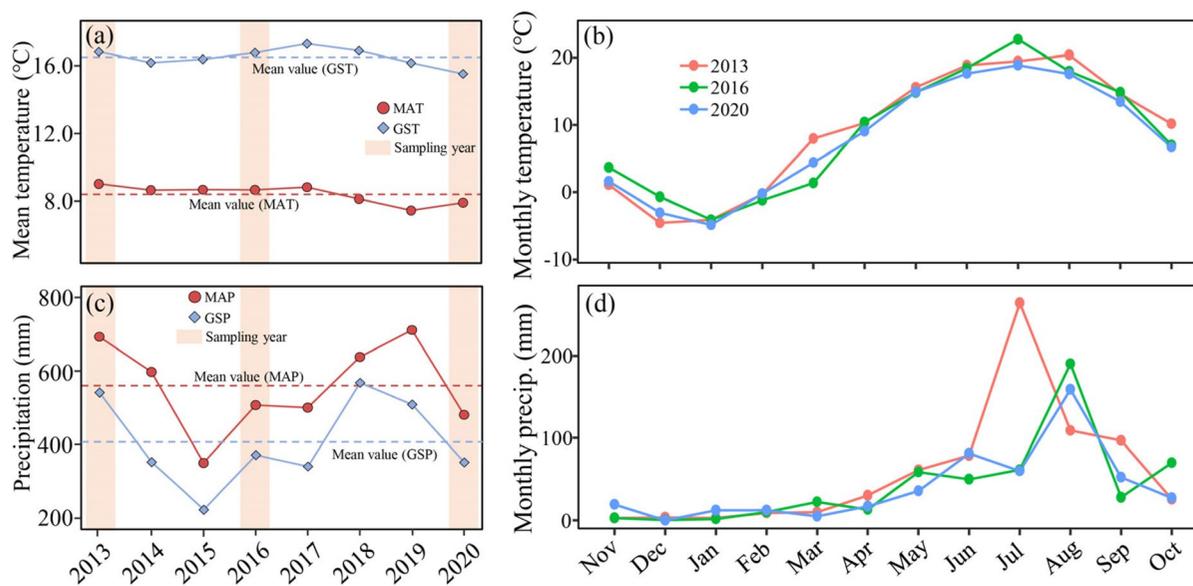Foliar functional traits varied significantly among the three years, with the exception of LDMC, Pg,

Fig. 1 Variations in temperature and precipitation among selected years. (**a**) and (**c**) were annual and growing season mean temperature and precipitation, respectively; (**b**) and (**d**) were monthly temperature and precipitation, respectively. MAT, mean annual temperature; MAP, mean annual precipitation; GST, growing season temperature; GSP, growing season precipitation. Mean value refers to the average value from 2013 to 2020

and N:P ratio in green leaves ([N:P]g) (Table S1). In graminoids, leaf functional traits significantly differed among years, except for LDMC, Ng, and Ns (Fig. 2a–i). In forbs, LT, Ng, [N:P]g, Ns, and Ps varied among years (Fig. 2a–i). Additionally, functional group well explained variation in all functional traits (Table S1). Lower values of SLA, Ng, Pg, Ns, and Ps were observed in graminoids than forbs (Fig. 2b, d, e, g, h). In contrast, LT, LDMC, [N:P]g, and N:P ratio in senesced leaves ([N:P]s) were significantly higher in graminoids than forbs (Fig. 2a, c, f, i).

Functional group and sampling year alone and their interactions did not affect foliar NuRE (Table S1). However, the NRE and PRE of graminoids varied markedly among survey years, ranging from 44.83% to 59.93% and from 45.25% to 62.82%, respectively (Fig. 2j, k; Table S1). In comparison, the NuRE of forbs varied much less, with values ranging from 51.64% to 56.39% for NRE and from 49.82% to 61.66% for PRE (Table S1). Notably, NuRE did not differ between graminoids and forbs (Fig. 2j, k). Moreover, standard major axis analysis supported that NRE and PRE were almost equal within each functional group (Fig. S3). Values of ln-NRE:PRE ranging from −0.16 to 0.16 potentially indicate

co-limitation by N and P, and values observed in the present study fall within this range: the ln-NRE:PRE ratio was -0.047 (95% CI: -0.098 to 0.004) for graminoids and -0.008 (95% CI: -0.061 to 0.045) for forbs (Fig. S3).

Correlations between nutrient resorption efficiency and its abiotic and biotic regulators

In graminoids, precipitation (both MAP and GSP) was negatively correlated with Ng and positively correlated with Pg, and thus also negatively correlated with [N:P]g (Fig. 3a). In forbs, negative correlations were found between MAT/GST and Ng, as well as between MAP/GSP and Pg. As a result, MAP and GSP were positively related to [N:P]g in forbs (Fig. 3b). All climatic factors were positively correlated with LT and SLA in graminoids. In forbs, only precipitation (MAP and GSP) was significantly positively correlated with LT and SLA (Fig. 3). NuRE in graminoids were positively related to GST (Fig. 3a). For forbs, there was a positive relationship between GST and NuRE and a negative relationship between GSP and NuRE, although they were insignificant (Fig. 3b). Compared to the significant effects
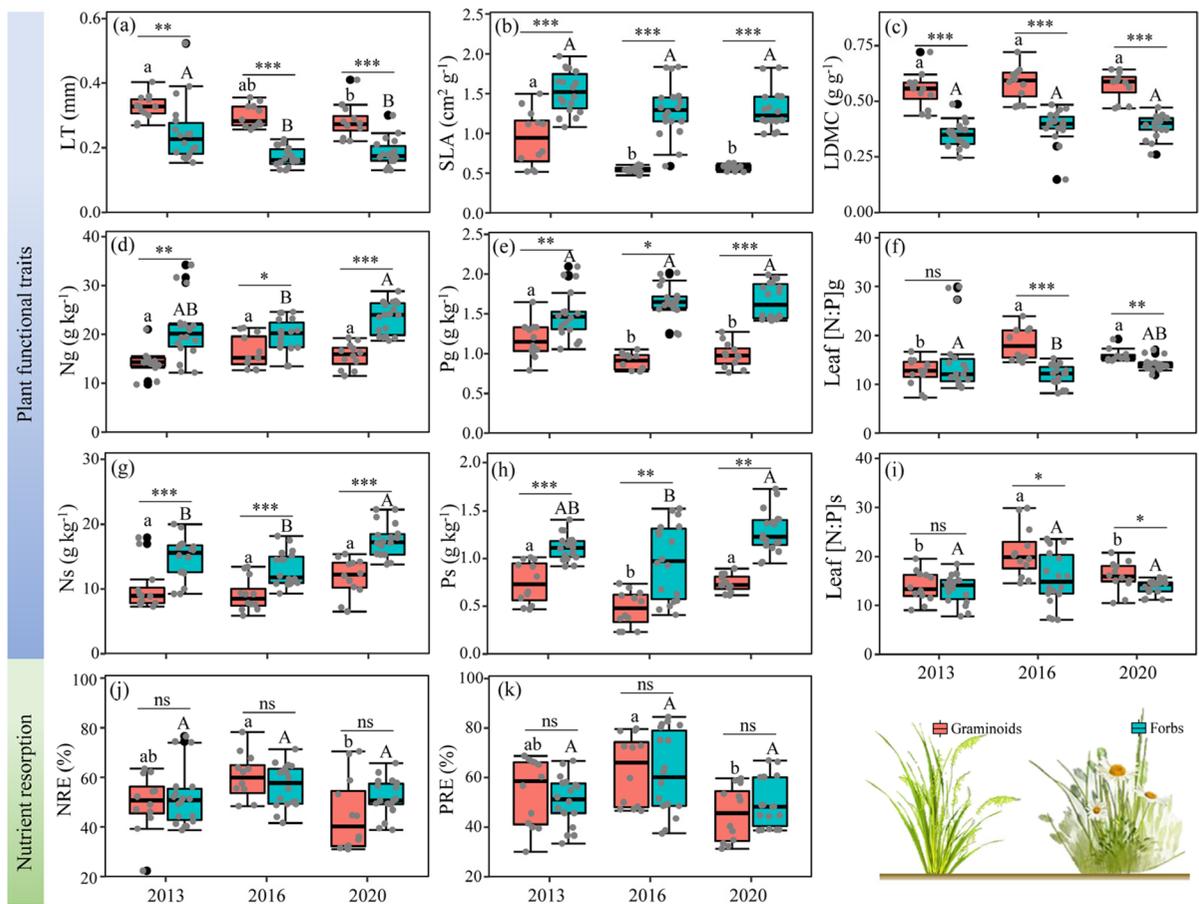
Fig. 2 Inter-annual variations in leaf functional traits (**a-i**) and nutrient resorption efficiency (**j-k**). Different lowercase and uppercase letters indicate that the significant differences among the three surveyed years in graminoids and forbs ($P<0.05$), respectively. The asterisks (*, **, ***, or "ns") on top indicate the significant ($P<0.05$, 0.01, 0.001, respectively) or insignificant ($P>0.05$) differences of relevant variables between grami-
noids and forbs. LT, leaf thickness; SLA, specific leaf area; LDMC, leaf dry matter content; Ng, N concentration in green leaf; Pg, P concentration in green leaf; leaf [N:P]g, N:P ratio in green leaf; Ns, N concentration in senesced leaf; Ps, P concentration in senesced leaf; leaf [N:P]s, N:P ratio in senesced leaf; NRE, nitrogen resorption efficiency; PRE, phosphorus resorption efficiency

of climatic variables, few correlations were detected between soil nutrient indicators or foliar functional traits and NuRE in two functional groups (Fig. S4). For example, soil AP was significantly negatively related to SLA and Pg but positively correlated to [N:P]g in graminoids (Fig. S4a). Moreover, soil AP was significantly negatively associated with LT but positively related to Pg in forbs (Fig. S4b).

In addition to the above correlation analysis, the influence of foliar functional traits on NRE and PRE was further examined in both graminoids and forbs. The [N:P]g was more strongly correlated with NuRE than other foliar traits (Fig. 4). In particular, both NRE and PRE in forbs were correlated with [N:P]g ($P<0.01$). In graminoids, NRE and [N:P]g were not significantly correlated (Mantel's r>0.4). Pairwise correlations among all functional traits further suggested that [N:P]g may be a reliable indicator of nutrient resorption. In graminoids, Ng and Pg were positively and negatively correlated to [N:P]g, respectively, while in forbs, a negative correlation was observed between Pg and [N:P]g (Fig. 4). Finally, foliar morphological traits, especially SLA in graminoids, were strongly related to green leaf nutrient concentrations and [N:P]g (Fig. 4a), However, these correlations were not present in forbs (Fig. 4b).

Fig. 3 Partial correlation between climatic factors and nutrient resorption efficiencies and leaf functional traits. MAT, mean annual temperature; MAP, mean annual precipitation; GST, growing season temperature; GSP, growing season precipitation. All other abbreviations here were the same as those in Fig. 2. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$
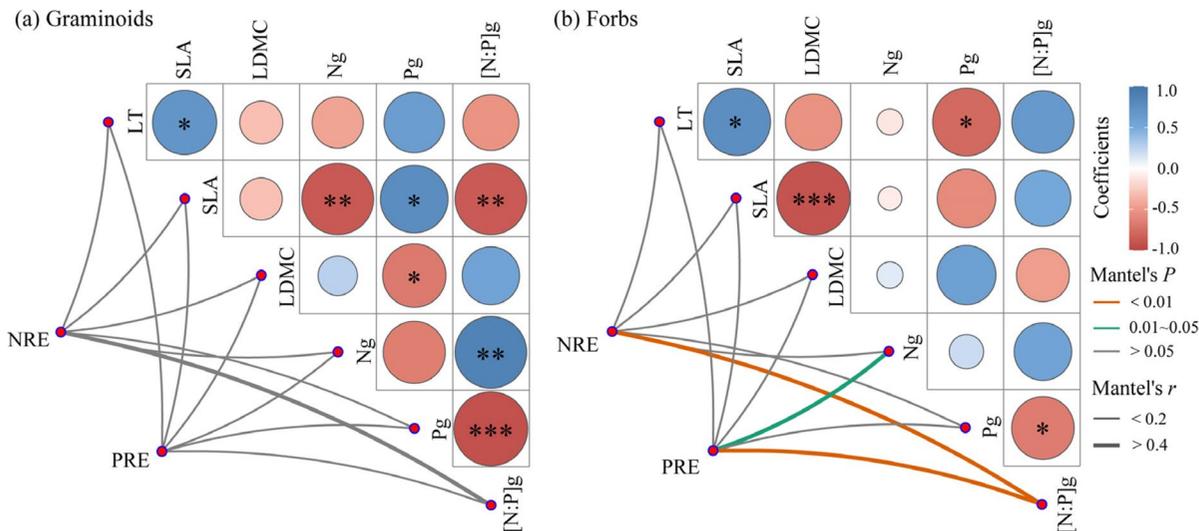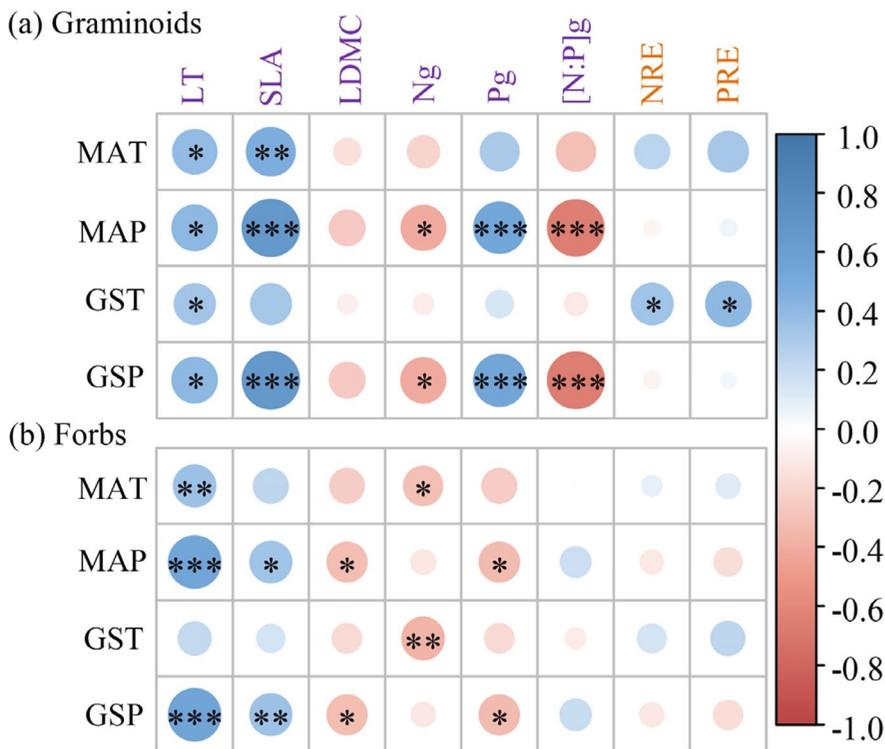

Fig. 4 Pairwise correlations of leaf functional traits and Mantel tests between nutrient resorption efficiencies and each leaf functional trait. The meanings of all abbreviations could be found in Fig. 2. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$
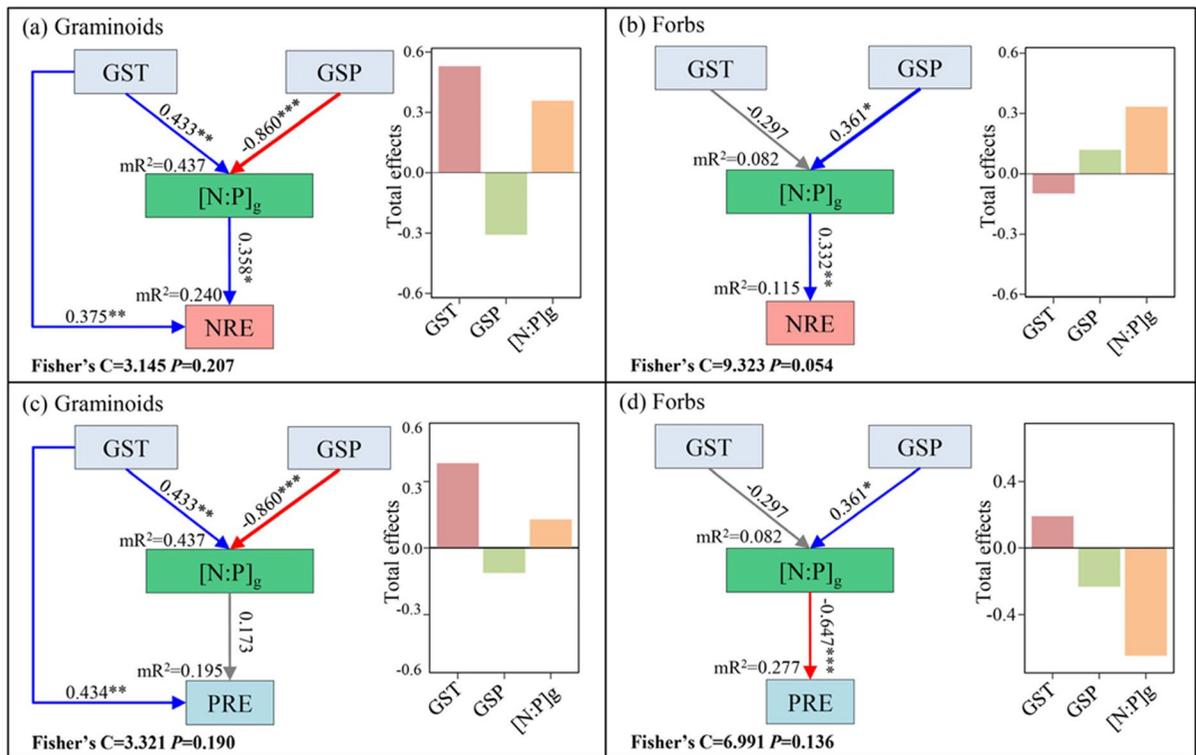
Fig. 5 The piecewiseSEM with linear mixed effect component models determined the direct and indirect relationships between mean temperature and precipitation in the growing season, N:P ratio in green leaf, and nutrient resorption efficiencies. The corresponding values on the solid line arrows are the normalized path coefficient. The blue, red, and grey arrows show significant positive, negative, and insignificant correlations, respectively (*$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$). mR^2, the R^2 of marginal coefficients of determination (i.e., the explanatory power of fixed effect) in a mixed effect model. Total effects were defined by the sum of the direct and indirect effects of all pathways. The meanings of all abbreviations could be found in Fig. 2

Impacts of climatic variables and plant functional traits on foliar nutrient resorption efficiency

Based on the above results (depicted in Figs. 3, 4; Fig. S4), four key abiotic and biotic factors (i.e., GST, GSP, [N:P]g, and AP) were found to be linked to NuRE. These factors were then used to determine the direct and indirect impacts on foliar NuRE with piecewiseSEM, while soil AP was excluded from final models (Fig. 5; Fig. S1). Primarily, NRE and PRE were positively and negatively correlated with [N:P]g, respectively (Fig. 5). Meanwhile, the positive relationships were found between NRE and PRE and between NRE:PRE ratio and [N:P]g (Fig. 6), implying a stoichiometric control on foliar NuRE. Further exploration for relationships between NuRE and foliar nutrients and between NuRE and [N:P] g suggested that no evidence supported the nutrient concentration control and nutrient limitation control strategies (Fig. S5).

Taking the effects of climatic variables into consideration, in graminoids, GST not only had direct positive effects on both NRE and PRE, but also indirectly influenced nutrient resorption via regulation of [N:P]g (i.e., via foliar stoichiometric control strategy). Compared to GST, GSP showed almost opposite effects on NRE and PRE in graminoids (Fig. 5a, c). As for forbs, the impact of GST on NuRE was negligible, with no significant direct or indirect effects (Fig. 5b, d). In contrast, GSP affected NRE and PRE in forbs via indirect effects on [N:P] g. Intriguingly, climate variations during the growing season seemed to have dramatically opposed impacts on NuRE between graminoids and forbs. Warmer and
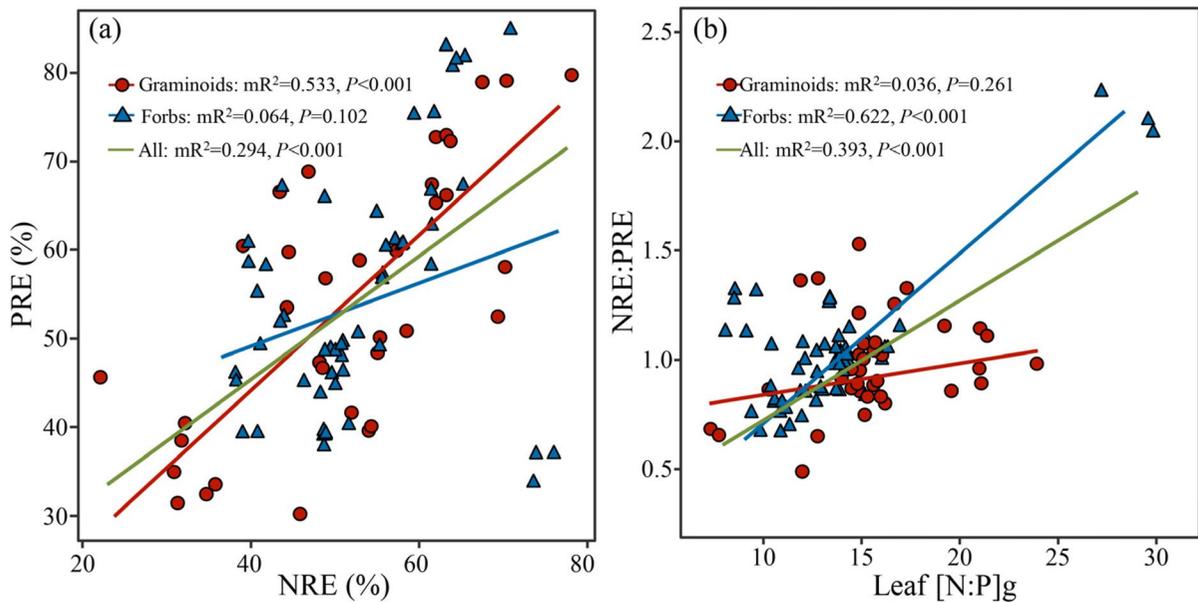
Fig. 6 Relationships between NRE and PRE (**a**) and between leaf N:P ratio and NRE:PRE ratio (**b**) based on linear mixed effect model. Each data point represented the data of a species in each plot in each year. mR^2, the R^2 of marginal coefficients of determination (i.e., the explanatory power of fixed effect) in a mixed effect model. Leaf [N:P]g, N:P ratio in green leaf. NRE, nitrogen resorption efficiency; PRE, phosphorus resorption efficiency

drier growing seasons favored foliar NRE and PRE in graminoids, while drought attenuated NRE in forbs but unexpectedly improved PRE (Fig. 5).

Discussion

Variations in foliar nutrient resorption in plant functional groups

There was a significant variation of NuRE across selected years in graminoids but not in forbs (Fig. 2j, k), partially supporting the first hypothesis. Compared to forbs (coefficient of variation [CV] of 17.99% for NRE and 24.94% for PRE), graminoids showed greater variation in NuRE (26.01% for NRE and 27.16% for PRE). This implied that NuRE in graminoids was more plastic than forbs, which might be explained by examining the relative costs and benefits of nutrient resorption (Güsewell 2005; Tang et al. 2013). Generally, plants can absorb nutrients either from the soil or their own senescing tissues (Wright and Westoby 2003; Rejmánková, 2005), and optimize the relative costs and benefits of drawing nutrients from different sources for a given habitat

(Tang et al. 2013; Brant and Chen 2015). Graminoid species, the dominant group in the studied grassland, better captured nutrients from the soil using their highly branched, fibrous root systems (Peng et al. 2020). This gave graminoid species more flexible trade-offs between capturing nutrients from senesced tissues versus the soil. Although there was no statistically significant difference, soil nutrient availability increased slightly from 2013–2020 (Fig. S2). Meanwhile, both the NRE and PRE of graminoid species decreased, especially from 2016 to 2020 (Fig. 2j, k), which indicated that N and P acquisition from soils was more cost-effective in graminoids (Kobe et al. 2005; Ratnam et al. 2008; Zhang et al. 2022). Additionally, graminoids have higher stoichiometric N:P flexibility (Fig. 2f), further explaining the more flexibility in their NuRE based on the stoichiometric control strategy (Figs. 5 and 6), which means graminoids will increase their dominance here (Hou et al. 2023).

Notably, no significant difference in NuRE was found between graminoids and forbs (Fig. 2j, k), and NRE and PRE were essentially equal within each functional group (Fig. S3a). These findings are inconsistent with previous global data analyses (Aerts 1996; Wang et al. 2018) and several site-level

reports (Zhang et al. 2022). However, several studies of the Tibetan Plateau grasslands have also found that NRE and PRE were equivalent among graminoids and forbs (Jiang et al. 2012; Zhao et al. 2017). The relative resorption of N and P (i.e., NRE:PRE or ln-NRE:PRE) is commonly used to describe the limitations of N or P on plant growth (Reed et al. 2012; Yan et al. 2017). Taking the poor-nutrient status of Loess Plateau soils (Chen et al. 2020) into consideration, the observed value of ln-NRE:PRE within a range of -0.16 to 0.16 further suggested a possible co-limitation by N and P (Du et al. 2020). The similar ln-NRE:PRE values and equal foliar NRE and PRE of graminoids and forbs in this study (Fig. S3) implied that plants in this grassland were likely co-limited by N and P.

Climatic and leaf functional trait controls of nutrient resorption efficiency

As predicted by our second hypothesis in which climatic variables would affect plant traits and then control foliar nutrient resorption indirectly. We found, in the current study, only GST directly affected NuRE in graminoids (Fig. 5a, c), while GST and GSP both controlled NRE and PRE in graminoids and forbs, mostly through indirect effects on [N:P]g (Fig. 5). Such findings were consistent with the results of a previous study conducted in the Tibetan Plateau grasslands, where annual precipitation influenced NRE and PRE through the regulation of foliar N and P concentrations and their ratio (Zhao et al. 2017). Compared to these results, this study highlighted the importance of temperature and precipitation during the growing season, which more strongly affected foliar NuRE than the annual means of these variables (Figs. 3 and 5).

Foliar N and P concentrations and [N:P]g are reliable physiological and ecological indicators of plant nutrient status, nutrient limitations, plant life-history strategies, and differentiation among functional groups (Ratnam et al. 2008; Lü et al. 2013; Tao et al. 2016). In this study, [N:P]g was positively and negatively correlated with NRE and PRE, respectively (Fig. 5). Meanwhile, positive relationships were found between NRE and PRE and between the NRE:PRE ratio and [N:P]g (Fig. 6). These implied the stoichiometric control strategy on NuRE, where plants resorb N and P according to their leaf stoichiometry

and consequently show proportional shifts in resorption ability with changing [N:P]g (Fig. 6; Güsewell 2005; Lü et al. 2013; Chen et al. 2021). This could be ascribed to the fact that changes in [N:P]g directly reflect the difference between N and P inputs to plant leaves (Drenovsky and Richards 2004; Ratnam et al. 2008; Zhao et al. 2017). As a result, in nutrient-poor environments (such as our study area), to cope with climate-induced changes in [N:P]g, plants might regulate NRE and PRE to maintain proportional inputs of N and P (Fig. 6). This represents a reasonable strategy when considering that regulation might be achieved (without too much energy) via osmotic differences between source and sink (Chen et al. 2021).

The interesting finding was the disparate effects of GSP on [N:P]g in graminoids versus forbs. This might be attributable to differences in the response of Ng and Pg (between functional groups) to precipitation, and especially to variation in Pg (Figs. 3, 4 and 5), as [N:P]g was primarily determined by Pg (Güsewell and Koerselman 2002; Ordoñez et al. 2009). Here, Ng increased but Pg declined with decreasing GSP in graminoids (Fig. 3a), resulting in a negative correlation between GSP and [N:P]g (Fig. 5a, c). A possible explanation for this result is that graminoids, as the functional group with higher [N:P]g (Fig. 2f; Li et al. 2022), utilized more resources to obtain N (rather than P) when drought stress limited root activity, as well as the solubility and diffusion of soil nutrients (Tian et al. 2020; Ghiloufi and Chaieb 2021; Matías et al. 2021). Physiologically, increasing foliar N would maintain net photosynthetic efficiency (via the synthesis of more chlorophyll) and also stabilize internal water content and cellular osmotic pressure, affording graminoid species greater tolerance to drier environments (Pons and Westbeek 2004; Yu et al. 2020; Mu and Chen 2021). Furthermore, graminoids also show greater foliar P-use efficiency (i.e., leaf production per foliar P accumulation, Kuznetsova et al. 2010) instead of more P capture under drought-induced nutrient limitations (Tian et al. 2020; Lambers 2022). When GSP decreased, this finally led to an increase in [N:P]g in study graminoids (Figs. 3a and 5a, c). Increasing soil nutrient availability could also promote plant growth, thus diluting Pg and increasing [N:P]g in graminoids (Fig. S2; Zong et al. 2018). Together, the potential processes and mechanisms discussed above help explain the negative correlation between GSP and [N:P]g in graminoids.

In contrast, for forbs, Pg increased as GSP decreased (Fig. 3b), likely as a consequence of how

forbs adapted to drought conditions. Forbs generally do not possess drought-tolerant leaves, and therefore increasing Pg might improve their hydraulic efficiency, helping to maintain a greater leaf water potential (Ocheltree et al. 2020). This shift would lead to a decline in the daily transpiration rate from leaves, thus allowing them a greater water-use efficiency (WUE) and drought tolerance (Singh et al. 2000; Sardans et al. 2008). Additionally, lower GSP could enhance soil available P content as more substantial rock weathering occurs under arid conditions (Chen et al. 2013; Delgado-Baquerizo et al. 2013; Zhao et al. 2017). As a result, greater P availability could positively affect WUE, as plants might obtain P more efficiently from the soil, further increasing Pg (Sardans et al. 2008; Yan et al. 2016), which ultimately leads to a decrease in [N:P]g and positive correlation between GSP and [N:P]g in forbs (Fig. 5b, d).

Finally, positive correlations were detected between GST and both NRE and PRE in graminoids, but not in forbs (Fig. 5). Generally, higher GST enhances soil N mineralization rates, resulting in greater foliar N content (Craine et al. 2012; Wang et al. 2012; Zong et al. 2018). Higher GST also accelerates soil water loss, leading to drought conditions (Li et al. 2016). Consequently, as discussed above, graminoids might preferentially absorb N rather than P to adapt to drier soil conditions (Tian et al. 2020; Lambers 2022). This would result in a higher [N:P]g in graminoids, which further caused a positive relationship between GST and NRE (rather than PRE) by stoichiometric control strategy (Figs. 5a and 6). In contrast, the direct positive correlation between GST and PRE observed in graminoids would require follow-up analyses to uncover the underlying mechanisms, such as the regulation of leaf enzyme and species composition (Lü et al. 2019; Liu et al. 2022). While both GST and GSP impacted [N:P]g in graminoids (in different directions), GSP seemed to dominate the forb [N:P]g response to climate variation. In brief, nutrient resorption in graminoids was controlled by GST and GSP. However, only GSP influenced NRE and PRE in forbs. Therefore, graminoids are expected to maintain their dominance in grassland communities in future climates that are warmer and drier.

Limitations and implications

Understanding the regulators of nutrient resorption will help to expand our knowledge of plant nutrient cycling. Here, patterns and potential regulators of foliar NuRE are examined based on a long-term field survey. However, some caution should be taken in interpreting the study results. First, significant effects of soil nutrients on foliar nutrient resorption were not found, although this has been observed in other studies (Wang et al. 2018; Zhang et al. 2022), which might be because that soil nutrient concentration, as a relative instantaneous index for nutrient supply, has the lower representativeness than nutrient supply capability (e.g., nutrient net mineralization rate). Thus, further exploration is necessary and urgent. Secondly, the mechanisms examined collectively explained a relatively low amount of variation (11.5%–27.7%) in nutrient resorption (Fig. 5). It remains unclear whether there may be other regulators that were not included here, such as leaf enzyme and species composition (Lü et al. 2019; Liu et al. 2022). Additionally, slight variations in soil nutrients and disturbance resistance among plant species may be causes of the above limitations (Craine et al. 2013; Lind et al. 2013; Heilmeier 2019). Nonetheless, the results of this study do have important implications for our understanding of foliar NuRE in semi-arid grassland ecosystems. For example, GST and GSP were found to directly control foliar NuRE and indirectly affect NRE and PRE via [N:P]g. To some extent, these results emphasized that climatic factors during the growing season rather than soil nutrient control plant nutrient resorption via foliar stoichiometric control strategies. More research is needed to understand better the interactions between nutrient resorption and other environmental factors (especially extreme climatic conditions), as well as how climate, plant traits (such as leaf enzyme and species composition), and soil properties interact to determine nutrient resorption on greater temporal and spatial scales. This study presents an accurate and thorough assessment of nutrient resorption, aiding our understanding and improving predictions of nutrient resorption responses to climate change.

Conclusions

In this study, variation in foliar nutrient resorption was examined using a long-term field survey in *situ* in a semi-arid grassland of the Loess Plateau. NuRE

showed greater interannual variation in graminoids versus forbs, suggesting that graminoid species may have more flexible nutrient resorption strategies in the face of climatic variation. NRE and PRE were not different within, and between, graminoids and forbs, implying a co-limitation of N and P in this region. Mean temperatures and precipitation during the growing season affected the [N:P]g of graminoids, and further controlled NRE and PRE via a foliar stoichiometric control strategy. However, in forbs, growing season precipitation, rather than temperature, most strongly impacted NRE and PRE through stoichiometric controls. Overall, these findings suggested that climatic factors during the growing season control nutrient resorption via a foliar stoichiometric control strategy. Meanwhile, graminoids, as the dominant group here, would maintain their dominance in future warm-dry climates in this region. This study expanded our understanding of the factors driving foliar nutrient resorption and the mechanisms maintaining dominant species in this nutrient-poor grassland ecosystem.

Data availability The data that support this study are available from the corresponding author upon reasonable request.

Declarations

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