

Interspecific interactions alter plant functional strategies in a revegetated shrub-dominated community in the Mu Us Desert, China

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- **Background and Aims** Previous studies investigating plant–plant interactions have focused on plant growth, context dependence and shifts in interactive outcomes. However, changes in functional traits in the context of interactions have been inadequately explored; few studies have focused on the effects of interactions on the plasticity of functional strategies.
- **Methods** We conducted a 4-year removal experiment for the xeric shrub *Artemisia ordosica* and perennial graminoids (PGs) in the Mu Us Desert, northern China. Soil nutrient content, biomass and 12 functional traits related to plant morphology and nutrient status were measured for the shrub species and a dominant PG species (i.e. *Leymus secalinus*) in the presence and absence of shrubs and PGs.
- **Key Results** Shrubs affected the functional traits of *L. secalinus*, reducing leaf dry matter content and increasing plant height, which probably promoted the functional strategy of *L. secalinus* towards a more resource-acquisitive and competitive strategy. In contrast, when the shrubs were affected by PGs, they shifted towards a resource-conservative and stress-tolerative strategy, by increasing leaf dry matter content and decreasing specific leaf area. Moreover, the shrub species relied more on internal nutrient recycling (higher nitrogen resorption efficiency) rather than on external nitrogen uptake under nitrogen competition; instead, *L. secalinus* tended to exhibit higher external nitrogen uptake from soil during nitrogen shortages.
- **Conclusions** This study indicated that the functional strategies and nutrient cycling of the shrub species and the dominant PG were altered by each other. The shifts in functional traits may help plants to coexist in the community for a relatively long time. Our findings highlighted that interspecific interactions alter plant functional strategies and provided new insights into community assembly and succession mechanisms in a revegetated shrubland for ecological restoration of drylands.

Key words: *Artemisia ordosica*, beneficiary feedback effects, facilitation, functional traits, *Leymus secalinus*, Mu Us Desert, nitrogen resorption efficiency.

INTRODUCTION

Plant–plant interactions are defined as the effect of one or more plants on the survival, growth and reproduction of their neighbouring plants (Callaway, 2007). These interactions, including both facilitation and competition, profoundly influence species occurrence and community assembly (Pugnaire *et al.*, 1996; Brooker, 2006; Wang *et al.*, 2021). The pioneering concept of facilitation was proposed by Clements (1916) more than 100 years ago, but was neglected by most studies for decades owing to the importance given to competition (Grime, 1973; Tilman, 1982). In the past two decades, numerous studies have focused on facilitation and defined it as a positive interaction among organisms (Bruno *et al.*, 2003; Michalet *et al.*, 2016). Facilitation was traditionally attributed to the amelioration of limiting environmental conditions of stressful microenvironments, such as enrichment of resources (Turkington and Harper, 1979), relief from physical stress (Callaway, 1995) and defence from herbivores (Louthan *et al.*, 2014). However, most previous

studies have focused on the natural environmental stress amelioration by nurse species that can facilitate the growth and development of other species (Pueyo *et al.*, 2009; Zhang *et al.*, 2017). Recently, the roles of functional traits in the functional strategies during plant–plant interactions have gained attention (Grassein *et al.*, 2010; Gorné *et al.*, 2020).

Functional traits are morphological, physiological and biochemical characteristics of plants and their organs. They contribute to important plant functional strategies, such as stress defence [e.g. leaf dry matter content (LDMC)], competitive ability (e.g. plant height, and canopy area), resource acquisition [e.g. specific leaf area (SLA)], nutrient cycle (e.g. nutrient resorption efficiency and $\delta^{15}\text{N}$ values), and nutrient storage [e.g. leaf nitrogen and leaf phosphorus (Gaudet and Keddy, 1998; Robinson, 2001; Wright *et al.*, 2004; Pérez-Harguindeguy *et al.*, 2013; Díaz *et al.*, 2016; Wang *et al.*, 2019)]. Furthermore, these strategies represent plant responses to environmental factors (Westoby *et al.*, 2002; Schöb *et al.*, 2013). Therefore, various functional traits can predict how beneficiaries

respond to microenvironmental modifications caused by benefactor species (Schöb, 2012; Butterfield et al., 2013). More specifically, the presence of nurse species ameliorates the effects of microenvironmental stress (e.g. strong wind and intense radiation). Therefore, the beneficiary species are predicted to invest considerable resources in developing acquisitive traits (e.g. higher SLA). In contrast, in the absence of nurse species, beneficiary species are predicted to invest considerable resources in developing traits that can resist abiotic stress [i.e. higher LDMC and leaf carbon content, and lower SLA (Pugnaire et al., 1996; Poorter et al., 2009; Pistón et al., 2018)]. Thus, detecting the functional traits of beneficiaries in response to their nurse species is important for understanding how plants adapt to their neighbours, particularly in stressful environments.

In natural communities with nurse species, although the nurse species exert positive effects on the beneficiaries, the latter may also exert feedback effects on the former (i.e. beneficiary feedback effects, BFEs). Furthermore, these BFEs have been shown to be positive (Pugnaire et al., 1996), neutral (Armas and Pugnaire, 2005) or negative (Holzapfel and Mahall, 1999). In recent years, evidence from alpine ecosystems has shown that the beneficiary species negatively affect the reproductive output of nurse species (Michalet et al., 2011; Cranston et al., 2012; Schöb et al., 2014b). In addition, a global study has further confirmed that the negative BFEs are driven primarily by resource competition from benefitting graminoids (Michalet et al., 2016). However, compared to the known feedback effects under competitive interactions (Keddy, 2001), we are only just beginning to understand the mechanisms of BFEs associated with the positive effects in plant communities (Bronstein, 2009; Schöb et al., 2014a). In particular, knowledge remains limited on how BFEs contribute to changes in the functional strategies of nurse species.

Similar to alpine ecosystems, desert ecosystems are characterized by extreme climate and resource deficiency (Maestre et al., 2016). Therefore, the beneficiaries in desert areas are susceptible to generating negative BFEs due to competition for resources (Banuet et al., 1991; Holzapfel and Mahall, 1999). *Artemisia ordosica* Krasch. is a dwarf shrub widely used for revegetating desert regions in northern China, particularly in the Mu Us Desert (Li et al., 2011). The presence of these shrubs facilitates the recruitment and growth of associated herbaceous plants, particularly perennial graminoids (PGs), increasing the coverage and biomass of the species (Lu et al., 2018). In turn, the enrichment of PGs negatively affects the fitness of the shrubs (Bai et al., 2018). Studies have suggested that the developed beneficiary species may compete for resources with the nurse plants (Banuet et al., 1991; Holzapfel and Mahall, 1999). However, the mechanism of nurse shrubs responding to negative feedback by regulating their nutrient strategies remains unknown.

In this study, we performed a 4-year removal experiment of shrubs and PGs in an *A. ordosica* community in the Mu Us Desert. The study focused on the changes of plant functional traits, leaf nutrient resorption, biomass and soil nutrient contents in the presence and absence of each other. We used *Leymus secalinus* (Georgi) Tzvel. as a representative species of PGs and hypothesized that: (1) the presence of the nurse shrub (*A. ordosica*) alters the functional strategies of *L. secalinus* towards a more resource-acquisitive and competitive strategy; (2)

the BFEs of PGs, in turn, change the functional strategies of *A. ordosica* towards more a resource-conservative and defence-allocation strategy, resulting from competition for nutrients; and (3) during nutrient competition, the shrubs and *L. secalinus* would develop diverse nutrient cycling strategies – that is, shrub species would rely more on internal nutrient recycling, and instead *L. secalinus* would tend to exhibit higher external nutrient uptake. Therefore, the study seeks to: (1) detect whether the nurse shrubs affect the functional traits such as SLA, LDMC, plant height and nutrient strategies of *L. secalinus*; (2) clarify whether PGs in turn affect the functional traits of the shrubs; and (3) elucidate how the shrubs and PGs alter their functional and nutrient strategies to fit the long-term interactions.

MATERIALS AND METHODS

Study site

This study was conducted at the Yanchi Research Station (37°40′–38°100′N, 106°300′–107°410′E, 1550 m a.s.l.), located in the southwestern fringe of the Mu Us Desert, northern China. The area is characterized by a semi-arid continental climate (Jia et al., 2018). Mean annual temperature and precipitation were 8.1 °C and 292 mm, respectively. Approximately 80 % of the precipitation occurs between May and September. Pan evaporation was markedly higher than local precipitation, up to 2024 mm (data from Yanchi Weather Station). Wind erosion in this area is frequent and strong, and mean annual wind velocity wind is 2.6 m s⁻¹ (Bao et al., 2013; Kapp et al., 2015). According to the US Soil Taxonomy, the soil category of the investigated area is quartisamment (Gao et al., 2014). The soil total nitrogen content (0–20 cm) is 0.11–0.29 g kg⁻¹ (Bai et al., 2018). The plants in this region show severe nutrient deficiency, especially for nitrogen (She et al., 2020).

The natural landscape of the study site is a dry steppe. However, after the 1950s, the area was subject to intense ecological destruction and land degradation, resulting in mobile dunes with mosaic vegetation due to intensive anthropogenic activities (i.e. over-grazing by livestock, and collection of fuel and medicinal materials). Since the late 1990s, large-scale ecological restoration measures have been implemented, including fencing, prohibition of grazing and sowing of xeric shrubs by aerial seeding, to promote the ecological restoration of this degraded ecosystem (Wang et al., 2013). Presently, the area is dominated by the native dwarf shrub *A. ordosica* (Li et al., 2011). The presence of this shrub species facilitates the recruitment and growth of associated herbaceous plants and promotes biodiversity (Bai et al., 2019). The dominant herbaceous species in the region are PGs (e.g. *L. secalinus* and *Pennisetum flaccidum* Grisebach), and herbaceous plants including perennial forbs [e.g. *Ixeris chinensis* (Thunb.) Nakai, *Cynanchum thesioides* (Freyn) K. Schum., and *Silene aprica* Turcx. ex Fisch. et Mey] and annual plants [e.g. *Setaria viridis* (L.) Beauv., *Chenopodium aristatum* L., and *Corispermum puberulum* Iljin; Supplementary Data Table S1].

Experimental design and sampling

The experimental plots were established in a 4-km² shrubland area (Fig. 1). The experimental area had a gentle slope and was

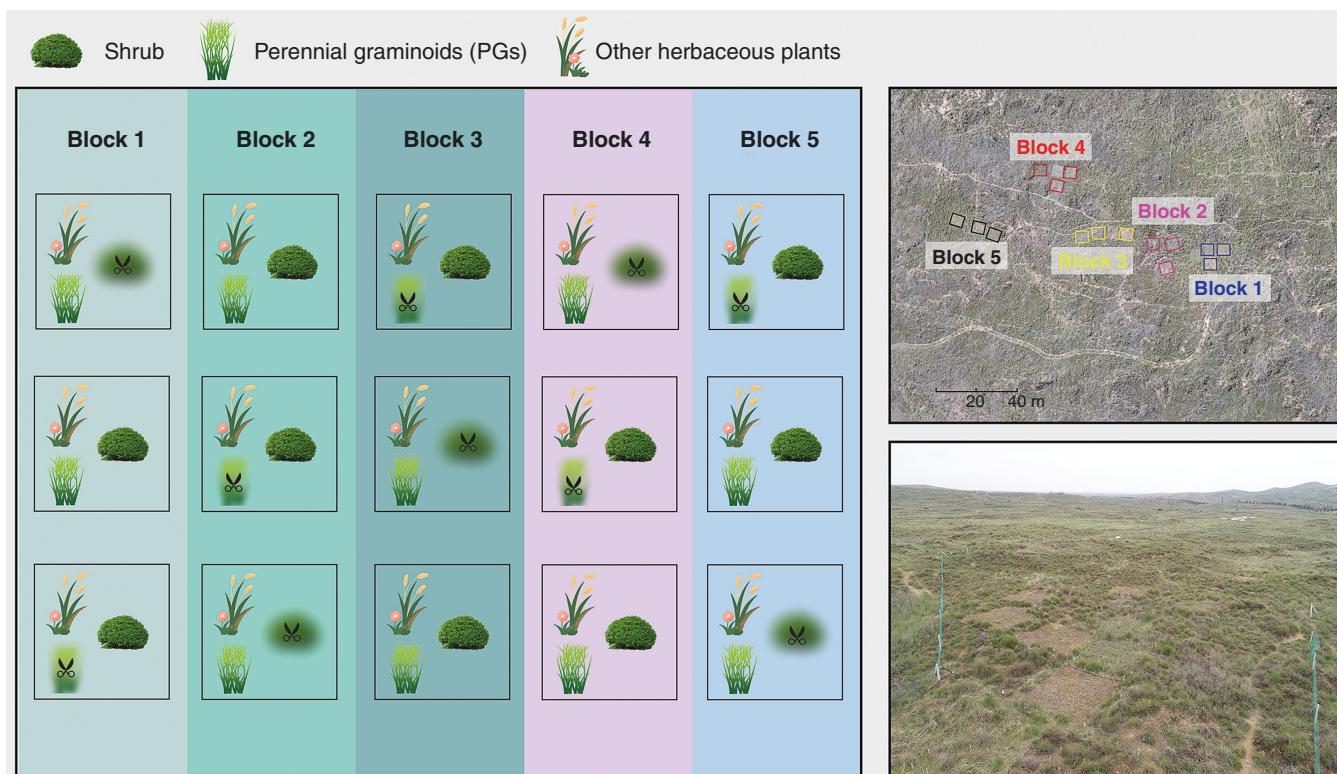


FIG. 1. Experimental design. Left: schematic of the removal experiment; top right: distribution of the experimental plots from above; and bottom right: actual image of the experimental plots.

fenced to prevent grazing. *Artemisia ordosica* was the only shrub species in the experimental plots, and the dominant PG was *L. secalinus* (~75 % above-ground biomass of PGs). The two species accounted for ~70 % of the community above-ground biomass (Supplementary Data Table S1). A randomized complete block design was used to eliminate the impacts of topography and microenvironmental heterogeneity. The experiment consisted of three treatments: (1) presence of both shrub species and all PGs (Control); (2) absence of shrub species but presence of PGs (ReSH); and (3) presence of shrub species but absence of PGs (RePG). Each treatment was replicated five times, giving a total of 15 plots. Each plot was 6 × 6 m. A 1-m buffer zone was left to reduce the effect of neighbouring plots. The above-ground parts of the shrub species or all PGs were removed by cutting the stems with scissors at 2 cm below the ground surface (Fig. 1). All cut plant materials were discarded. The removal treatments were performed twice per month throughout the growing season, from May to late September. This experiment was conducted from 2016 to 2019.

At the end of August 2019, three 1 × 1-m quadrats were randomly selected in each plot, and the above-ground parts of all herbaceous species were harvested, oven-dried at 75 °C for 48 h and weighed. The coverage percentages of shrub patches were measured along three parallel 6-m lines (Bai et al., 2018). The above-ground biomass of shrubs was estimated using a non-destructive method based on the length and number of twigs, following the method described by She et al. (2016). The abundance of *L. secalinus* and shrubs in each plot was recorded, and therefore the above-ground biomass could be calculated at both the plot level (using a coverage- and abundance-based

weighting method) and individual level (biomass divided by abundance).

Twelve functional traits related to plant morphology and nutrient status were measured for both the shrub species and *L. secalinus*: SLA, LDMC, plant height, green leaf carbon content (GLC), green leaf nitrogen content (GLN), green leaf phosphorus content (GLP), green leaf $\delta^{15}\text{N}$ values (GL- $\delta^{15}\text{N}$), senesced leaf carbon content (SLC), senesced leaf nitrogen content (SLN), senesced leaf phosphorus content (SLP), leaf nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE).

At the beginning of September 2019, five shrubs and ten *L. secalinus* plants with no visible etiolation were randomly selected to determine the functional traits in each plot, because the effects of etiolation can lead to abnormal growth (Priestley and Ewing, 1923). Plant height was measured as the shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) on a plant and the ground level. In each plot, we collected over 100 leaves for shrubs and ten leaves for *L. secalinus*. Leaves from all individuals were combined within each plot, and a sample (approximately one-third) was used to determine SLA and LDMC, and then all samples were ground to analyse GLC, GLN and GLP contents and GL- $\delta^{15}\text{N}$ values. Although this method may result in a lower nutrient value of leaves due to leaching, it can reflect differences between treatments and reduce sampling disturbance. SLA was calculated as the leaf area [the projected leaf area was captured by an EPSON V19 scanner (EPSON, Los Alamitos, CA, USA) at 300 dpi, and was calculated using MATLAB R2016a] divided by the dry weight (dried at 75 °C

for 48 h). LDMC was calculated as the dry weight divided by the saturated weight (soaked in water for 8 h).

In December 2019, fully senesced leaves were collected from the previously sampled plants and analysed for SLC, SLN and SLP contents. Leaf carbon and nitrogen content were determined using a Vario EL cube CHNS Elemental C/N analyser (Elementar Analysensysteme, Munich, Germany), and leaf phosphorus was digested with HNO_3 and determined using inductively coupled plasma-optical emission spectrometry (iCAP 6300 spectrophotometer, Thermo Fisher Scientific, MA, USA). Leaf nitrogen isotope ratios (GL- $\delta^{15}\text{N}$) were determined using a DELTA V Advantage isotope ratio mass spectrometer with a precision of 0.2 ‰ (Thermo Fisher). The $\delta^{15}\text{N}$ values representing the nitrogen isotopic composition of the samples relative to that of atmospheric dinitrogen (‰) were calculated using the following formula:

$$\delta^{15}\text{N} (\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

where R_{sample} is the sample isotope ratio ($^{15}\text{N}/^{14}\text{N}$) and R_{standard} is the $^{15}\text{N}/^{14}\text{N}$ ratio for atmospheric N_2 .

Simultaneously, five soil cores of 3.8 cm diameter and at 0–20 cm depth were randomly collected from each plot and composited to create one sample for each plot, giving a total of 15 soil samples. Each composite sample was mixed, homogenized, and sieved through a 2-mm mesh to remove gravel and litter. Total soil organic carbon content (SOC) was determined using the dichromate oxidation method (Schumacher *et al.*, 2002). Total soil nitrogen content (STN) was determined using a Kjeldahl Nitrogen Analyser (Kjeltec 2200 Auto Distillation Unit, Foss, Sweden) according to Bremner (1996). Total soil phosphorus content (STP) was extracted with HNO_3 - HClO_4 -HF and was measured using inductively coupled plasma emission spectrometry (iCAP 6300 ICP-OES model; Thermo Fisher) according to Fixen and Grove (1990). Soil available phosphorus content (SAP) was determined by Olsen-phosphorus, a commonly used measure of plant-available phosphorus, which was obtained by extracting with 0.5 mol L^{-1} NaHCO_3 and was measured using the Mo-Sb colorimetric method with a UV-2550 ultraviolet–visible spectrophotometer (Shimadzu, Kyoto, Japan) (Olsen, 1954). The soil-available nitrogen content (including NH_4^+ -N, and NO_3^- -N) was extracted with 2 M KCl solution at a 1 : 5 ratio of soil to solution. Ammonium was analysed using the salicylate method (Kempers and Zweers, 1986) with a DR3900-UV-Visible spectrophotometer (HACH, Loveland, CO, USA). Nitrate was analysed using a UV spectrophotometer (Shimadzu) according to Sah (1994). Soil nitrogen isotope ratios (soil $\delta^{15}\text{N}$) were measured using a DELTA V Advantage isotope ratio mass spectrometer (Hauck, 1983) and calculated as described in eqn (1).

Nutrient resorption efficiency

Nutrient resorption efficiency (N_{RE}) was calculated as the proportion of the mature leaf nutrient pool that is resorbed, using the following equations:

$$NRE (\%) = \left[\frac{N_{gr} - N_{sen}}{N_{gr}} \right] \times 100 \% \quad (2)$$

$$PRE (\%) = \left[\frac{P_{gr} - P_{sen}}{P_{gr}} \right] \times 100 \% \quad (3)$$

where NRE (%) and PRE (%) are the nutrient resorption efficiencies of nitrogen and phosphorus, respectively; and N_{gr} (%) and P_{gr} (mg g^{-1}) are the nitrogen and phosphorus concentrations from the green leaves. N_{sen} (%) and P_{sen} (mg g^{-1}) are the nitrogen and phosphorus concentrations from senesced leaves, respectively. NRE (%) and PRE (%) were calculated for shrubs and *L. secalinus*.

Statistical analysis

We performed linear mixed effects model analysis using neighbouring plants (shrub or PGs) as fixed variables and block as a random variable to determine the effects of neighbouring plants on the soil nutrient content. Therefore, seven variables (SOC, STN, STP, SAP, NH_4^+ -N, NO_3^- -N and soil $\delta^{15}\text{N}$ values) were analysed separately. Furthermore, to investigate the effects of the neighbouring plants on the functional traits, nutrient resorption efficiency and biomass of target plants (the effects of shrub species on PGs and vice versa), we performed another linear mixed effects model analysis using the neighbouring plants as fixed variables and block as a random variable; accordingly, 14 response variables (SLA, LDMC, plant height, GLC, GLN, GLP, GL- $\delta^{15}\text{N}$, SLC, SLN, SLP, NRE, PRE, and biomass at the plot and individual level) were analysed. In addition, separate models for each species were used.

All statistical analyses were performed using R v.4.1.1 software (R Core Team, 2021). All data were tested for homogeneity of variances using Levene's test in the 'car' package (Fox and Weisberg, 2019), and subsequently tested for normality using the Shapiro–Wilk test. The log-transformation was used to improve the normality when necessary. We used the 'lme4' and 'lmerTest' packages to fit linear mixed effects models (Bates *et al.*, 2015; Kuznetsova *et al.*, 2017), and the 'ggplot2' package for figure output (Wickham, 2016).

RESULTS

Soil nutrient content

The removal of shrubs had no effects on soil nutrients, including SOC, STN, STP, SAP, NH_4^+ -N, NO_3^- -N and soil $\delta^{15}\text{N}$ values ($P > 0.05$; Fig. 2; Supplementary Data Table S2). In contrast, when PGs were removed, STN ($P < 0.05$) and NH_4^+ -N ($P < 0.01$) increased compared to the control treatments (Fig. 2; Table S2). However, SOC, STP, SAP, NO_3^- -N and soil $\delta^{15}\text{N}$ values did not change (all $P > 0.05$).

Plant functional traits

Morphological traits of the shrub species and *L. secalinus* had contrasting responses to removing the corresponding neighbouring plants (Fig. 3; Supplementary Data Table S3). Shrub removal increased LDMC ($P < 0.05$) and reduced plant height ($P < 0.01$) of *L. secalinus* significantly, but had no effect

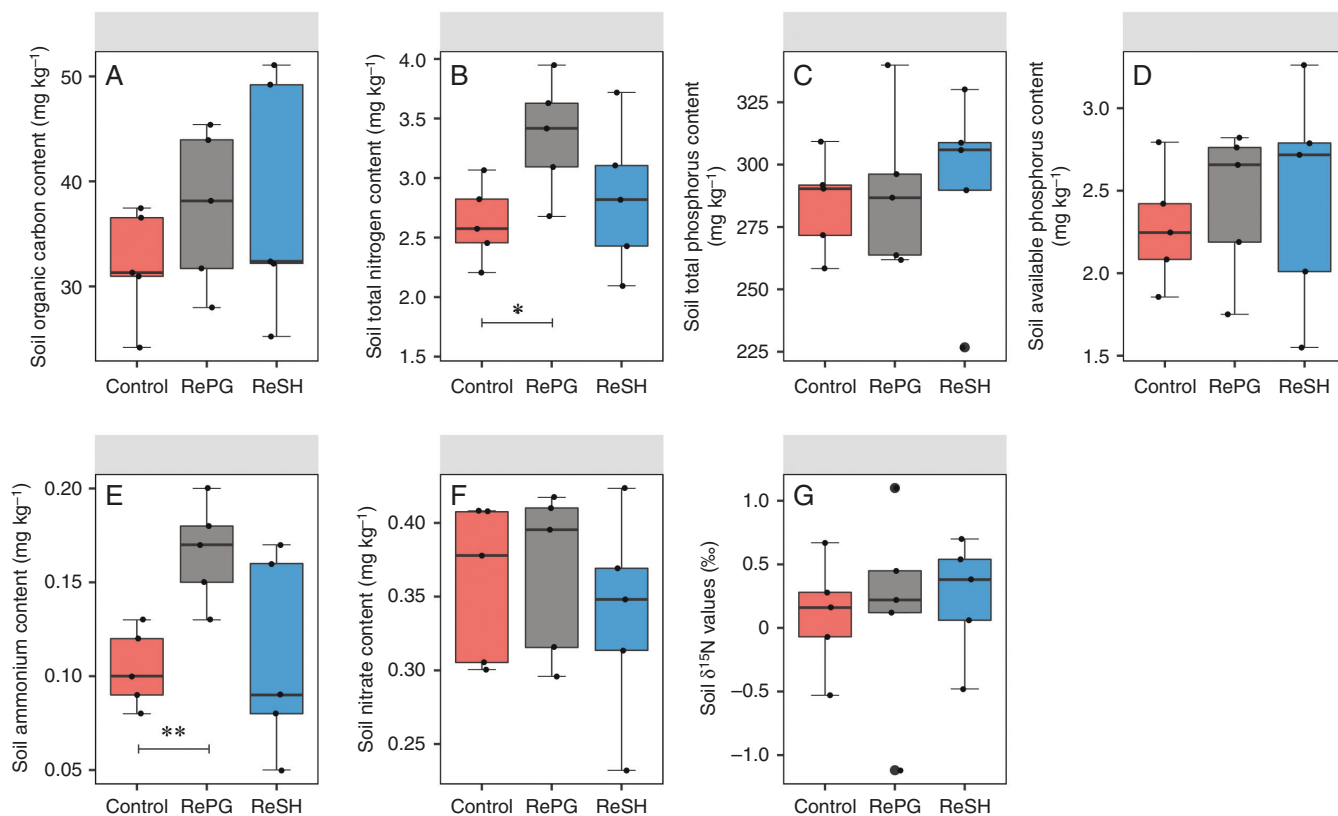


FIG. 2. Soil organic carbon content (A), soil total nitrogen content (B), soil total phosphorus content (C), soil-available phosphorus content (D), soil ammonium content (E), soil nitrate content (F) and soil $\delta^{15}\text{N}$ values (G) in the different treatments. Soil-available phosphorus was determined based on Olsen-phosphorus, a commonly used measure of plant-available phosphorus. PGs, perennial graminoids; Control, with shrubs and PGs; RePG, with shrubs and without PGs; and ReSH, with PGs and without shrubs. Significance: **, $P < 0.01$; *, $P < 0.05$.

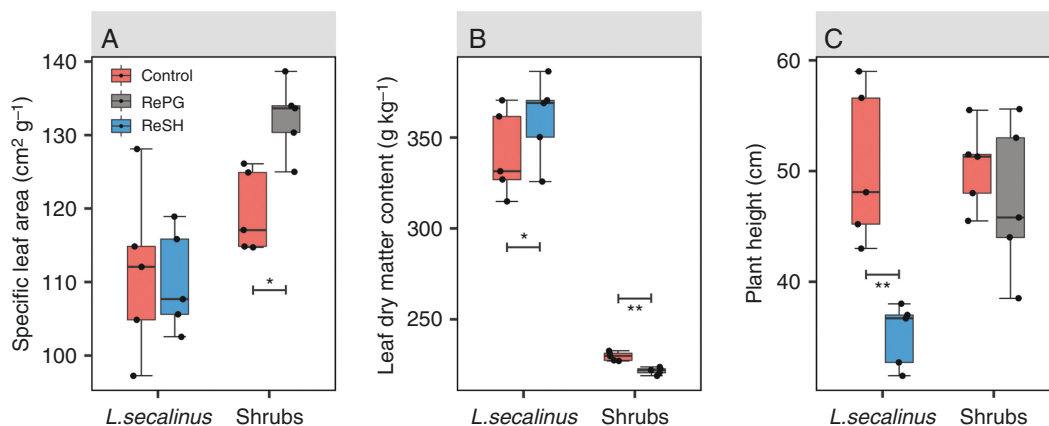


FIG. 3. Specific leaf area (A), leaf dry matter content (B) and plant height (C) of shrubs and *L. secalinus* in the different treatments. PGs, perennial graminoids; Control, with shrubs and PGs; RePG, with shrubs and without PGs; and ReSH, with PGs and without shrubs. Significance: **, $P < 0.01$; *, $P < 0.05$.

on their SLA ($P > 0.05$). For shrubs, the removal of PGs increased SLA ($P < 0.05$) and decreased LDMC ($P < 0.01$), but there was no effect on shrub height ($P > 0.05$).

Green leaf nutrients in *L. secalinus* were affected by shrub removal (Fig. 4; Supplementary Data Table S4). For *L. secalinus*, GLN, GLP and $\text{GL-}\delta^{15}\text{N}$ increased when shrubs were removed (all $P < 0.01$), but GLC did not increase ($P > 0.05$). The green

leaf nutrients of the shrubs did not respond to the removal of PGs ($P > 0.05$; Fig. 4; Table S4).

For the *L. secalinus* senesced leaves, shrub removal notably decreased SLC and SLN (both $P < 0.01$), but had no effect on SLP ($P > 0.05$; Fig. 4; Supplementary Data Table S4). For shrubs, only SLN significantly increased in the absence of PGs ($P < 0.05$), but SLC and SLP did not change (all $P > 0.05$; Fig. 4; Table S4).

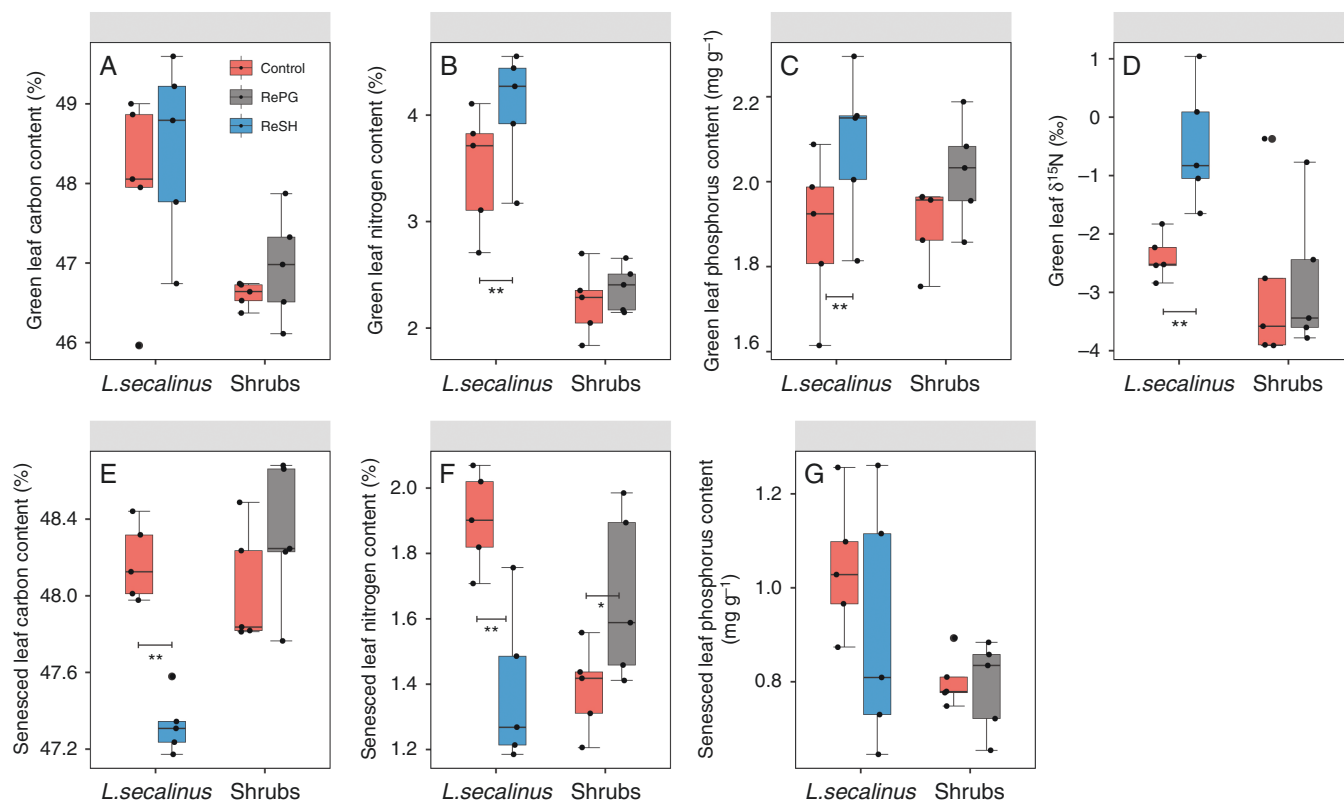


FIG. 4. Green leaf carbon content (A), green leaf nitrogen content (B), green leaf phosphorus content (C), green leaf $\delta^{15}\text{N}$ values (D), senesced leaf carbon content (E), senesced leaf nitrogen content (F) and senesced leaf phosphorus content (G) of shrubs and *L. secalinus* in different treatments. PGs, perennial graminoids; Control, with shrubs and PGs; RePG, with shrubs and without PGs; and ReSH, with PGs and without shrubs. Significance: **, $P < 0.01$; *, $P < 0.05$.

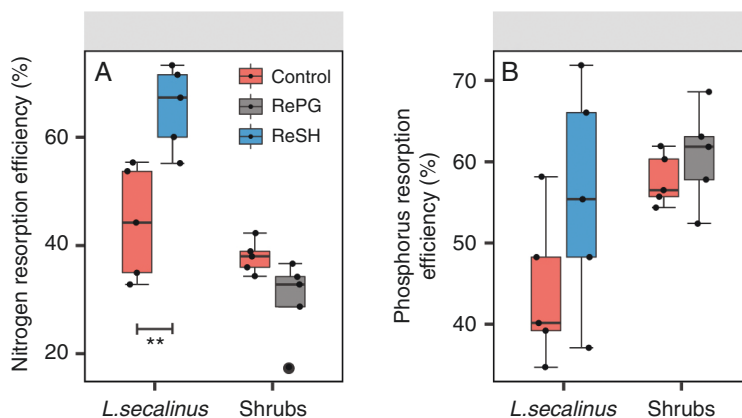


FIG. 5. Nitrogen resorption efficiency (A) and phosphorus resorption efficiency (B) of shrubs and *L. secalinus* in different treatments. PGs, perennial graminoids; Control, with shrubs and PGs; RePG, with shrubs and without PGs; and ReSH, with PGs and without shrubs. Significance: **, $P < 0.01$.

Nutrient resorption strategy

Only *L. secalinus* showed regulation of nitrogen resorption efficiency (Fig. 5; Supplementary Data Table S5). NRE of *L. secalinus* increased in response to shrub removal ($P < 0.01$), but that of shrub species did not change when PGs were absent ($P > 0.05$). For phosphorus resorption efficiency, neither shrubs nor *L. secalinus* responded to the removal treatment (both $P > 0.05$; Fig. 5; Table S5).

Above-ground plant biomass

At the plot level, above-ground biomass of both shrub species and *L. secalinus* showed no response to the corresponding removal treatment (both $P > 0.05$; Supplementary Data Fig. S1; Table S6). At the individual level, the removal of shrub species significantly decreased the biomass of *L. secalinus* ($P < 0.01$; Fig. S1; Table S6), and the removal of PGs considerably increased the biomass of shrub species ($P < 0.05$).

DISCUSSION

How does the nurse shrub species affect the dominant perennial grass?

As expected, *L. secalinus* had lower LDMC and higher plant height when the shrubs were present in the community (Fig. 3), indicating that *L. secalinus* may shift towards resource-acquisitive and competitive strategies. Previous studies have also shown that some dominant shrubs in harsh environments influence the functional traits of associated herbaceous plants, such as LDMC and height, due to environmental amelioration (Carlsson and Callaghan, 1991, Gómez et al., 2008; Schöb et al., 2012). In the present study, shrubs may have weakened the disturbance caused by winds and facilitated the height of beneficiaries (Niklas, 1998; Nick, 2000; Bai et al., 2019). In addition, LDMC of *L. secalinus* increased when shrubs were removed (Fig. 3). Generally, leaves with higher LDMC are more resistant to abiotic stress and have a low potential relative growth rate (Cornelissen et al., 2003). Furthermore, in this study, the individual biomass of *L. secalinus* decreased when shrubs were removed ($P < 0.01$; Supplementary Data Fig. S1; Table S6), suggesting that *L. secalinus* may alter its functional strategy towards slow growth and enhance its stress-tolerance ability in response to the absence of nurse shrubs.

In this study, SLA of *L. secalinus* was not affected by the presence of shrubs (Fig. 3), contrasting with the findings of several studies where nurse plants enhanced SLA of beneficiaries in desert ecosystems (Rolhauser and Pucheta, 2016; González et al., 2020). SLA is recognized as a proxy related to resource availability (Chapin et al., 1980; Wright et al., 2001). In this study, the presence of *A. ordosica* had no effects on soil resources (Fig. 2). Thus, it did not affect SLA of *L. secalinus*.

We also found that GLN, GLP and GL- $\delta^{15}\text{N}$ of *L. secalinus* significantly decreased with the presence of shrubs (Fig. 4), suggesting nutrient competition between *L. secalinus* and shrubs, due to positive average soil- $\delta^{15}\text{N}$ values under each treatment (Fig. 2). Our results suggest that the effects of the nurse shrubs on *L. secalinus* can be attributed not only to positive interactions, but also to competitive interactions for soil nutrients. Several studies in harsh ecosystems found that the interacting species demonstrate competitive effects while exerting facilitative effects (Cramer et al., 2010; Allegranza et al., 2016). In addition, the barren and aerated conditions in desert soils are conducive to the occurrence of nitrification (Huang et al., 2021), leading to an increase in ^{15}N atoms in soil ammonium. In this study, the increase in GL- $\delta^{15}\text{N}$ values implied that *L. secalinus* preferred ammonium when shrubs were removed. The soil inorganic nitrogen results could indirectly support a nitrogen-source shift, which showed that the soil ammonium content decreased when PGs were present (Fig. 2). However, future studies could use effective methods, such as ^{15}N tracer addition, to clarify whether shrubs alter the nitrogen source of PGs, thus improving our understanding of the plasticity of nutrient strategies involved in the desert plant community.

Furthermore, we found that NRE of *L. secalinus* increased when shrubs were removed (Fig. 5). Therefore, we speculated that the nutrient stress of *L. secalinus* was partially reduced by removing shrubs, increasing their GLN (Fig. 4). However, with the growth and reproduction of *L. secalinus*, they may still be subject to ambient nitrogen limitation. In addition, the main

nutrient competitor might probably have shifted from interspecific shrubs to intraspecific *L. secalinus* individuals. Thus, *L. secalinus* preferred to resorb nitrogen from senesced leaves, resulting in a decrease in SLN and an increase in NRE.

In a previous study, *L. secalinus* changed its water use strategy to adapt to interspecific competition (Liu et al., 2020). Our study further provided another mechanism for nutrient competition. These shifts in resource-acquisition strategies may be important mechanisms explaining how herbaceous plants cope with limited resources in harsh environments. However, in this study, although the assumption of the plant strategies was based on limited traits and biomass, other functional traits (e.g. below-ground traits) and processes (e.g. symbioses between plants and microbes) may contribute to the shifts in resource-acquisition strategies of interactive plants. Therefore, more functional traits and further analysis of the trait trade-off should be incorporated to reveal the complex interactions in future studies.

How does the dominant perennial grass in turn affect the nurse shrubs?

Consistent with our second hypothesis, the results show that the presence of *L. secalinus* reduced SLA and increased LDMC of the shrubs (Fig. 3). Moreover, the individual biomass of shrubs decreased in the presence of *L. secalinus* ($P < 0.05$, Supplementary Data Fig. S1; Table S6), indicating that the functional strategies of *A. ordosica* shifted towards resource conservation and defence allocation. Previous studies showed that beneficiaries negatively affect the reproductive output of nurse plants, such as flower density and fruit set (Schöb et al., 2014b; Michalet et al., 2016) and seedling survival (Banuet et al., 1991). However, in the present study, the results show that the beneficiary could affect the functional strategies of the nurse plants by reducing their resource-acquisition ability (lower SLA, and individual biomass) and increasing their stress-tolerant ability (higher LDMC). This could have resulted in *L. secalinus* out-competing the shrubs in the resource-limited environment. Nevertheless, long-term field data are needed to confirm this assumption. In addition, disturbances, such as drought, grazing, plant diseases and insects, are important factors that hamper the resource-acquisition process and should be explored in future studies.

When PGs were present in the community, although there was no significant change in NRE of shrub species ($P > 0.05$, Fig. 5), we found a decrease in SLN of the shrubs (Fig. 4), along with no significant differences in leaf $\delta^{15}\text{N}$ values for shrubs between the PG-retention and PG-removal treatments (Fig. 4); we can therefore infer that the shrub species may tend to hold more nutrients (increased nitrogen resorption from senesced leaves) rather than increasing absorption from the soil (enhanced nutrient content in the green leaves) to alleviate nitrogen stress. Thus, this capacity may enable shrubs to endure nitrogen deficiency. Evidence from alpine and arid ecosystems (Pornon and Lamaze, 2007; Hall et al., 2011; Yahdjian et al., 2014), such as the Patagonian Steppe, has indicated that shrubs assimilate a small fraction of nitrogen content from the soil annually when in competition with grasses (Sala et al., 2012). These reports support our inference.

Previous studies have attributed the mechanism of BFEs to competition for water, especially from grass species

(Schöb *et al.*, 2014a; Michalet *et al.*, 2016; Liu *et al.*, 2020). However, in the present study, the results further show that nutrient competition is an important mechanism of BFEs. Thus, the conservative nutrient strategy of shrubs may help them adapt to the negative BFEs from herbaceous plants. Nevertheless, given the relatively short timeframe of nutrient monitoring, future research should focus on growth, defence, reproduction and trade-offs when assessing BFEs to reveal the adaptive strategies of nurse plants.

Would the interactions lead to the exclusion of shrubs in the future community?

Overall, our study showed that the relationship between shrub species and the dominant PG was antagonistic in the present state. Consequently, the shrubs may alter the functional strategies of *L. secalinus* toward resource acquisition and competition. In turn, the BFEs from PGs may shift the shrubs toward resource-conservative and defence-allocative strategies. This implies that the shifts in the functional strategy of the shrubs and dominant PG will contribute to their coexistence in the community. However, previous studies of the Mu Us Desert argued that the *A. ordosica* community was in a stable disclimax under continuous grazing (Zhang, 1994). However, when stress was excluded, the community gradually shifted to a grass-dominated one (Guo *et al.*, 2000; Wang *et al.*, 1997). Recent studies conducted in the Mu Us Desert also showed that resource competition in the *A. ordosica* community would drive the succession from shrub-dominated to herbaceous-dominated landscapes (Bai *et al.*, 2018; Qiao *et al.*, 2019). With increased precipitation and nitrogen deposition, it was shown that the shrubs might eventually be excluded from the community due to competition for resources (She *et al.*, 2021). A study in the degraded subalpine ecosystems also showed that beneficiaries could replace the nurse plants because of their competitive effect (Nuche and Alados, 2018).

Nevertheless, the final outcome of plant–plant interactions between nurse plants and beneficiary species may not only be restricted by the limited resources, but also depend on the functional strategies of the interactive plants (Liancourt *et al.*, 2005; Maestre *et al.*, 2009). During community succession under antagonistic interactions, nurse species can be envisaged in at least two strategies, i.e. either tolerate or escape the neighbouring plants that benefit from them (Bronstein, 2009). Both these strategies were observed in the present study, i.e. the nurse shrubs adapted to the negative BFEs by investing in defensive traits (higher LDMC) and shifting nitrogen resorption strategies. The modifications helped the nurse shrubs to decrease their niche overlap with herbaceous plants and contribute to the long-term coexistence in severely stressed ecosystems. Thus, although we argue that the drastic resource competition may ultimately exclude the shrubs from the community, this process may continue for a long time due to adaptive trait plasticity in the shrub species.

Notably, although we predicted the community dynamics based on interspecific interactions, further fieldwork needs to explore whether other mechanisms, such as soil modification and seed trapping (Filazzola and Lortie, 2014), contribute to

the succession. In addition, an important caveat is that disturbances, such as grazing, would affect the balance of interactions, thereby altering the consequence of interactions resulting in suspending or even reversing succession (Milchunas and Vandever, 2014). Therefore, we suggest that, for the purpose of recovering the current vegetation to a dry steppe, grazing should be continually prohibited, guaranteeing that native grasses ultimately outcompete the nurse shrubs.

CONCLUSIONS

The current study, based on an interspecific interaction in a revegetated community, showed that the shrubs and the dominant PG might alter the functional strategies of each other. The dominant PG was inclined towards resource-acquisitive and competitive strategies when affected by shrubs. However, the BFEs altered the functional strategy of the shrubs towards resource-conservative and defence allocative strategies. Thus, the interactions would stimulate a shift from a shrub-dominated to a herbaceous-dominated community. However, the plasticity in the nutrient strategies of the interactive plants will contribute to their long-term coexistence. Although the present study was a short-term experiment, our results highlighted the interaction mechanisms of the revegetated community in a harsh ecosystem. Moreover, we provide insight into the mechanism of community assembly and succession in a revegetated ecosystem. This can contribute to species selection and our understanding of community dynamics for dryland ecological restoration. More traits and control experiments mimicking the disturbances need to be incorporated to reveal the interspecific relationships and provide more direct and robust field-based data to understand community dynamics. Furthermore, the coexistence time of the interactive species needs to be identified.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Fig. S1. The plot-level biomass, and individual biomass of shrubs and *L. secalinus* from different treatments. Table S1. Species and their biomass proportion in the control plot. Table S2. Results of the linear mixed effects models on the effects of plant removal on soil nutrient content. Table S3. Results of the linear mixed effects models on the effects of the neighbouring plant on plant morphological traits. Table S4. Results of the linear mixed effects models on the effects of the neighbouring plant on leaf nutrient traits. Table S5. Results of the linear mixed effects models on the effects of the neighbouring plant on nutrient resorption efficiency. Table S6. Results of the linear mixed effects models on the effects of the neighbouring plant on biomass at the plot level and individual level.

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