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Original Articles

Arbuscular mycorrhizal fungi alter plant N and P resorption of dominant species in a degraded grassland of northern China

Yue Shen [a,b], Fei Zhang [a], Ying Yang [a], Guoqing Lu [a], Xin Yang [a,b,*]

[a] Ningxia University, School of Agriculture, Yinchuan, Ningxia, China
[b] Ningxia Grassland and Animal Husbandry Engineering Technology Research Center, China

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ABSTRACT

Plant nutrient resorption is an important regulator of biogeochemical cycling and decomposition. Arbuscular mycorrhizal fungi (AMF) may influence this process by helping plants absorb nutrients, although the mechanism by which this occurs remains unclear. We examined variations in nutrient resorption over a period of 3 years in three dominant species, namely, *Artemisia frigida*, *Potentilla acaulis*, and *Stipa krylovii*, treated with or without fungicide in a degraded grassland in Inner Mongolia in 2017. Our results showed that AMF increased the nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) in *A. frigida* but decreased NRE and PRE in *S. krylovii* and PRE in *P. acaulis.* The inconsistent nutrient resorption responses of *A. frigida* and *S. krylovii* to AMF were primarily attributed to the changes in biomass in the presence of AMF, thereby changing the nutrient requirements. For *P. acaulis*, the reduction in PRE with AMF was because AMF-induced its N limitation, which is consistent with the relative nutrient resorption hypothesis. AMF increased internal nutrient cycling in *A. frigida*, which may promote its dominance in degraded grassland in Inner Mongolia, China. Moreover, AMF reduced senesced leaf N concentrations, thereby reducing the carbon (C):N ratio in senesced leaves, which may affect nutrient return to the soil. Our findings indicate that AMF substantially affect the biomass and nutrient requirements of dominant plant species, potentially leading to changes in nutrient resorption during grassland degradation, which may provide a deep insight into plant nutrient retranslocation in degraded grasslands.

1. Introduction

Nutrient resorption is the process through which plants translocate nutrients from senescing structures before abscission. Translocated nutrients are either redistributed to other living tissues or stored for later use. Nutrient resorption is the dominant mechanism of nutrient conservation (Aerts, 1996). A previous study reported that approximately 31% of plant nitrogen and 40% of plant phosphorus are recycled via nutrient resorption worldwide (Vergutz et al., 2012). Consequently, nutrient resorption substantially affects primary productivity (Cleveland et al., 2013), especially in grasslands, where soil nutrient availability is usually low (Craine and Jackson, 2010). Microbial activities are vital for nutrient absorption by grassland species (Smith and Read, 2008). However, gaps remain in our knowledge of the roles that microorganisms (Sessitsch et al., 2004), especially arbuscular mycorrhizal fungi (AMF), play in plant nutrient resorption (Zhang et al., 2018).

Nutrient resorption efficiency is defined as the percentage of the total nutrient translocated from green leaves before leaf abscission (Aerts and Chapin, 2000). Plants with greater nutrient resorption efficiency might be more competitive in low-nutrient environments, such as overgrazed grasslands in Inner Mongolia (Han et al., 2008a), as reduced nutrient loss can reduce the need to absorb new nutrients from the soil (Aerts, 1996). This lessens plant dependence on soil nutrient availability and accordingly enhances adaptability in nutrient-poor habitats. Moreover, greater nutrient resorption tends to lead to lower nutrient concentrations and C/N ratios in senesced leaves, resulting in slow or incomplete litter decomposition (Stephan et al., 2011). This in turn lowers nutrient availability in the soil, which provides an advantage to species that are well-adapted to low-nutrient habitats (Aerts and Chapin, 2000). Therefore, nutrient resorption influences the quantity of nutrients that plants must absorb from the soil as well as the rate at which litter nutrients become available to plants and microbes in the soil by influencing senesced leaf nutrient concentrations, ultimately affecting plant community compositions (Zhang et al., 2018).

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* Corresponding author.
E-mail address: yangxin@nxu.edu.cn (X. Yang).

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Previous studies have mainly quantified the responses of plant nutrient resorption to climatic factors, such as nitrogen deposition and precipitation (Huang et al., 2009; Lü and Han, 2010; Shen et al., 2017). However, the roles and contributions of AMF to nutrient resorption are less well understood (Zhang et al., 2018). AMF can develop a symbiotic relationship with many plant species, assisting plants in taking up soil nutrients, particularly P (Smith and Read, 2008), and they can increase N and P concentrations in green leaves. AMF may alleviate P deficiencies in species with positive mycorrhizal growth response (MGR) or aggravate P deficiencies in species with negative MGR in grasslands mainly characterized by N limitation or co-limitation by N and P (Harpole et al., 2011). The relative nutrient resorption hypothesis posits the type of nutrient resorbed by plants depends on their nutrient limitation status (Chen et al., 2021; Güsewell, 2005). In this regard, plants have a tendency to increase nitrogen resorption efficiency (NRE) when N is limited (van Heerwaarden et al., 2003), while P-limited growth may similarly encourage plants to increase phosphorus resorption efficiency (PRE) (Güsewell, 2005; Lü et al., 2013). AMF may help species with positive MGR absorb N or P and thus change plants' nutrient limitation status, which may directly affect nutrient resorption. Thus, we speculated that AMF may alter nutrient resorption in plants by altering nutrient concentration and nutrient limitation status. Additionally, nutrient resorption may help determine the quality of senesced leaves added to soil (Killingbeck, 1996). The quality and decomposition rates of senesced leaves can control the long-term deposition of soil organic matter in grassland ecosystems. Thus, if AMF affect plant nutrient resorption, their effects on leaf litter decomposition and global carbon cycles may be significant (Phillips et al., 2013; Wurzburger and Enj, 2017). Exploring the effects of AMF on plant nutrient resorption and senesced leaf nutrient concentrations is crucial for understanding nutrient cycling in grassland ecosystems.

Overgrazing induces grassland degradation and has severely weakened grassland ecosystem structure and functions in China (Han et al., 2008a; Han et al., 2008b) and even globally (Eldridge et al., 2016; Herrero-Jáuregui and Oesterheld, 2018). In typical steppe grasslands, overgrazing results in a shift in the plant community from *Stipa krylovii* to *Artemisia frigida* and *Potentilla acaulis*. The proportions of *S. krylovii*, *P. acaulis*, and *A. frigida*, the dominant members of the plant community, exhibit different stages of degradation in typical steppe grasslands (Liu et al., 2002). *A. frigida* and *P. acaulis* are perennial, stoloniferous and dicotyledonous forbs, with high and positive MGR, whereas *S. krylovii* is a perennial monocotyledonous grass, with low and negative MGR (Fig. 1c) (Yang et al., 2018; Zhou et al., 2022). Our latest study revealed that AMF assisted plants in taking up P, not N, and enhanced the growth of species with positive MGR (Yang et al., 2018). The increased biomass with AMF might increase the demand for nutrients, ultimately reducing N concentration in green leaves (Zheng et al., 2018), which may aggravate N deficiencie for species with positive MGR. It has been reported that resorption efficiency decreases with increasing green leaf nutrient concentrations, and there is a positive relationship between senesced and green leaf N and P concentrations, based on a global data set (Kobe et al., 2005). Therefore, we hypothesized that (1) AMF would increase NRE and reduce PRE in *A. frigida* and *P. acaulis*, this is because AMF might help *A. frigida* and *P. acaulis* (species with high and positive MGR) absorb P, increase their biomass, and reduce their green leaf N concentration. AMF would reduce NRE and increase PRE for *S. krylovii*, this is because AMF might reduce P concentration in green leaf and biomass in *S. krylovii* (a species with low and negative MGR), and increase N concentration in green leaf; (2) AMF would increase the senesced leaf C:N ratios in *A. frigida* and *P. acaulis*, by reducing their senesced leaf N concentrations, but reduce the senesced leaf C:N ratio in *S. krylovii*, by increasing its senesced leaf N and P concentrations. Understanding the impact of AMF on nutrient conservation is especially important for understanding nutrient cycling processes and how plants adapt to nutrient-poor conditions in degraded grasslands.

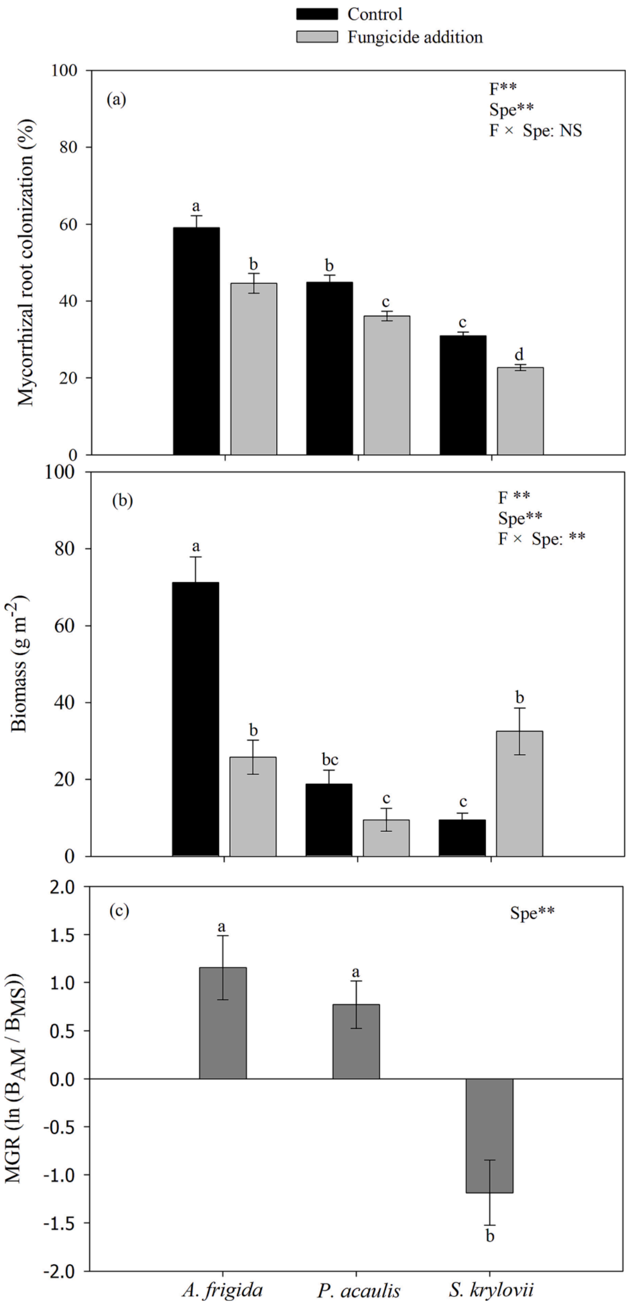

Fig. 1. Effects of fungicide addition (F), species (Spe) and their interaction on mycorrhizal root colonization (a), biomass (b) and mycorrhizal growth response (MGR)(c) of *A. frigida*, *P. acaulis*, and *S. Krylovii*. Data are means ± SE ($n = 6$). $^{**}p < 0.01$, NS $p > 0.05$. Letters above the bars show the results of Duncan's test. Different lowercase letters above bars indicate significant differences among different treatments at $p < 0.05$.

2. Materials and methods

2.1. Study area

This study was conducted on a temperate grassland community at the Duolun Station in Inner Mongolia, China (42°02′N, 116°17′E; elevation 1,324 m). The monthly mean temperature was 13.4 °C–21.5 °C from May to September. The mean annual precipitation is 378 mm (1953–2010). The study area was under heavy cattle grazing for a long period, until it was fenced in 2003. The plant species include *A. frigida*, *P. acaulis*, *S. krylovii*, *Cleistogenes squarrosa*, *Agropyron cristatum*, and *Leymus chinensis*, and the biomass of the first three species accounted for>70% of the aboveground biomass in this region (Yang et al., 2014). The soils at this site are Haplic Calcisols. The plant-available N (mg kg^{-1}), plant-available P (mg kg^{-1}), and soil bulk density (g cm^{-3}) were 11.51, 5.79, and 1.13, respectively, in the 0–10-cm soil layer. The amounts of precipitation during growing season (May to September) in 2015, 2016, and 2017 were 191, 146, and 241 mm, respectively.

2.2. Experimental design

An experiment was conducted using a randomized block design in a homogeneous and flat field in May 2015. Each block contained two plots with dimensions of 2 m × 2 m, and there were six blocks in total. AMF treatments (control vs. fungicide addition) were randomly assigned to plots within each block. Each plot was separated by a 2-m buffer. Every 2 weeks, the fungicide addition plots received 6 g of an active ingredient: benomyl (fungicide) dissolved in 10 L water m^{-2}, whereas 10 L water m^{-2} was applied to the control plots. These treatments were carried out from June to August each year from 2015 to 2017 (Kula and Hartnett, 2015; Yang et al., 2018). A total of 60 L water m^{-2} was applied to each plot each year, which is equivalent to 60 mm precipitation. The impact of benomyl on plant community compositions reported in previous studies is attributed to AMF suppression, with the lowest effects on other soil microbes or soil properties (Qiao et al., 2019; Zhang et al., 2016), which was also proved in our analysis (Tables S1 and S2).

2.3. Field sampling and chemical analyses

Green leaf materials were collected on August 17 (the time of peak biomass), and senesced leaf materials were sampled on October 25 (the end of the growing season during which all plant materials turn yellow and become ready for abscission) in 2017 (the third year of the onset of treatment). Two sampling quadrants with dimensions of 0.5 × 0.5 m were randomly laid out within each plot, and then all aboveground plant material from each species was clipped at the soil surface at each sampling time. Within each plot, the materials from the two sampling quadrants were pooled. The leaves and stems of *S. krylovii*, *A. frigida*, and *P. acaulis* were divided, dried at 65 °C for 48 h, and weighed separately. The sum of leaves and stems was calculated as the aboveground biomass of the three species separately. The leaves were ground using a ball mill. Plant N concentrations were analyzed using the FOSS Kjeltec 2300 Analyzer Unit (Hillerød, Sweden). Plant P concentrations were measured by first digesting the plant material in HNO_3–$HClO_4$ and subsequently measuring the concentrations using a spectrophotometer. Ammonium molybdate and ascorbic acid were used as color reagents (Carter & Gregorich 2008). Total carbon (C) concentrations in the plant material were determined using the $K_2Cr_2O_7$–H_2SO_4 oxidation method to quantify the plant C:N ratio.

Three soil cores (10-cm diameter × 10-cm depth) were collected on August 17 from each plot, thoroughly mixed into one composite soil sample, and then passed through a sieve (2 mm) to filter plant material and stones. The soil samples were then stored in an ice-box (4 °C), transported to the analysis center within 2 h, and divided into two parts. One part was used to determine the concentration of soil inorganic N and soil-available P, while the other part was stored at − 80 °C and then used to determine the relative abundance of microbial functional groups (gram-positive and gram-negative bacteria, saprophytic fungi, and AMF) using the phospholipid fatty acid (PLFA) method. Qualitative and quantitative PLFA analyses were performed using the Agilent 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA, USA) and SHERLOCK software (MIDI Inc., Newark, NJ, USA). The fatty acids a15:0, i15:0, i16:0, a17:0, and i17:0 were chosen to represent gram-positive bacteria; 16:1w7, cy17:0, and cy19:0 were chosen to represent gram-negative bacteria; 16:1w5c was used to represent AMF; and 18:2w6 and 18:2w9 were used to represent saprophytic fungi (Schnoor et al. 2011). Soil inorganic N (NH_4^+–N and NO_3^-–N) concentrations were determined using the Flow-Solution analyzer (Flowsys, Ecotech, Germany). Soil-available P concentration was determined using the Olsen method (Carter and Gregorich, 2008).

We randomly placed a 0.5 × 0.5 sample square in each plot, in which we randomly dug 10 plants for each species. The roots of each plant were sampled from 0 to 10-cm soil and then immediately transported to the laboratory, cleaned with tap water, and cut into 1-cm segments. The root segments were soaked in 10% KOH (w/v) at 90 °C in a water bath for 2 h, acidified with 2% (w/v) HCl for 5 min, and then washed and stained with 0.05% (w/v) trypan blue. Five segments were randomly chosen for each plant, and a total of 50 segments from each species were used to evaluate mycorrhizal root colonization (Trouvelot, 1986).

2.4. Resorption calculation and data analysis

Nutrient resorption efficiency was determined using the following equation:

$$\text{Nutrient resorption efficiency} = \left(1 - \frac{X_{sen}}{X_{gr}} MLCF\right) \times 100 \tag{1}$$

where X_{sen} and X_{gr} are the N or P concentration in senesced and green leaves, respectively. MLCF denotes the mass loss correction factor, which has a value of 0.640 for forbs and 0.713 for graminoids, according to Vergutz et al. (2012).

Resorbed leaf N:P ratios were calculated as follows:

Resorbed N:P = $([N]_{gr} - [N]_{sen})/([P]_{gr} - [P]_{sen})$, (2).

Where $[N]_{gr}$, $[P]_{gr}$, $[N]_{sen}$ and $[P]_{sen}$ represent green and senesced leaf N and P concentrations, respectively. $([N]_{gr} - [N]_{sen})$ and $([P]_{gr} - [P]_{sen})$ represent absolute N and P resorption, respectively (Sohrt et al., 2018).

The MGR of each species was calculated as follows:

MGR = ln (B_{AM} / B_{MS}), (3).

where B_{AM} is the mean dry biomass of plants without benomyl fungicide addition, and B_{MS} is the mean dry biomass of plants receiving benomyl fungicide addition (Hoeksema et al., 2010).

Levene's test was used to determine the normality of the data. Values greater than triple the standard deviation from the mean were considered non-normally distributed, resulting in one outlier being replaced with the mean value prior to all analysis. Green and senesced leaf N:P ratios ($[N:P]_{gr}$, $[N:P]_{sen}$) and senesced leaf C:N ratio ($[C:N]_{sen}$) were log-transformed before analyses (Isles, 2020). A two-way ANOVA was performed to detect both interactions and primary effects of blocks, fungicide additions, the plant species, and their interactions on mycorrhizal root colonization, biomss, MGR as well as $[N]_{gr}$, $[P]_{gr}$, $[N]_{sen}$, $[P]_{sen}$, $\ln[N:P]_{gr}$, $\ln[N:P]_{sen}$, $\ln[C:N]_{sen}$, and NRE and PRE for each of the three species. Duncan's test ($p < 0.05$) was used to evaluate all of the indices among different treatments. SPSS (version 17.0; SPSS Inc., New York, USA) was used to perform all statistical analyses.

3. Results

3.1. Mycorrhizal root colonization

Both fungicide addition and plant species significantly affected on mycorrhizal root colonization (Table S3; $p < 0.01$, Fig. 1a). Fungicide addition reduced mycorrhizal root colonization in *A. frigida*, *P. acaulis*, and *S. Krylovii* by 24.5%, 19.6%, and 26.8%, respectively (Fig. 1a).

Fungicide addition reduced the biomass of *A. frigida* by 63%, had no significant effects on the biomass of *P. acaulis*, and increased the biomass of *S. krylovii* by 241% ($p < 0.05$, $p > 0.05$, and $p < 0.05$, respectively, Fig. 1b). *A. frigida* and *P. acaulis* had a high and positive MGR, whereas *S. Krylovii* had a low and negative one (Fig. 1c).

3.2. Green leaf N and P concentrations

Fungicide addition significantly affected $[N]_{gr}$ (Table S3; $p < 0.01$, Fig. 2a), increasing $[N]_{gr}$ in *A. frigida*, *P. acaulis*, and *S. Krylovii* by 24%, 51%, and 47%, respectively (Fig. 2a). Significant species effects on $[N]_{gr}$ and $[P]_{gr}$ were observed (Table S3; $p < 0.01$, Fig. 2a and b), and the interaction between fungicide addition and species significantly affected $[P]_{gr}$ (Table S3; $p < 0.01$, Fig. 2b). Fungicide addition reduced $[P]_{gr}$ by 18% in *A. frigida* but had no significant effect on $[P]_{gr}$ in *P. acaulis* and *S. Krylovii* (Fig. 2b).

3.3. NRE and PRE

NRE and PRE were significantly affected by plant species (Table S3; $p < 0.05$ and $p < 0.01$, respectively, Fig. 3a and b), and significant interactive effects of fungicide addition and species on NRE and PRE were observed (Table S3; $p < 0.01$ and $p < 0.01$, respectively, Fig. 3a and b). Fungicide addition decreased NRE and PRE in *A. frigida* by 13% and 14%, respectively (Fig. 3a and b), increased NRE and PRE in *S. krylovii* by 26% and 15.4%, respectively (Fig. 3a and b), and increased the PRE of *P. acaulis* by 9.0% (Fig. 3b). With fungicide addition, the NRE of *P. acaulis* and *S. krylovii* was higher than that of *A. frigida*; without fungicide addition, the NRE of *A. frigida* and *P. acaulis* was higher than that of *S. krylovii* (Fig. 3a).

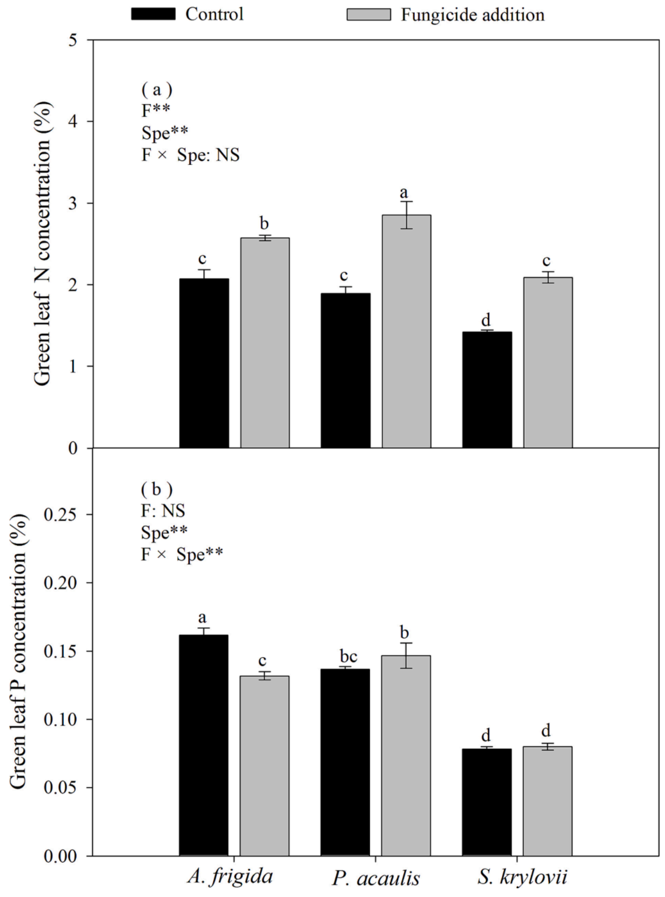

Fig. 2. Effects of fungicide addition (F), species (Spe) and their interaction on green leaf N (a) and P (b) concentration in *A. frigida*, *P. acaulis*, and *S. Krylovii*. Data are means ± SE (n = 6). ** $p < 0.01$, NS $p > 0.05$. Letters above the bars show the results of Duncan's test. Different lowercase letters above bars indicate significant differences among different treatments at $p < 0.05$.

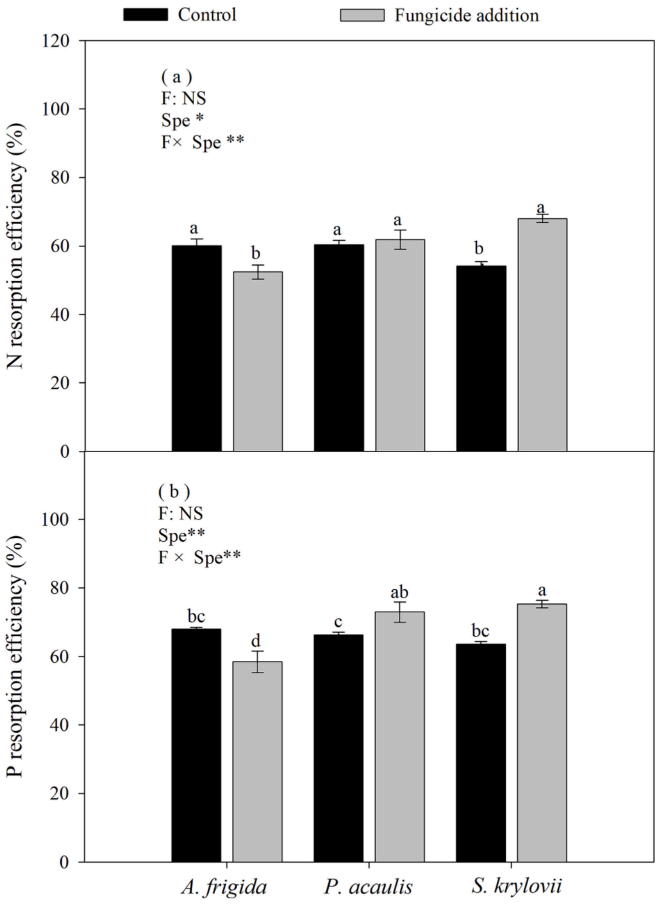

Fig. 3. Effects of fungicide addition (F), species (Spe) and their interaction on N (a) and P (b) resorption efficiency in *A. frigida*, *P. acaulis*, and *S. Krylovii*. Data are means ± SE (n = 6). ** $p < 0.01$, * $p < 0.05$, NS $p > 0.05$. Letters above the bars show the results of Duncan's test. Different lowercase letters above bars indicate significant differences among different treatments at $p < 0.05$. Values greater than triple the standard deviation from the mean were considered non-normally distributed, resulting in one outlier being replaced with the mean value prior to analysis (b).

3.4. Senesced leaf N and P concentrations

Both fungicide addition and plant species significantly affected $[N]_{sen}$ (Table S3; $p < 0.01$, Fig. 4a), and the interaction between fungicide addition and species was also significant (Table S3; $p < 0.01$, Fig. 4a). Fungicide addition increased $[N]_{sen}$ in *A. frigida* and *P. acaulis* by 46% and 42%, respectively ($p < 0.05$, Fig. 4a) but had no significant effect on that in *S. krylovii* ($p > 0.05$, Fig. 4a). $[P]_{sen}$ differed significantly among species (Table S3; $p < 0.01$, Fig. 4b). The interaction between fungicide addition and species significantly affected $[P]_{sen}$ (Table S3; $p < 0.01$, Fig. 4b). With fungicide addition, $[N]_{sen}$ was ranked in the order of *A. frigida* > *P. acaulis* > *S. krylovii* ($p < 0.05$, Fig. 4a). Without fungicide addition, the $[N]_{sen}$ of *A. frigida* and *P. acaulis* was higher than that of *S. krylovii* ($p < 0.05$, Fig. 4a), similar to $[P]_{sen}$ (Fig. 4b).

3.5. Green and senesced leaf N:P and C:N ratios

Fungicide addition and plant species significantly affected $\ln[N{:}P]_{gr}$ (Table S3; $p < 0.01$, Fig. 5). Fungicide addition increased $\ln[N{:}P]_{gr}$ in *A. frigida, P. acaulis, and S. krylovii* by 16%, 13%, and 12%, respectively, which were all greater than ln16 (Fig. 5). N:P ratio>16 generally means that P is limiting (Koerselman and Meuleman, 1996). Therefore, there was a P limitation for all species with fungicide addition.

Moreover, fungicide addition and plant species both significantly

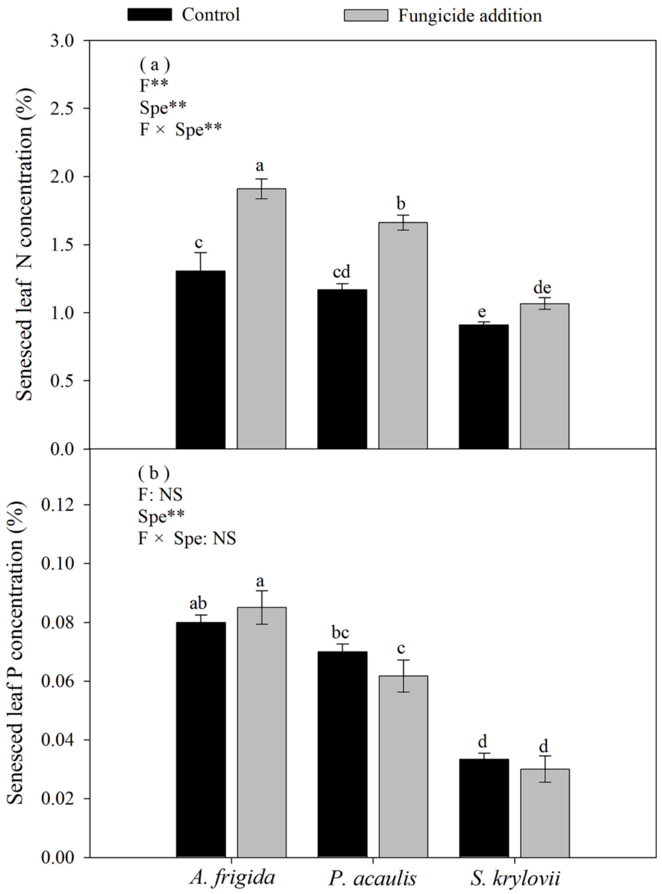

Fig. 4. Effects of fungicide addition (F), species (Spe) and their interaction on senesced leaf N (a) and P (b) concentration in *A. frigida*, *P. acaulis*, and *S. Krylovii*. Data are means ± SE (n = 6). ** $p < 0.01$, NS $p > 0.05$. Letters above the bars show the results of Duncan's test. Different lowercase letters above bars indicate significant differences among different treatments at $p < 0.05$.

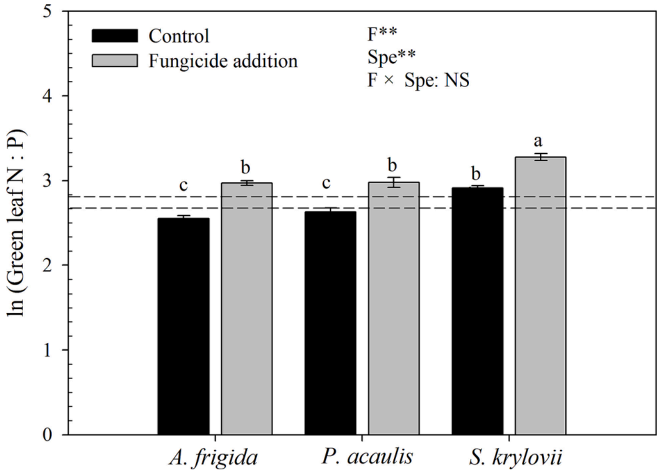

Fig. 5. Effects of fungicide addition (F), species (Spe) and their interaction on green leaf N:P ratio in *A. frigida*, *P. acaulis*, and *S. Krylovii*. Data are means ± SE (n = 6). ** $p < 0.01$, NS $p > 0.05$. Letters above the bars show the results of Duncan's test. Different lowercase letters above bars indicate significant differences among different treatments at $p < 0.05$. The above short dashed line represents ln16, and the below short dashed line represents ln14.

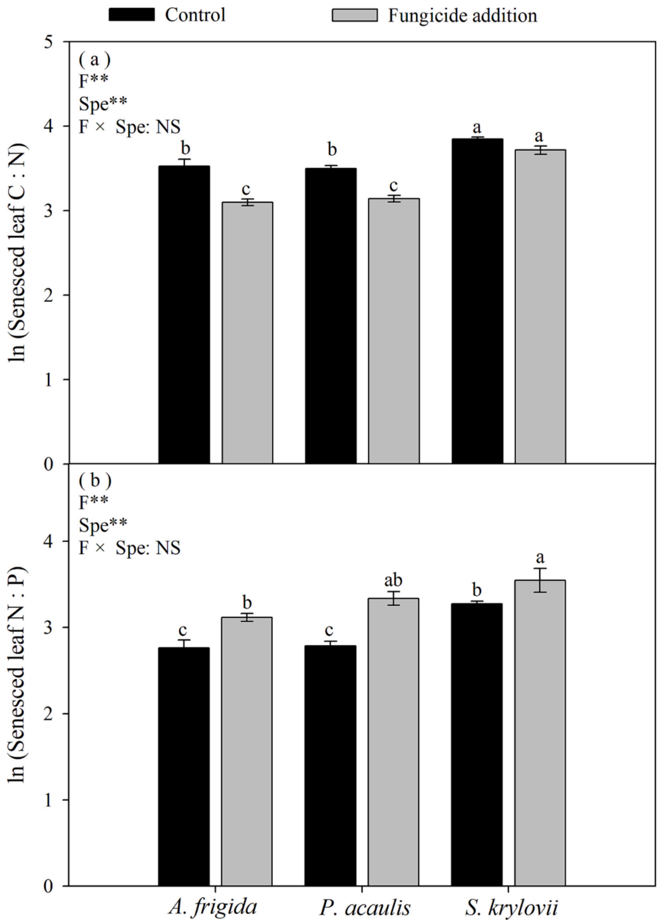

Fig. 6. Effects of fungicide addition (F), species (Spe) and their interaction on senesced leaf C:N (a) and N:P ratio (b) in *A. frigida*, *P. acaulis*, and *S. Krylovii*. Data are means ± SE (n = 6). ** $p < 0.01$, NS $p > 0.05$. Letters above the bars show the results of Duncan's test. Different lowercase letters above bars indicate significant differences among different treatments at $p < 0.05$.

affected $\ln[C:N]_{sen}$ and $\ln[N:P]_{sen}$ (Table S3; $p < 0.01$, Fig. 6a and b). $\ln[C:N]_{sen}$ in *A. frigida* and *P. acaulis* reduced by 12% and 10%, respectively (Fig. 6a) but $\ln[N:P]_{sen}$ in *A. frigida*, *P. acaulis*, and *S. krylovii* increased by 13%, 20%, and 8%, respectively (Fig. 6b) with fungicide addition. Regardless of fungicide addition, $\ln[C:N]_{sen}$ was greater in *S. krylovii* than in *A. frigida* and *P. acaulis* (Fig. 6a).

3.6. Relationships between NRE, PRE, $[N:P]_{gr}$, and biomass

Biomass of *A. frigida* was positively correlated with NRE and PRE ($p < 0.05$, $r^2 = 0.50$; $p < 0.01$, $r^2 = 0.50$; Fig. 7a and d). Biomass of *S. krylovii* was positively correlated with NRE and PRE ($p = 0.06$, $r^2 = 0.31$; $p < 0.05$, $r^2 = 0.41$; Fig. 7c and f).

Negative correlations were observed between NRE, PRE, and $\ln[N:P]_{gr}$ for *A. frigida* ($p < 0.05$, $r^2 = 0.46$; $p < 0.05$, $r^2 = 0.43$; Fig. 8a and d), whereas positive correlations were observed between PRE and $\ln[N:P]_{gr}$ for *P. acaulis* ($p < 0.05$, $r^2 = 0.45$; Fig. 8e) and between NRE, PRE, and $\ln[N:P]_{gr}$ for *S. krylovii* ($p < 0.01$, $r^2 = 0.69$; $p < 0.05$, $r^2 = 0.49$; Fig. 8c and f).

4. Discussion

Partly support our first hypothesis, our results showed that AMF significantly increased NRE and PRE in *A. frigida* and reduced PRE in *P. acaulis* and NRE and PRE in *S. krylovii*. Such an increase in the NRE and PRE of *A. frigida* might primarily result from the increased biomass of

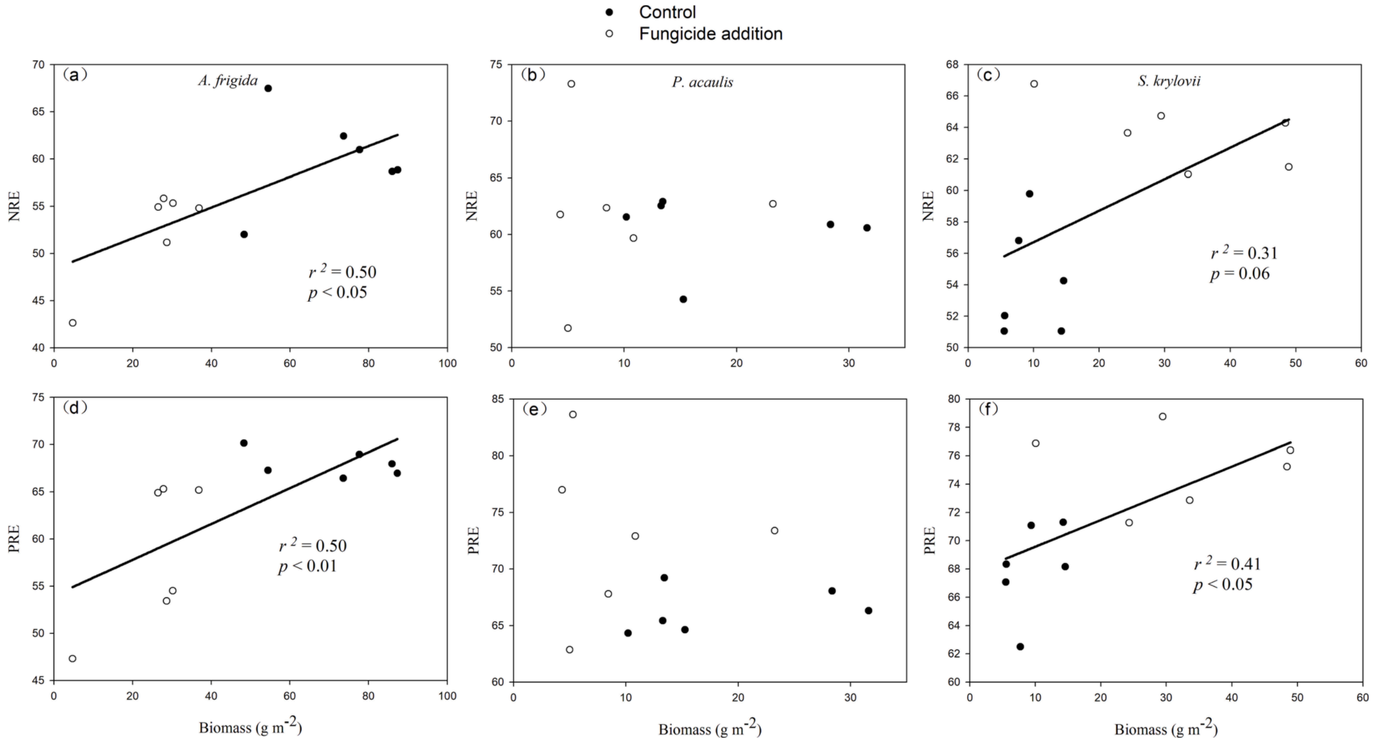

Fig. 7. Relationships between NRE, PRE and biomass of *A. frigida* (a and d), *P. acaulis* (b and e) and *S. krylovii* (c and f). Values greater than triple the standard deviation from the mean were considered non-normally distributed, resulting in one outlier being replaced with the mean value prior to analysis (f).

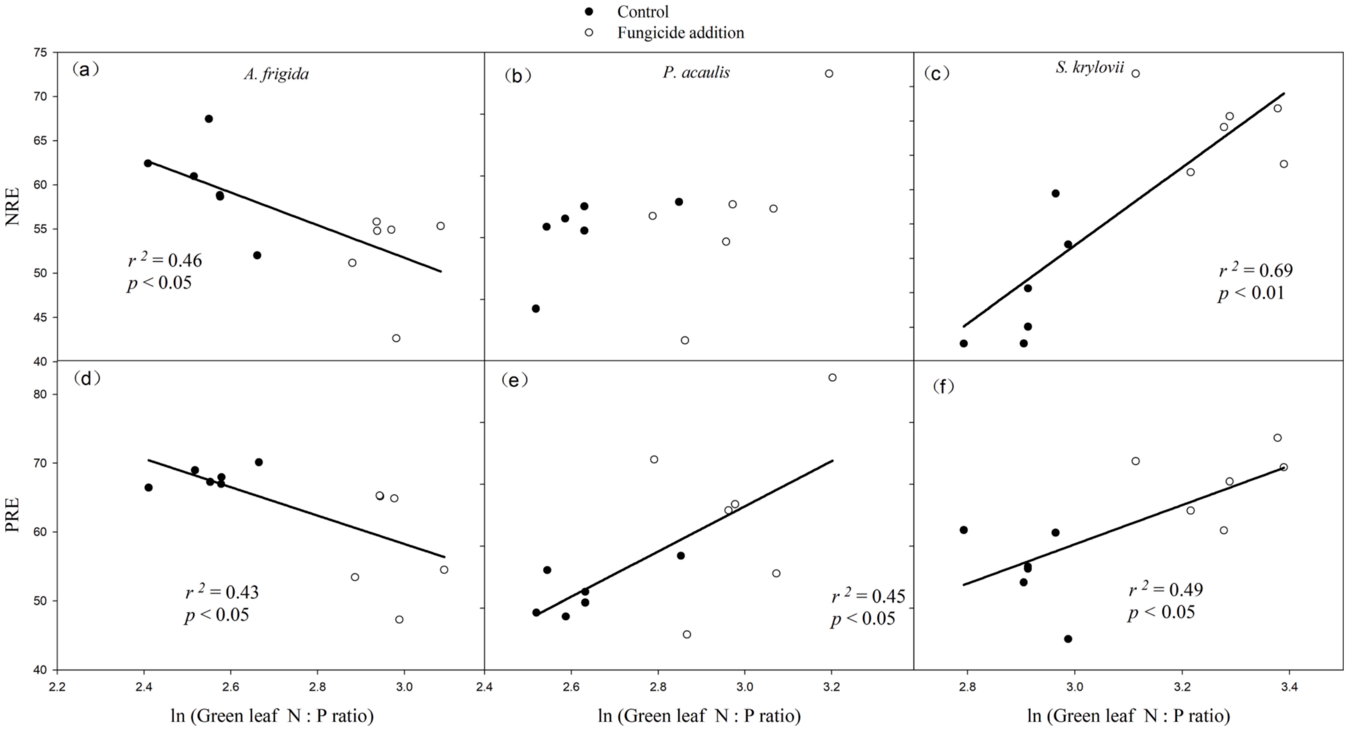

Fig. 8. Relationships between NRE and green leaf N:P ratio, PRE and green leaf N:P ratio for *A. frigida* (a and d), *P. acaulis* (b and e) and *S. krylovii* (c and f). Values greater than triple the standard deviation from the mean were considered non-normally distributed, resulting in one outlier being replaced with the mean value prior to analysis (f).

A. frigida with AMF. We found biomass of *A. frigida* was positively correlated with NRE and PRE, suggesting that plants tend to increase nutrient resorption as they grow because of increased nutrient requirements (Zheng et al., 2018). The increased biomass of *A. frigida* with AMF diluted the green leaf N concentrations (Fig. S1a) (Wright and Westoby, 2003; You et al., 2018). However, in contrast to $[N]_{gr}$ in *A. frigida*, a positive relationship was observed between $[P]_{gr}$ and biomass in *A. frigida* (Fig. S1d), indicating that *A. frigida* has a higher competitive ability for P than N, especially with AMF (Lambers, 2022). Similarly, a positive correlation between nutrient resorption and plants biomass has also been found in previous studies (Ren et al., 2015; Zheng et al., 2018), suggesting that an increase in biomass enhances nutrient withdrawn from senesced leaves. Moreover, Koerselman and Meuleman (1996) suggested that an N:P molar ratio < 14 indicates that N is limiting, that > 16 indicates that P is limiting, and that between 14 and 16 indicates co-limitation by N and P. The $\ln[\text{N:P}]_{gr}$ value was 2.55 in *A. frigida* (<ln14), and it was an N limitation for *A. frigida* without fungicide addition. This was consistent with the findings of a previous study in that it was mainly N limitation (Bai et al., 2015). AMF alleviate P limitation and lead to N limitation in *A. frigida*. Theoretically, according to the relative nutrient resorption hypothesis, AMF would reduce the PRE of *A. frigida* under N limitation conditions, and $\ln[\text{N:P}]_{gr}$ is expected to show a negative relationship with NRE but a positive relationship with PRE. However, the result showed that AMF increased the PRE of *A. frigida*, and there was a negative relationship between PRE and $\ln[\text{N:P}]_{gr}$. It is likely that AMF-induced increase in *A. frigida* biomass primarily increased NRE and PRE, resulting from increased nutrient requirement as plants grow. In other words, for the *A. frigida* response, AMF-induced biomass changes have a more important role than AMF-caused changes in root nutrient acquisition. Furthermore, the positive NRE–PRE relationship is probably attributed to increased nutrient limitation as plants grow (Fig. S2a). However, for *S. krylovii*, AMF substantially reduced its biomass, and there were positive relationships between NRE/PRE and biomass of *S. krylovii*. It is likely that AMF-induced biomass changes decreased the NRE and PRE of *S. krylovii* with AMF symbiosis. AMF reduced the biomass of *S. krylovii*; thus, nutrients available in soil are sufficient to fulfill plant's nutrient requirements, which weakens the internal nutrient cycling (i.e., decreases in NRE and PRE). Thus, AMF-induced biomass changes in *A. frigida* and *S. krylovii* primarily controlled their nutrient concentration and resorption.

Our results also showed that AMF reduced PRE in *P. acaulis*. AMF reduced $[\text{N}]_{gr}$ in *P. acaulis*, which resulted in its N limitation (Koerselman and Meuleman, 1996). Moreover, there was a positive relationship between PRE and $\ln[\text{N:P}]_{gr}$ in *P. acaulis*. Therefore, to compensate for N deficiency caused by AMF, *P. acauli* reduced its PRE and withdrew less P from senesced leaves (Huang et al., 2016). For *P. acaulis*, AMF-induced changes in root nutrient acquisition have a more important role than AMF-caused biomass changes; that is, the relative nutrient resorption hypothesis is a more important mechanism (Rejmánková, 2005; Reed et al., 2012). In the present study, fungicide addition reduced the biomass of *A. frigida* but increased that of *S. krylovii*. Such changes in biomass were mainly attributed to the difference in mycorrhizal root colonization and MGR for the three species. Moreover, the suppression of AMF might reduce the competitive ability of *A. frigida*, which has positive MGR and high mycorrhizal root colonization, thereby increasing the competitive ability of *S. krylovii*, which has negative MGR and low mycorrhizal root colonization (Yang et al., 2014). In addition, the precipitation was higher during the growing season in 2017 in our study site (Zhang et al., 2022). The increase in plant biomass in the presence of AMF is more under high precipitation than under low precipitation, and high precipitation can facilitate the growth of forbs more than that of grasses (DeMalach et al., 2017). AMF affects the biomass of *A. frigida*, *P. acaulis* and *S. krylovii* not only through changing mycorrhizal responsiveness but also altering competitive interaction among them, potentially leading to cascade influences on plant nutrient resorption. Our results suggest that AMF form mutualistic symbiotic associations with *A. frigida*, which promote *A. frigida* adaptations to nutrient-poor conditions, not only because AMF help *A. frigida* absorb P (Smith and Read, 2008) but also because AMF increase the nutrient resorption of *A. frigida*, that is, AMF enhance nutrient conservation strategies (Zhang et al., 2018). Grassland degradation related to heavy grazing pressure is often associated with the removal of nutrients from soil (Han et al., 2008a). In our study sites, the dominant grass species *S. krylovii* lost its competitive advantage to forbs such as *A. frigida* under heavy grazing. Our results showed that AMF increased the nutrient resorption of *A. frigida* and reduced that of *S. krylovii*. Plants with greater NRE could be more competitive in low-nutrient environments (Aerts, 1996). Our results may partly explain why *A. frigida* replaces *S. krylovii* as the dominant species in degraded grasslands (Liu et al., 2002) and imply that AMF might play a vital role in vegetation succession in grassland degradation in Inner Mongolia, China.

Our results showed that AMF reduced $[\text{N}]_{gr}$ in all three species. This result was inconsistent the results of previous studies, which reported that AMF could enable plants to absorb N (Leigh et al., 2009). AMF increased the biomass of *A. frigida*, and a negative relationship was found between $[\text{N}]_{gr}$ and its biomass (Fig. S1a). Consequently, the AMF-induced increase in biomass led to a reduced in $[\text{N}]_{gr}$ in *A. frigida*. According to our results, this was mainly N limitation (Koerselman and Meuleman, 1996). The positive correlation between $[\text{N}]_{gr}$ and *S. krylovii* biomass (Fig. S1c) indicated that *S. krylovii* had a higher competitive ability for N (Xia and wan, 2008). In our study, $[\text{P}]_{gr}$ in *A. frigida* increased with AMF, which is consistent with the observation that AMF generally help plants absorb P (Smith and Read, 2008). Compared with *P. acaulis* and *S. krylovii*, *A. frigida* has higher MGR and mycorrhizal root colonization. The interactive effects on $[\text{P}]_{gr}$ between fungicide addition and species indicated that AMF mainly helps plants with high mycorrhizal dependency absorb P (Yang et al., 2018).

Partly in support of our second hypothesis, our results showed that AMF increased leaf C:N ratios in *A. frigida* and *P. acaulis*; this finding can be attributed to the AMF-induced reduction in $[\text{N}]_{gr}$ in *A. frigida* and *P. acaulis* as well as the positive relationship between $[\text{N}]_{gr}$ and $[\text{N}]_{sen}$ (Fig. S3). This phenomenon has also been found in a global data set (Kobe et al., 2005). The positive relationship between senesced and green leaf nutrient concentrations was attributed to physiological (such as phloem transport) and biochemical (such as solubility of compounds containing nitrogen) constraints to nutrient resorption (Aerts and Chapin, 2000; Kobe et al., 2005). The increased leaf C:N ratios in *A. frigida* and *P. acaulis* caused by AMF indicated that AMF might inhibit litter degradation, which might drive the plant community to become more N limited. Greater resorption of N may result in lower N availability in the soil, as N-depleted litter undergoes less effective microbial decomposition, resulting in slower or incomplete litter decomposition (Güsewell and Gessner, 2009). In this way, AMF not only influences nutrient resorption but also nutrient cycling by producing plants with lower quality, slower-cycling litter. Additionally, we found that the ln(senesced leaf C:N ratio) was lower in *A. frigida* than in *S. krylovii* and that AMF significantly increased the biomass of *A. frigida*, whereas it reduced the biomass of *S. krylovii*. This finding indicates that more high-quality litter will descend and become incorporated into the soil, thereby returning more nutrients to the soil with progressing grassland degradation. However, compared with fungicide addition, AMF significantly increased the ln(senesced leaf C:N ratio) in *A. frigida* and *P. acaulis*, which might lead to slower or incomplete litter decomposition (Stephan et al., 2011). Overall, our results suggest that predicting the role of AMF in nutrient cycling outcomes may be more complex than previously considered.

Our results demonstrated that fungicide addition significantly reduced the mycorrhizal root colonization and the PLFA concentrations of AMF but had no significant effects on those of other soil microbes (Table S1). Previous studies on fungicide addition also revealed that it had no significant effects on soil biota and nutrient availability (Qiao et al., 2019; Zhang et al., 2016). Although the use of fungicide may control fungal pathogens, which indirectly facilitates plant growth (Maron et al. 2011), their effects could be negligible according to recent studies (Qiao et al., 2019; Zhang et al., 2016).

5. Conclusion

Previous studies have largely focused on the role of AMF in plant nutrient absorption. However, we found that AMF also had important effects on plant nutrient resorption, which in turn would affect senesced leaf quality and nutrient return to the soil (Zhang et al., 2018). *A. frigida*, *P. acaulis*, and *S. krylovii*, the three dominant species in degraded grassland, exhibited different patterns of nutrient resorption with AMF. AMF increased internal nutrient cycling in *A. frigida*, as evidenced by greater NRE and PRE in *A. frigida*, and reduced internal nutrient cycling in *S. krylovii*, as evidenced by reduced NRE and PRE in *S. krylovii*. The inconsistent nutrient resorption responses of *A. frigida* and *S. krylovii* to AMF were primarily attributed to the changes in biomass in the presence of AMF, thereby changing the nutrient requirements. For *P. acaulis*, the reduction in PRE with AMF was because AMF-induced its N limitation, which is consistent with the relative nutrient resorption hypothesis. Moreover, our results showed that AMF increased the senesced leaf C:N ratio in *A. frigida* and *P. acaulis*, which might lead to slower or incomplete litter decomposition, ultimately affecting nutrient cycling in degraded grasslands in Inner Mongolia, China. Unfortunately, because the functions of AMF cannot be completely suppressed, their effects on plant nutrient resorption may be underestimated.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110195.

References

Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? J. Ecol. 84 (4), 597.

Aerts, R., Chapin, F.S., 2000. The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns. Advances in ecological research 30, 1–67. https://doi.org/10.1016/s0065-2504(08)60016-1.

Bai, W., Guo, D., Tian, Q., Liu, N., Cheng, W., Li, L., Zhang, W.-H., McCulley, R., 2015. Differential responses of grasses and forbs led to marked reduction in below-ground productivity in temperate steppe following chronic N deposition. Journal of Ecology 103 (6), 1570–1579.

Carter, M.R., Gregorich, E.G., 2008. Soil Sampling and Methods of Analysis, 2nd edn. CRC Press, Boca Raton.

Chen, H., Reed, S.C., Lü, X., Xiao, K., Wang, K., Li, D., 2021. Coexistence of multiple leaf nutrient resorption strategies in a single ecosystem. Science of The Total Environment 772, 144951. https://doi.org/10.1016/j.scitotenv.2021.144951.

Cleveland, C.C., Houlton, B.Z., Smith, W.K., Marklein, A.R., Reed, S.C., Parton, W., Del Grosso, S.J., Running, S.W., 2013. Patterns of new versus recycled primary production in the terrestrial biosphere. Proc Natl Acad Sci U S A 110 (31), 12733–12737.

Craine, J.M., Jackson, R.D., 2010. Plant nitrogen and phosphorus limitation in 98 North American grassland soils. Plant and Soil 334, 73–84. https://doi.org/10.1007/s11104-009-0237-1.

DeMalach, N., Zaady, E., Kadmon, R., 2017. Contrasting effects of water and nutrient additions on grassland communities: A global meta-analysis. Global Ecology and Biogeography 26, 983–992. https://doi.org/10.1111/geb.12603.

Eldridge, D.J., Poore, A.G.B., Ruiz-Colmenero, M., Letnic, M., Soliveres, S., 2016. Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. Ecological Applications 26, 1273–1283. https://doi.org/10.1890/15-1234.

Güsewell, S., 2005. High nitrogen: phosphorus ratios reduce nutrient retention and second-year growth of wetland sedges. New Phytologist 166, 537–550. https://doi.org/10.1111/j.1469-8137.2005.01320.x.

Güsewell, S., Gessner, M.O., 2009. N : P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. Functional Ecology 23, 211–219. https://doi.org/10.1111/j.1365-2435.2008.01478.x.

Han, G., Hao, X., Zhao, M., Wang, M., Ben, H.E., Walter, W., Wang, M., 2008a. Effect of grazing intensity on carbon and nitrogen in soil and vegetation in a meadow steppe in Inner Mongolia. Agriculture, Ecosystems & Environment 125, 21–32. https://doi.org/10.1016/j.agee.2007.11.009.

Han, J.G., Zhang, Y.J., Wang, C.J., Bai, W.M., Wang, Y.R., Han, G.D., Li, L.H., 2008b. Rangeland degradation and restoration management in China. Rangeland Journal 30, 233–239. https://doi.org/10.1071/RJ08009.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., Smith, J.E., 2011. Nutrient co-limitation of primary producer communities. Ecology Letters 14, 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x.

Herrero-Jáuregui, C., Oesterheld, M., 2018. Effects of grazing intensity on plant richness and diversity: a meta-analysis. Oikos 127, 757–766. https://doi.org/10.1111/oik.04893.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Umbanhowar, J., 2010. A meta-analysisof context-dependency in plant response to inoculation withmycorrhizal fungi. Ecology Letters 13, 394–407. https://doi.org/10.1111/j.1461-0248.2009.01430.x.

Huang, J., Yu, H., Li, L., Yuan, Z., Bartels, S., 2009. Water supply changes N and P conservation in a perennial grass Leymus chinensis. Journal of Integrative Plant Biology 51, 1050–1056. https://doi.org/10.1111/j.1744-7909.2009.00872.x.

Huang, J., Yu, H., Lin, H., Zhang, Y.u., Searle, E.B., Yuan, Z., 2016. Phosphorus amendment mitigates nitrogen addition-induced phosphorus limitation in two plant species in a desert steppe, China. Plant Soil 399 (1-2), 221–232.

Isles, P.D.F., 2020. The misuse of ratios in ecological stoichiometry. Ecology 101 (11), e03153. https://doi.org/10.1002/ecy.3153.

Killingbeck, K.T., 1996. Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. Ecology 77, 1716–1727. https://doi.org/10.2307/2265777.

Kobe, R.K., Lepczyk, C.A., Iyer, M., 2005. Resorption efficiency decreases with increasing green leaf nutrients in a global data set. Ecology 86, 2780–2792. https://doi.org/10.1890/04-1830.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied 33 (6), 1441.

Kula, A.A.R., Hartnett, D.C., 2015. Effects of mycorrhizal symbiosis on aboveground arthropod herbivory in tallgrass prairie: an in situ experiment. Plant Ecology 216, 589–597. https://doi.org/10.1007/s11258-015-0461-0.

Lambers, H., 2022. Phosphorus Acquisition and Utilization in Plants. Annual Review of Plant Biology 73, 17–42. https://doi.org/10.1146/annurev-arplant-102720-125738.

Leigh, J., Hodge, A., Fitter, A.H., 2009. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. New Phytologist 181, 199–207. https://doi.org/10.1111/j.1469-8137.2008.02630.x.

Liu, Z. L., Wang, W., Hao, D. Y., and Liang, C. Z. (2002). Probes on the Degeneration and Recovery Succession Mechanisms of Inner Mongolia Steppe. Journa1 of Arid Land Resources and Environment 16:84-91. DOI: 10.1088/1009-1963/11/5/313.

Lü, X.T., Han, X.G., 2010. Nutrient resorption responses to water and nitrogen amendment in semi-arid grassland of Inner Mongolia, China. Plant and Soil 327, 481–491. https://doi.org/10.1007/s11104-009-0078-y.

Lü, X., Reed, S., Yu, Q., He, N., Wang, Z., Han, X., 2013. Convergent responses of nitrogen and phosphorus resorption to nitrogen inputs in a semiarid grassland. Global Change Biology 19, 2775–2784. https://doi.org/10.1111/gcb.12235.

Maron, J.L., Marler, M., Klironomos, J.N., Cleveland, C.C., 2011. Soil fungal pathogens and the relationship between plant diversity and productivity. Ecology letters 14, 36–41. https://doi.org/10.1111/j.1461-0248.2010.01547.x.

Phillips, R.P., Edward, B., Midgley, M.G., 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytologist 199, 41–51. https://doi.org/10.1111/nph.12221.

Qiao, Y., Bai, Y., Zhang, Y., She, W., Lai, Z., Qin, S., 2019. Arbuscular mycorrhizal fungi shape the adaptive strategy of plants by mediating nutrient acquisition in a shrub-dominated community in the Mu Us Desert. Plant and Soil 443, 549–564. https://doi.org/10.1007/s11104-019-04253-0.

Reed, S.C., Townsend, A.R., Davidson, E.A., Cleveland, C.C., 2012. Stoichiometric patterns in foliar nutrient resorption across multiple scales. New Phytologist 196, 173–180. https://doi.org/10.1111/j.1469-8137.2012.04249.x.

Rejmánková, E., 2005. Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. New Phytologist 167, 471–482. https://doi.org/10.1111/j.1469-8137.2005.01449.x.

Ren, H., Xu, Z., Huang, J., Lu, X., Zeng, D.-H., Yuan, Z., Han, X., Fang, Y., 2015. Increased precipitation induces a positive plant-soil feedback in a semi-arid grassland. Plant and Soil 389, 211–223. https://doi.org/10.1007/s11104-014-2349-5.

Schnoor, T.K., Mårtensson, L.-M., Olsson, P.A., 2011. Soil disturbance alters plant community composition and decreases mycorrhizal carbon allocation in a sandy grassland. Oecologia 167 (3), 809–819.

Sessitsch, A., Gyamfi, S., Tscherko, D., Gerzabek, M.H., Kandeler, E., 2004. Activity of microorganisms in the rhizosphere of herbicide treated and untreated transgenic glufosinate-tolerant and wildtype oilseed rape grown in containment. Plant and Soil 266, 105–116. https://doi.org/10.1007/s11104-005-7077-4.

Shen, Y., Yang, X., Sun, X., Chen, W., Yang, G., Liu, N., Chen, J., Zhang, Y., 2017. Increased precipitation modulates the influence of nitrogen and litter inputs on the nutrient resorption proficiency rather than efficiency of Leymus chinensis. Plant Ecology 219, 217–230. https://doi.org/10.1007/s11258-017-0790-2.

Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis, 3th edition. Elsevier, New York.

Sohrt, J., Herschbach, C., Weiler, M., 2018. Foliar P-but not N resorption efficiency depends on the P-concentration and the N: P ratio in trees of temperate forests. Trees 32, 1443–1455. https://doi.org/10.1007/s00468-018-1725-9.

Stephan, H., Sylvain, C., Sandra, B., Ira, T.H., 2011. Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. New Phytologist 189, 950–965. https://doi.org/10.1111/j.1469-8137.2010.03483.x.

Trouvelot, A. 1986. Mesure du taux de mycorhization VA d'un systeme radiculaire. Recherche de methodes d'estimation ayant unesignificantion fonctionnelle. pp 217–221 in Physiological and genetical aspects of mycorrhizae = aspects physiologiques Etgenetiques des mycorhizes: Proceedings of the European Symposium on Mycorrhizae, Dijon, 1–5 July. INRA, Paris, France.

van Heerwaarden, L.M., Toet, S., Aerts, R., 2003. Nitrogen and phosphorus resorption efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen fertilization. Journal of Ecology 91, 1060–1070. https://doi.org/10.1046/j.1365-2745.2003.00828.x.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., Jackson, R.B., 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecological Monographs 82, 205–220. https://doi.org/10.1890/11-0416.1.

Wright, I.J., Westoby, M., 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. Functional Ecology 17 (1), 10–19. https://doi.org/10.1046/j.1365-2435.2003.00694.x.

Wurzburger, N., Enj, B., 2017. Experimental evidence that mycorrhizal nitrogen strategies affect soil carbon. Ecology 98, 1491–1497. https://doi.org/10.1001/ecy.1827.

Xia, J., Wan, S., 2008. Global response patterns of terrestrial plant species to nitrogen addition. New Phytologist 179, 428–439. https://doi.org/10.1111/j.1469-8137.2008.02488.x.

Yang, G., Liu, N., Lu, W., Wang, S., Kan, H., Zhang, Y., Xu, L., Chen, Y., van der Heijden, M., 2014. The interaction between arbuscular mycorrhizal fungi and soil phosphorus availability influences plant community productivity and ecosystem stability. Journal of Ecology 102 (4), 1072–1082.

Yang, X., Shen, Y., Liu, N., Wilson, G.W.T., Cobb, A.B., Zhang, Y., 2018. Defoliation and arbuscular mycorrhizal fungi shape plant communities in overgrazed semiarid grasslands. Ecology 99, 1847–1856. https://doi.org/10.1002/ecy.2401.

You, C., Wu, F., Yang, W., Xu, Z., Tan, B., Yue, K., Ni, X., 2018. Nutrient-limited conditions determine the responses of foliar nitrogen and phosphorus stoichiometry to nitrogen addition: A global meta-analysis. Environmental Pollution 241, 740–749. https://doi.org/10.1016/j.envpol.2018.06.018.

Zhang, B., Li, S., Chen, S., Ren, T., Yang, Z., Zhao, H., Liang, Y., Han, X., 2016. Arbuscular mycorrhizal fungi regulate soil respiration and its response to precipitation change in a semiarid steppe. Scientific Reports 6, 19990. https://doi.org/10.1038/srep19990.

Zhang, H.-Y., Lü, X.-T., Hartmann, H., Keller, A., Han, X.-G., Trumbore, S., Phillips, R.P., Xu, X., 2018. Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. Global Ecology and Biogeography 27 (7), 875–885.

Zhang, J., Ru, J., Song, J., Li, H., Li, X., Ma, Y., Li, Z., Hao, Y., Chi, Z., Hui, D., Wan, S., 2022. Increased precipitation and nitrogen addition accelerate the temporal increase in soil respiration during 8-year old-field grassland succession. Global Change Biology 28, 3944–3959. https://doi.org/10.1111/gcb.16159.

Zheng, J., She, W., Zhang, Y., Bai, Y., Qin, S., Wu, B., 2018. Nitrogen enrichment alters nutrient resorption and exacerbates phosphorus limitation in the desert shrub Artemisia ordosica. Ecology and Evolution 8, 9998–10007. https://doi.org/10.1002/ece3.4407.

Zhou, M., Guo, Y., Sheng, J., Yuan, Y., Zhang, W.-H., Bai, W., 2022. Using anatomical traits to understand root functions across root orders of herbaceous species in a temperate steppe. New Phytologist 234, 422–434. https://doi.org/10.1111/nph.17978.