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Facilitation by leguminous shrubs increases along a precipitation gradient

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Abstract

1. Combining nutrient dynamics (plant nutrient uptake and soil fertility) can help uncover mechanisms of shrub–grass interactions and assess the validity of the stress-gradient hypothesis, which predicts that facilitation between plants increases in stressful environments. However, how facilitation via shrub-mediated nutrient increases varies with precipitation is poorly resolved.
2. We first synthesized a global dataset from 66 studies and evaluated how shrubs affected soil organic carbon (C) and nitrogen (N) in grasslands along a precipitation gradient. We then made new measurements in a single-grassland type encroached by leguminous shrubs from the same genus (*Caragana*) to constrain the variations caused by combining different grassland types and shrubs traits in the meta-analysis. Specifically, we investigated how shrubs mediated N dynamics and how shrub–grass interactions varied along a precipitation gradient (147–342 mm) in a temperate steppe of China.
3. At the global scale, leguminous shrub-mediated effects on soil nutrients increased with precipitation, while no relationship was found for non-leguminous shrub. For the field experiment, greater N and lower δ^{15}N in *Caragana* compared to non-leguminous shrub (reference shrub, *Salsola collina*) suggested active N-fixation in *Caragana*. We found that *Caragana* enhanced N concentration and leaf quality (low C:N ratio) in neighbouring plants more on mesic sites than on xeric sites. Thus, facilitation increased via higher soil N and with decreasing environmental stress, at least along this relatively arid precipitation gradient.
4. Our results highlight the importance of precipitation in determining the nutritional facilitation to neighbouring grasses from encroaching leguminous shrubs. Conceptual frameworks for plant facilitation may therefore need to include shrub characteristics (N-fixers vs. non-fixers) and positive effects of higher precipitation on this type of facilitation to characterize plant interactions along stress gradients.

KEYWORDS
competition, dryland, facilitation, Inner Mongolia, nurse plant, nutrient dynamics, shrub encroachment, stress gradient hypothesis

1 | INTRODUCTION

Woody plant encroachment, defined as an increase in abundance of indigenous woody plants in formerly grass-dominated ecosystems, has dramatically altered land cover patterns of global drylands over the past 150 years (Archer, Scifres, Bassham, & Maggio, 1988; D'Odorico, Okin, & Bestelmeyer, 2012; Stevens, Lehmann, Murphy, & Durigan, 2017; Van Auken, 2000). Shrubs can modulate the landscape and community structure via positive and/or negative effects on their neighbour herbaceous vegetation (Knapp et al., 2008; Lortie et al., 2004; Segoli, Ungar, Giladi, Arnon, & Shachak, 2012). The stress-gradient hypothesis (SGH) predicts an increase in the importance of positive plant–plant interactions with increasing environmental severity (Bertness & Callaway, 1994; Brooker, 2006; Callaway et al., 2002). Some field and meta-analysis studies across the precipitation gradient support SGH (e.g., Armas, Rodríguez-Echeverría, & Pugnaire, 2011; Dohn et al., 2013; Holzapfel, Tielbörger, Parag, Kigel, & Sternberg, 2006; Pugnaire & Luque, 2001), while others do not (Butterfield, Betancourt, Turner, & Briggs, 2010; Maestre & Cortina, 2004; Tielborger & Kadmon, 2000). This inconsistency primarily exists at the extreme end of stress gradients: i.e. either positive interactions are observed as predicted by SGH, neutral interactions (Michalet et al., 2006), or even a switch from facilitation to competition with increasing severity (Maestre & Cortina, 2004; Michalet, Le Bagousse-Pinguet, Maalouf, & Lortie, 2014). Specifically for leguminous shrubs, experimental results from Armas et al. (2011) have supported the SGH whereas Michalet, Brooker, Lortie, Maalouf, and Pugnaire (2015) and Noumi, Chaieb, Le Bagousse-Pinguet, and Michalet (2016) suggest a reduction in facilitation with increasing aridity. The collapse of facilitation is typically driven by the reduced "nurse plant effect" under low rainfall condition (Michalet et al., 2014). Therefore, investigating nurse plant effects on resource availability could help uncover the mechanisms of shrub–grass interactions along aridity gradients (Le Bagousse-Pinguet, Forey, Touzard, & Michalet, 2013; Maestre & Cortina, 2004; Michalet & Pugnaire, 2016).

Formation of fertility islands beneath shrubs, mainly due to enhanced soil nutrient availability, represents one of the main mechanisms involved in the positive shrub–grasses interactions (Ludwig, De Kroon, Berendse, & Prins, 2004; Scholes & Archer, 1997). Increasing precipitation will increase shrub growth and nutrient accumulation and therefore might increase soil fertility with shrub encroachment (Aranibar et al., 2004). But other studies have shown that shrub encroachment in mesic grasslands could accelerate nitrogen (N) cycling (Binkley, Sollins, Bell, Sachs, & Myrold, 1992; Hellmann et al., 2011) and increase N loss during invasion (Baer, Church, Williard, & Groninger, 2006), leading to less soil nutrient accumulation beneath shrubs. Thus, how shrub-mediated soil fertility, particularly the difference of soil nutrients between within shrub canopy and in open grassland, changes along precipitation gradients is not well understood.

Using meta-analysis, Li et al. (2016) recently evaluated the effects of shrub encroachment on soil organic carbon (SOC) content (0–50 cm) in global grasslands and showed SOC increment was significantly and positively correlated with precipitation. Whether a similar pattern exists for soil N remains unknown. However, a meta-analysis from Dohn et al. (2013) in tree-grass co-dominated ecosystems suggested that the effects of woody encroachment on soil N concentrations had no relationship with rainfall. Therefore, whether precipitation can increase the shrub-mediated soil fertility remains controversial. Furthermore, recent studies showed that facilitation effects from woody plants on neighbour grass biomass (Mazía et al., 2016) and/or soil N (Blaser, Sitters, Hart, Edwards, & Venterink, 2013) are much stronger for N-fixers than that for non-fixers. But still, how this variation of shrub-mediated soil fertility changes with precipitation and whether these changes differ between leguminous and non-leguminous shrubs remain uncertain.

As the most limiting element for plant growth, N plays a central role in mediating plant–plant interactions in drylands (Haynes, 1986; Vitousek & Howarth, 1991). Many encroaching shrubs are N_2-fixing legumes (Eldridge et al., 2011) and their symbiotic N fixation is highly sensitive to water availability. Nitrogenase activities rely on the amount of carbohydrates supplied to nodules, and the supply decreases under water-limited conditions (Arfin-Khan, Grant, Beierkuhnlein, Kreyling, & Jentsch, 2014; Marino et al., 2007; Serraj, Sinclair, & Purcell, 1999). However, whether N benefits from leguminous shrub to neighbour grasses will reduce under water-limited ecosystems again remains unclear. Studies of the direct transfer of fixed-N between legume and non-legume species have been conducted in the greenhouse and/or at local scale in the field (Pirhofer-Walzl et al., 2012; Zhang et al., 2016), but lacking are regional scale assessments of how precipitation might affect N transfer from leguminous shrubs to neighbour grasses.

Investigating how nutrient respond to shrub encroachment will provide insights into the consequent changes in primary productivity and soil C sequestration (Hibbard, Archer, Schimel, & Valentine, 2001; Hughes et al., 2006). More than 5.1×10^6 ha of grasslands has been encroached by *Caragana* shrubs in northern China (Peng et al., 2013; Zhang, Wang, Nyren, & Jiang, 2006). Here, we first synthesized a global dataset to evaluate the net effects of shrub encroachment on soil organic C and N concentrations and how these effects change with precipitation. We also conducted a regional study focused on an arid to semi-arid precipitation gradient in a single grassland type encroached by shrubs from the same genus (*Caragana*). This allowed us to constrain some of the variation in the meta-analysis caused by different grassland types and shrub traits and to investigate where the most uncertainty exists in facilitation in the SGH. Along this precipitation gradient, *Caragana stenophylla* occurred in arid grasslands while *Caragana microphylla* in more mesic grasslands. As an important strategy to adapt to different water-stress conditions, *C. stenophylla* has narrower while *C. microphylla* has rather broad leaf shapes (Xie, Ma, Guo, Li, & Gao, 2014), but both are N-fixers. With this study, we explored how shrub-mediated C and N dynamics and plant–plant interactions change along a mean annual precipitation (MAP) gradient (147–342 mm). We addressed the following questions: (1) how does shrub-mediated soil fertility changes with precipitation at the regional and global scale? (2) do N benefits from *Caragana* to neighbour plants decrease at xeric sites (i.e. for *C. stenophylla*) while increase at mesic sites (i.e. for *C. microphylla*), thus supporting the collapse of facilitation?

2 | MATERIALS AND METHODS

2.1 | Synthesized dataset

We investigated the general effects of shrub encroachment in grasslands on soil C and N changes by synthesizing data from published literature. As the primary focus of our study were shrub-mediated effects on N facilitation, we first searched the Web of Science and Google Scholar using the following keywords (1) shrub* OR woody* OR shrubland* OR woodland* OR bush* OR grassland * OR encroachment* OR shrub abundance and (2) soil nitrogen. When studies also reported soil organic carbon, we included SOC responses in our dataset. We focused on studies that included pair-wise comparisons of shrub-encroachment plots with those without shrubs. We excluded any studies reporting heavy grazing in the study area from the meta-analysis. Overall, 32 articles with 114 cases for soil organic C and 66 articles with 207 cases for soil N met our criteria. These were mainly located in North America, Africa and Mediterranean regions (See Appendices S1 and S2 in Supporting Information). All points included in the meta-analysis are mean values of several replicates at the plot level (see similar in Dohn et al., 2013). Data reported at the same site but for different species were treated as separate data points. We calculated the effects of encroaching shrubs on soil fertility by comparing soil nutrients in the presence (subcanopy) and absence (open grassland) of shrubs within this dataset. Following Eldridge et al. (2011), we calculated normalized shrub effects using the log response ratio, LnRR = ln(encroach/non-encroach) in the meta-analysis, where encroach and non-encroach are the categories that define the ratio of any response variable beneath and outside the shrub canopy respectively. A positive LnRR indicated positive effects of shrubs and vice versa. We further identified whether woody plants were potential N fixers, according to Sprent (2009) or via searching the literature from the ISI Web of Knowledge to retrieve unambiguous information on plant legume types. Thus, our synthesized dataset contained LnRR for soil organic C and N, MAP (147–1,065 mm), N-fixation (N-Fixer or Non-fixer) and species identity of encroaching shrubs.

2.2 | Field study site

A complementary field study was conducted along a 1,200 km west-east transect across Inner Mongolia grasslands in northern China (108°71′–117°15′, 41°91′–48°50′; Appendix S3 in Supporting Information). Long-term MAP along the gradient ranges from 147 to 342 mm and mean annual temperature (MAT) ranges from −0.8 to 5.5°C. Rainfall in the study region mainly falls between May and September (growing season) and the annual peaks of standing biomass are in mid-August. Soil types are mainly arid, sandy, calcium rich brown loess, in the Kastanozem soil group in the Food and Agriculture Organization (FAO) classification system (Cheng, Chen, Xu, Han, & Li, 2009).

Along this transect, only sites with a mix of natural grassland and populations of *Caragana* shrubs were selected. In total, eight sites with *C. stenophylla* in the west and five sites with *C. microphylla* in the east were identified. *Caragana stenophylla* was mainly found in the more arid grassland sites with MAP ranging from 147 to 222 mm, whereas *C. microphylla* was found where MAP varied from 246 to 342 mm (See Appendix S3 in Supporting Information). The locations and elevations of the sampling sites were measured by GPS (eTrex Venture, Garmin, USA). A geographic information system point file was created from sampling sites coordinates (measured by GPS), using DIVA-GIS 7.5. Then, we extracted altitude, MAT, and MAP for each sampling site, using 2.5-min resolution interpolated climatic surfaces derived from the WorldClim dataset (http://www.worldclim.org/) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

2.3 | Field sampling

Field sampling was conducted during mid-August 2012. For each site, one large plot (50 m × 50 m) was set up and three to five paired subplots (1 m × 1 m) were established within the large plot. Each pair of subplots contained an encroached and a corresponding non-encroached subplot within a distance of *c.* 2 m (i.e. subplot beneath shrub canopy and subplot in open grassland, Figure S2 in Appendix S3). Shrubs were all medium-sized plants (up to 1 m tall and shrub canopy coverage within the encroached subplot was between 20% and 50%), typical for this grassland.

In all plots, aboveground plant organs (i.e. from the soil surface upwards) were harvested and sorted into species. Plant samples were rinsed with deionized water to remove dust particles. All plant organs were oven dried at 65°C for 72 hr. Only those species presented in both encroached and non-encroached subplots were selected for measuring N concentration and isotopes. Five individuals of each species within each subplot were randomly chosen for measuring plant N concentrations and damaged or senescent leaves were discarded. Besides *Caragana* and their neighbour plants, we further sampled the co-occurring non-leguminous shrub (*Salsola collina*) as a reference plant to assess if these leguminous shrubs *Caragana* fix N or not (Aranibar et al., 2004; Robinson, 2001). Within each subplot, five random soil samples (5.0 cm diameter, 20 cm deep) were collected by a soil corer and mixed as one composite sample (Figure S2). After removing roots from the samples, soils were sieved through a 2.0 mm sieve. Soil samples were dried at 65°C for 72 hr. Plant material and soil samples were milled to a fine powder.

2.4 | Laboratory analysis

Total SOC was measured using the Walkley–Black modified acid-dichromate $FeSO_4$ titration method (Nelson & Sommers, 1996). N concentration and natural abundance isotopic ratios of plants and soils were determined with an isotope-ratio mass spectrometer (IRMS; Deltaplus XP and Delta C prototype Finnigan MAT, respectively, Finnigan MAT, Bremen, Germany; 0.1‰ precision). The natural abundance of ^{15}N and ^{14}N ($\delta^{15}N$) is defined in per mil (‰) relative to atmospheric N_2, and expressed as follows:

$$\delta^{15}N(\%) = (R_{\text{sample}}/R_{\text{atmos}} - 1) \times 1{,}000 \tag{1}$$

where R_{sample} and R_{atmos} are the isotope ratio ($^{15}N/^{14}N$) of the sample and standard value of atmospheric N_2 (0.003677) respectively. Legumes typically contain higher tissue N and have $\delta^{15}N$ signatures close to the atmospheric N_2 value (0‰), being less enriched than plants that rely on soil N. Similarly, grasses that acquire N transferred from a leguminous shrub will have higher N concentrations and lower $\delta^{15}N$ values compared to those that rely only on the uptake of soil N (Robinson, 2001; Zhang et al., 2016).

2.5 | Soil C and N pool concentrations

Soil C and N pools by depth were calculated as follows:

$$\text{C(N) pool (kg m}^2) = \%\text{C(N)} \times \text{BD} \times \text{D} \times 10 \tag{2}$$

where %C (N) is the soil C (N) percent concentration; BD is the average bulk density of the soil profile (g/cm^3) and D is the depth of the soil profile (cm).

BD was calculated, using the equation adapted from Post and Kwon (2000):

$$\text{BD} = \frac{100}{\left[\left(\frac{\%\text{SOM}}{0.244}\right) + \frac{100-\%\text{SOM}}{1.64}\right]}, \tag{3}$$

where %SOM is the percentage of soil organic matter assuming that organic matter is equal to soil C concentration divided by 0.58 (Mann, 1986).

2.6 | Statistics analysis

For shrub-induced LnRR of SOC and total N from the global synthesized dataset, we applied linear mixed model (LMM) using LME4 package (Bates, Maechler, & Bolker, 2012), with MAP, legumes status (N-fixation shrub or non-N-fixation shrub), and their interaction as fixed effects while study sites as random effects. Similarly, LMM was also applied for LnRR of neighbour plants biomass, SOC, and soil N in our field study, with MAP as fixed effects and sample sites as random effects. Fixed effects were tested with ANOVA and the *F* test. We further correlated LnRR (from the synthesized and field dataset) with rainfall using regression analysis. The overall difference of LnRR in biomass, soil C and N between *C. stenophylla* and *C. microphylla* sites were compared by a two-tailed Wilcoxon two-sample rank sum test considering the small and unequal sample size between the two *Caragana* sites.

For our field data (except for the calculated LnRR), we tested data normality using the Shapiro–Wilk test and equality of variances using Levene's test. Data not meeting the requirement for analysis were log or square root transformed. For testing whether legumes fix N or not in the field study, we applied LMM to compare the difference in two situations: (a) the plant N status (concentrations and $\delta^{15}N$) between leguminous shrubs and non-leguminous shrubs (reference shrub) and (b) the soil N status (content and $\delta^{15}N$) between plots with and without shrubs. Fixed effects in situation (a) were legume (N-fixing shrub or non-N-fixing shrub), organ (leaf or stem), and their interaction while in situation (b) were shrub species (*C. stenophylla* or *C. microphylla*), encroach and their interaction. Fixed effects were tested, using ANOVA with *F* test. Random effects in situation (a) and (b) were sample sites. We then compared the contrast effects between *C. stenophylla* and

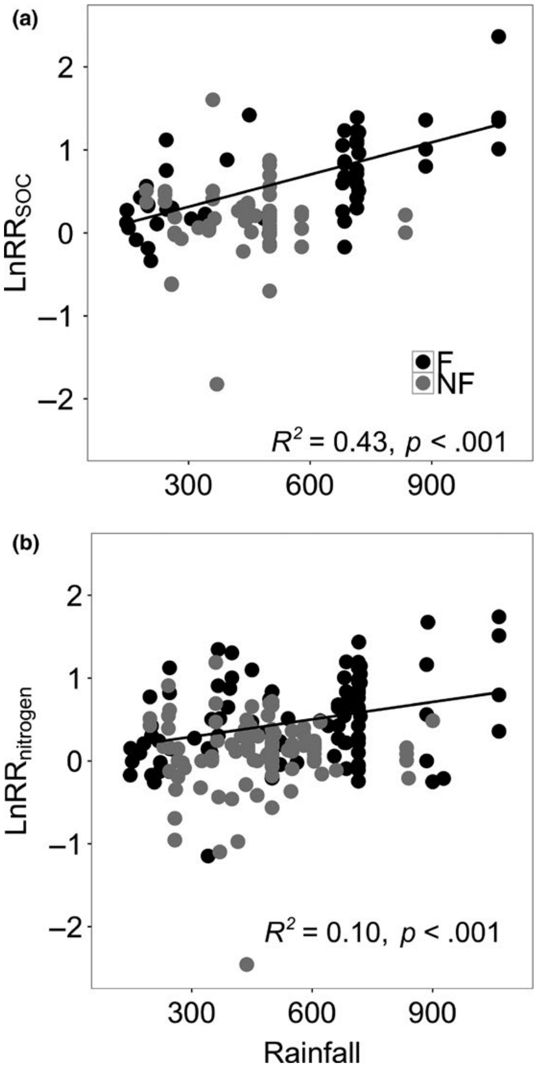

FIGURE 1 Regressions of rainfall with the log response ratio (LnRR), i.e. log (encroached/non-encroached), of soil carbon (LnRR$_{\text{carbon}}$, a) and nitrogen (LnRR$_{\text{nitrogen}}$, b) concentration at the global scale for non-N-fixing (NF, grey) and N-fixing (F, black) shrubs respectively. Liner regression analysis showed the correlations were only significant for leguminous shrubs. Statistical results see Table 1 and regression model details see the figure panel

TABLE 1 Effects of MAP, legume status and their interaction (fixed effects) on shrub-mediated log response ratio (LnRR), i.e. log (encroached/non-encroached) of soil carbon (LnRR_C) and nitrogen (LnRR_N) in the global meta-datasets. *F* test for fixed effects and *SD* that fitted for random effects (sites) from the mixed model are shown

	LnRR_C		LnRR_N	
Model	$F_{(1,74)}$	p	$F_{(1,129)}$	p
Fixed effects				
MAP	13.31	**<.001**	4.79	**.030**
Legume	11.66	**.001**	11.39	**.001**
Interaction	2.22	.141	0.06	.801
Random effects				
	SD		*SD*	
Sites	0.343		0.395	
Residual	0.335		0.344	

Note the significant effects ($p < .05$) are indicated in bold. Numbers within the bracket of *F* values were Num. *df* and Den. *df* respectively. Num. *df*, numerator degrees of freedom of fixed effects; Den. *df*, denominator degrees of freedom for fixed effects.

C. microphylla on soil N and δ^{15}N values using ANOVA with *F* test and multiple mean comparisons with *glht* function (Tukey test) in MULTCOMP packages. Paired *t* tests were used to compare shrub-mediated effects on neighbour-plant N concentration, C:N ratio and plant δ^{15}N in different plant species. All statistical analyses were performed, using R version 3.0.2 (R Core Team, 2013).

3 | RESULTS

For the synthesized dataset, we found LnRR for both soil C and N increased with increasing MAP (Figure 1, Table 1). However, when we included potential N-fixing, we found that, shrub-mediated effects on soil C ($\text{LnRR}_{\text{carbon}}$) and N ($\text{LnRR}_{\text{nitrogen}}$) increased as MAP increased only for N-fixers. On the contrary, $\text{LnRR}_{\text{carbon}}$ and $\text{LnRR}_{\text{nitrogen}}$ showed no relationship with MAP for non-leguminous shrubs (Figure 1).

Compared to the non-leguminous shrub (reference shrub, *S. collina*), *Caragana* had significantly greater N concentration and lower δ^{15}N values in both leaves and stems (Figure 2; Table 2). The encroachment by *C. microphylla* significantly increased soil N pools (+16.3%; Figure 3), whereas *C. stenophylla* had no significant effect, and the two shrubs significantly decreased soil δ^{15}N by 7.0% and 10.1% respectively (Figure 3; Table 3).

Caragana increased neighbour-plant N concentrations and decreased C:N ratios, but the shrub-mediated effects were greater for *C. microphylla* than for C. *stenophylla* (Figure 4a–d). Shrub encroachment had no significant effect on the δ^{15}N values of neighbour plants (Figure 4e,f, Table S2 in Appendix S3) except for *Artemisia frigida* on *C. microphylla* sites.

Shrub-mediated positive effects on neighbour-plant biomass increased as MAP increased (Figure 5, Table 4). *Caragana microphylla* had positive effects and *C. stenophylla* showed neutral effects on neighbour-plant biomass (Figure 6). The shrub-mediated positive effects on soil N increased as MAP increased. Overall, shrub-mediated effects on soil fertility, i.e. $\text{LNRR}_{\text{carbon}}$ (soil carbon pool) and $\text{LNRR}_{\text{nitrogen}}$ (soil N pool), were greater for *C. microphylla* than that for *C. stenophylla*, although the differences were statistically significant only for $\text{LNRR}_{\text{nitrogen}}$ (Figure 6).

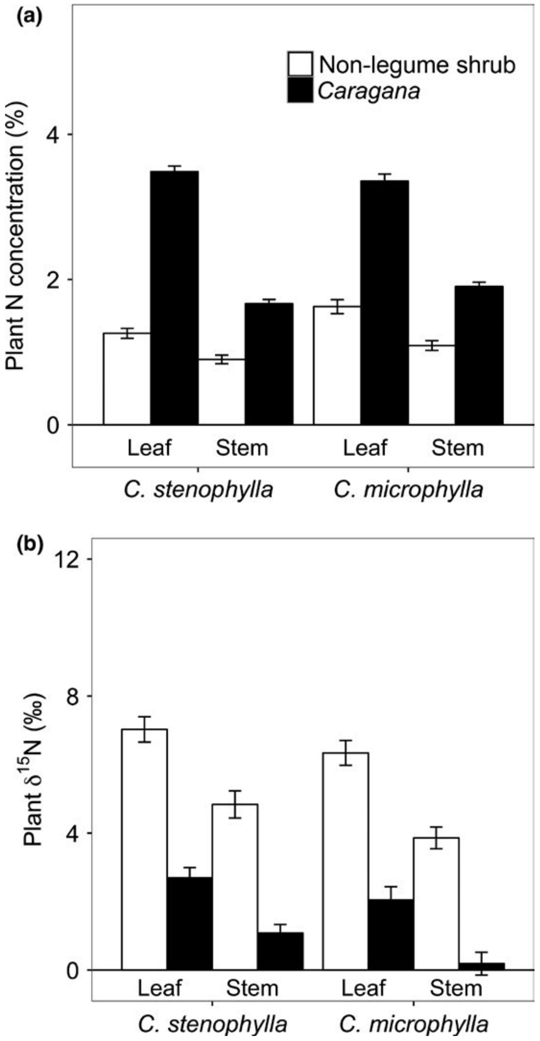

FIGURE 2 Nitrogen concentration (a) and δ^{15}N (b) in plant leaf and stem for co-occurring non-legume shrubs (reference plant, white, *Salsola collina*) and legume shrubs (black, *Caragana*) shrubs both for *Caragana stenophylla* and *Caragana microphylla*, respectively, across the transect. Values represent *M* ± 1 *SE*. Statistically significant effects of legume status (Non-leguminous shrub and *Caragana*), organs (leaf and stem) and interactions see Table 2

4 | DISCUSSION

4.1 | Soil fertility intensity from shrub encroachment at global scale

Although recent global meta-analysis found a positive precipitation-mediated effect of shrub encroachment on soil organic C pools (Li

TABLE 2 Effects of legume status (non-leguminous shrubs *Salsola collina* and leguminous *Caragana*), organs (leaf and stem) and their interactions on plant N concentration and δ^{15}N values across different sites (random effects) for *Caragana stenophylla* and *Caragana microphylla* respectively. *F* test for fixed effects and *SD* that fitted for random effects from the mixed model are shown

	C. stenophylla sites		*C. microphylla* sites	
	$F_{(1,63)}$	*p*	$F_{(1,35)}$	*p*
Plant N (%)				
Fixed effects				
Legume	347.95	**<.001**	240.03	**<.001**
Organ	399.75	**<.001**	141.02	**<.001**
Interaction	136.30	**<.001**	31.15	**<.001**
Random effects				
	SD		*SD*	
Sites	0.126		0.000	
Residual	0.264		0.278	
Plant δ^{15}N (‰)				
Fixed effects				
Legume	205.80	**<.001**	86.12	**<.001**
Organ	72.68	**<.001**	60.70	**<.001**
Interaction	1.73	.193	1.21	.280
Random effects				
	SD		*SD*	
Sites	1.023		1.025	
Residual	0.931		0.951	

Note the significant effects ($p < .05$) are indicated in bold. Numbers within the bracket of *F* values were Num. *df* and Den. *df* respectively. Num. *df*, numerator degrees of freedom of fixed effects; Den. *df*, denominator degrees of freedom for fixed effects.

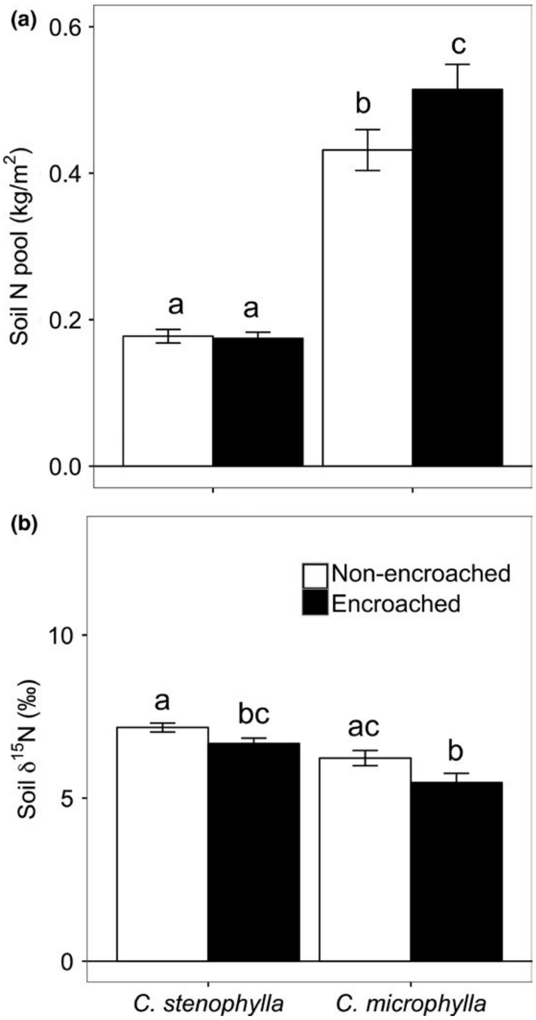

FIGURE 3 Soil N pool (a) and δ^{15}N (b) values in encroached (black) and non-encroached (white) subplots both for *Caragana stenophylla* and *Caragana microphylla*, respectively, across the field transect. Values represent *M* ± 1 *SE*. Note the significant effects ($p < .05$) are indicated by different letters. Statistical details see Table 3

et al., 2016), data on shrub-mediated effects on soil N were not included. In our study, when shrubs (i.e. leguminous and non-leguminous shrubs) were pooled together, we found a positive effect of precipitation on shrub-mediated effects both on soil C and N in our global synthesized datasets. By contrast, Dohn et al. (2013) showed no correlations between subcanopy to open grassland ratios and rainfall for soil N. These different findings might be due to the relatively limited data on soil N concentration (22 case studies on soil N concentration) in Dohn et al. (2013).

Interestingly, after subdividing our dataset by legume, we found that leguminous shrubs rather than non-leguminous shrubs mainly drove this positive correlation, indicating that the shrub encroachment effect on soil fertility (C and N) was more sensitive to precipitation for leguminous shrubs. In other words, legumes or plant-associated microbes (N-fixing bacteria) were an important predictor for sensitivity and magnitude of soil fertility increases and potential facilitation along the precipitation gradient (Michalet, 2006; Rodríguez-Echeverría, Lozano, & Bardgett, 2016). As investigations on changes in shrub–grass interactions or shrub-mediated facilitation along stress gradients will inevitably include different species, our results suggest that the N-fixing ability of shrubs will need to be taken into account. In addition, there was no correlation between MAP and shrub-mediated effects on SOC for non-N-fixing shrubs, thus, whether MAP promotes shrub-mediated effect on soil C sequestration (as concluded by Li et al., 2016) may depend on the N-fixing ability of the encroaching shrubs.

A recent global meta-analysis from Mazía et al. (2016) showed that facilitation from leguminous trees were broader than that from non-leguminous trees along a global aridity gradient. Our results corroborate this finding and, in turn, suggest that soil N is enhanced by woody plants in less stressful environments (Figure 1), extending the role of facilitation by leguminous plants. Greater sensitivity and magnitude of soil fertility increases from leguminous shrubs along the precipitation gradients might also contribute to the shrub encroachment rate at continental scales. Stevens et al. (2017) quantified savanna woody vegetation change spanning the last century and showed that woody cover in

TABLE 3 Effects of shrubtype (*Caragana stenophylla* or *Caragana microphylla*), encroachment and their interactions on soil N concentration and δ^{15}N values across different sites (random effects). *F* test for fixed effects and *SD* that fitted for random effects from the mixed model were shown in the table

	Soil N (%)		Soil δ^{15}N (‰)	
	F	*p*	*F*	*p*
Fixed effects				
Shrubtype $(_{1,\ 11})$	28.90	**<.001**	3.74	.079
Encroach $(_{1,\ 109})$	10.91	**.001**	44.92	**<.001**
Interaction $(_{1,109})$	17.77	**<.001**	2.02	.158
Random effects				
	SD		*SD*	
Sites	0.094		0.966	
Residual	0.055		0.497	

Note the significant effects ($p < .05$) are indicated in bold. Numbers within each fixed effects were Num. *df* and Den. *df* respectively. Num. *df*, numerator degrees of freedom of fixed effects; Den. *df*, denominator degrees of freedom for fixed effects.

Africa increased by two and a half times compared to Australian savannas. A possible explanation may be that Africa has a high abundance of leguminous woody plant from the family Fabaceae (Stevens et al., 2017). Therefore, shrub N-fixing ability is critical to predicting woody plant-mediated nutrient dynamics, plant–plant interactions and woody plant encroachment rate at the continental and even global scales.

4.2 | Does *Caragana* promote neighbour-plant N uptake and soil N pool?

We found that N inputs from leguminous shrubs could be important at local to regional scales. By definition, the δ^{15}N of atmospheric N_2 is 0‰ while soil δ^{15}N is relatively heavier. Legume species typically have δ^{15}N signatures close to the atmospheric N_2 value (0‰), i.e. lower δ^{15}N than plants that take up N from soils. Lower δ^{15}N and higher N concentration in both leaves and stems of *Caragana* than of reference shrubs (*S. collina*) indicate that N-fixation played a major role in the N utilization of *Caragana* (Figure 2, Robinson, 2001). Neighbour-plants that are close to leguminous shrubs likely will have higher N concentrations and lower δ^{15}N if they take up fixed-N directly, compared to neighbour-plants that are farther away from N-fixing shrubs and have to rely on the uptake of soil N only (Robinson, 2001). Based on this, Zhang et al. (2016) found that at local scales, the leguminous shrub *C. microphylla* directly transferred fixed-N to three dominant grasses. In the present study, the two species of leguminous *Caragana* both increased neighbour-plant N uptake at the regional scale as well, although evidence for direct sharing of fixed-N (depleted δ^{15}N) was lacking because most neighbour-plant δ^{15}N values did not show any depletion in proximity to leguminous shrubs (Figure 3).

The facilitative effects of *C. microphylla* on neighbouring plants and the surrounding soils were stronger than for *C. stenophylla*. Almost all coexisting species had higher N concentration when close to *C. microphylla* while only two species (*Stipa capillata* and *Cleistogenes squarrosa*) followed this pattern in association with *C. stenophylla* (Figure 3). Although N fixed by those two shrub species was not quantified, N-fixation from leguminous *Caragana* should be higher in more humid areas because energetic demands for N-fixation were alleviated at mesic areas (Aranibar et al., 2004). Woody plants tended to increase soil N concentration beneath the canopy (Dohn et al., 2013) and these effects were stronger for N-fixers than for non-fixers (Blaser et al., 2013). Our results went one step further, showing that even within N-fixers, shrubs in mesic areas increase soil N pools stronger than in xeric areas.

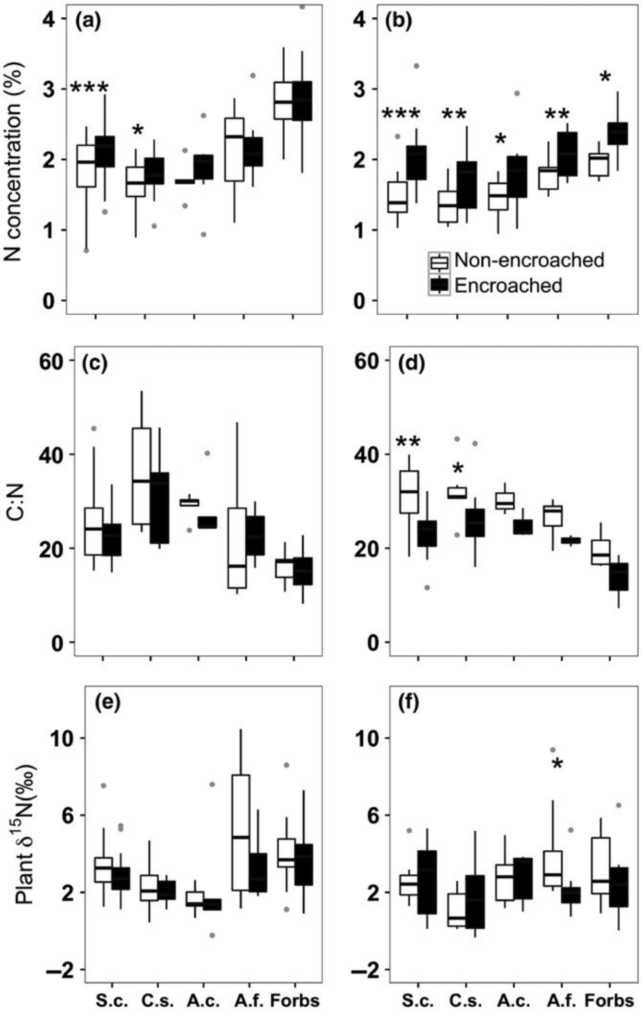

FIGURE 4 Neighbour plant foliar nitrogen (N) concentration, C:N ratio and δ^{15}N values in different species from encroached (black) and non-encroached (white) subplots at the *Caragana stenophylla* (a, c, e) and *Caragana microphylla* (b, d, f) sites. Neighbour species were belonging to different growth from: grasses (S.c., *Stipa capillata*, C.s., *Cleistogenes squarrosa*, A.c., *Agropyron cristatum*), sub-shrub (A.f., *Artemisia frigida*) and forbs. Grey points were outliers. The differences between encroached and non-encroached were compared by paired *t* test (*** if $p < .001$, ** if $p < .01$, * if $p < .05$, statistical results see Table S2)

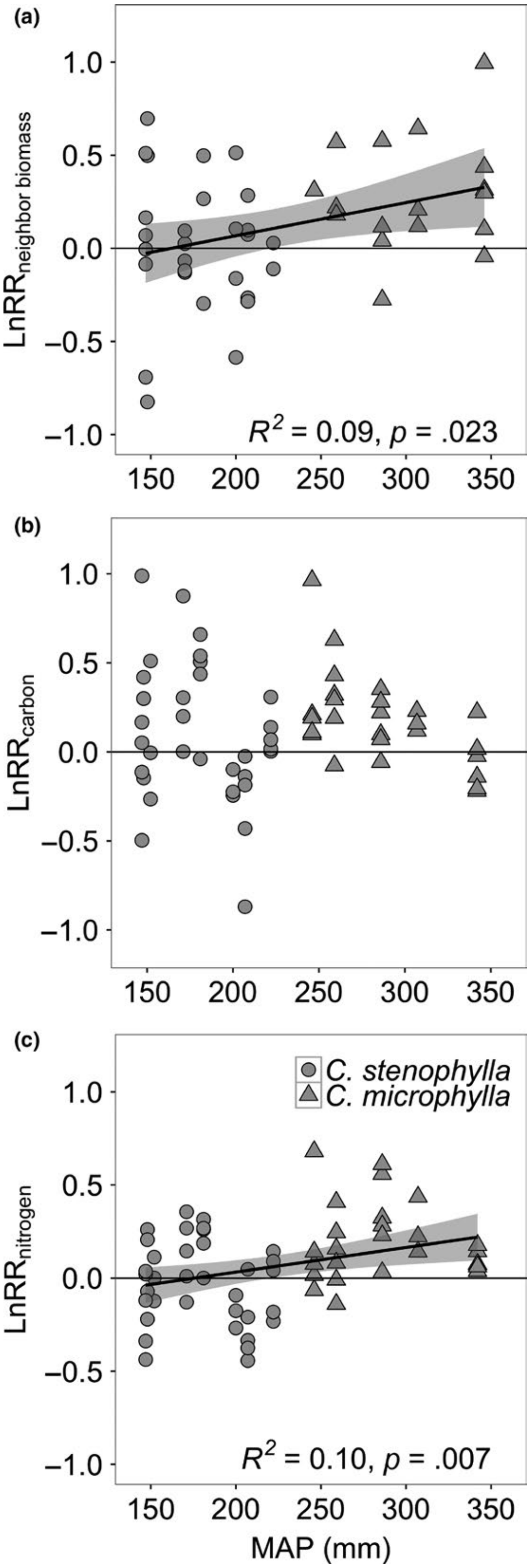

FIGURE 5 Regressions of mean annual precipitation (MAP) with the log response ratio (LnRR), i.e. log (encroached/non-encroached), of neighbour herbaceous biomass (g/m^2), soil carbon (C, kg/m^2), and nitrogen (N, kg/m^2) pools for *Caragana stenophylla* (circle) or *Caragana microphylla* (triangle) respectively. Statistical results see Table 4 and regression model details see the figure panel

TABLE 4 Effects of MAP (fixed effects) on shrub-mediated log response ratio (LnRR), i.e. log (encroached/non-encroached), of neighbour plant biomass (LnRR$_{biomass}$), soil carbon (LnRR$_C$) and nitrogen (LnRR$_N$) in the regional scale field study. *F* test for fixed effects and *SD* that fitted for random effects (sites) from the mixed model are shown

	LnRR$_{biomass}$		LnRR$_C$		LnRR$_N$	
Model	$F_{(1,9)}$	p	$F_{(1,9)}$	p	$F_{(1,9)}$	p
Fixed effects						
MAP	5.444	**.045**	0.031	.863	3.670	.088
Shrubtype	1.098	.322	5.484	**.044**	3.315	.110
Interaction	0.309	.592	0.020	.890	0.171	.689
Random effects						
	SD		*SD*		*SD*	
Sites	0.000		0.100		0.131	
Residual	0.343		0.348		0.187	

Note the significant effects ($p < .05$) are indicated in bold. Numbers within the bracket of *F* values were Num. *df* and Den. *df* respectively. Num. *df*, numerator degrees of freedom of fixed effects; Den. *df*, denominator degrees of freedom for fixed effects.

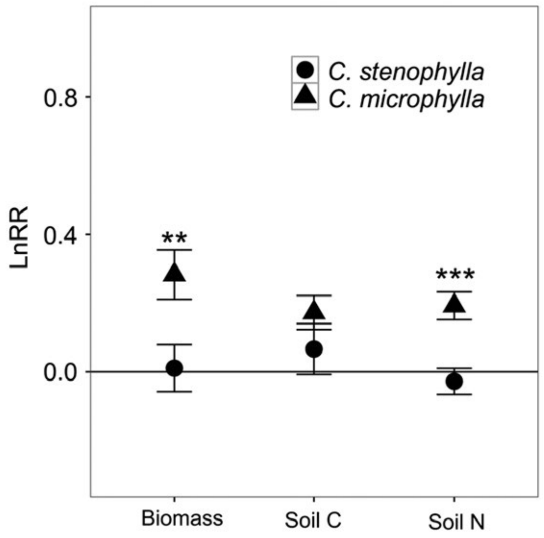

FIGURE 6 Log response ratio (LnRR), i.e. log (encroached/non-encroached), induced by shrub encroachment on neighbor plant biomass, soil carbon (C), and nitrogen (N) pool for *Caragana stenophylla* (circle) or *Caragana microphylla* (triangle) respectively. The difference in LnRR between *C. stenophylla* and *C. microphylla* were compared by a two-tailed Wilcoxon two-sample rank sum test (*** if $p < .001$, ** if $p < .01$)

4.3 | Shrub–grass interactions and the SGH

Michalet et al. (2014) suggested that in the most stressful environments, rather than facilitation dominating interactions, there may be a loss of facilitation and even a switch to primarily competitive interactions. We found that, *C. stenophylla* only had a neutral effect on their neighbour plants on more stressful (more arid) sites whereas *C. microphylla* had positive effects on more mesic sites, supporting the prediction of a collapse of facilitation. As N is the most limiting element for productivity in the majority of terrestrial ecosystems (Schuur & Matson, 2001), the contrasting responses of neighbour-plant biomass in our study may be explained by different N dynamics: i.e. positive effects at mesic grasslands in the present study should be related to increased N availability (both in neighbour plants and soil) beneath the shrubs (Maestre & Cortina, 2004; Tielborger & Kadmon, 2000). Similarly, Noumi et al. (2016) also found that positive effects from leguminous shrub species were associated with increasing nutrient content beneath their canopy and facilitation from encroached shrubs decreased with increasing aridity. In addition, as *C. stenophylla* and *C. microphylla* were found in locations with different precipitation, increased facilitation with increasing MAP may be due to differences between the two shrub species and thus may be confounded with MAP. However, non-significant effects shrub type and its interaction with precipitation strongly suggest that precipitation was causing these differences not species identity (Table 4).

Previous studies assessing the SGH in woody-grass co-dominated systems have included a much larger precipitation gradient (MAP 200–1,400 mm), and found that woody plants facilitated grass growth on xeric sites while depressing biomass on mesic sites due to light-limitation and/or nutrient competition (Blaser et al., 2013; Dohn et al., 2013). In our study, we focused on the more arid range of MAP (maximum MAP *c.* 360 mm). In these grasslands, the canopy cover and size of shrubs are low enough to not severely compete with the neighbour plants, especially for light. Hence, shrubs at the mesic grasslands along this MAP gradient in Inner Mongolia are most likely to promote neighbouring plant growth when they increase the supply of limiting resources (in this case, soil N) without excessively reducing light (Le Bagousse-Pinguet et al., 2013).

The functional strategy (stress tolerance and competitive ability) of the species involved in the interactions may also affect plant interactions (Michalet et al., 2014). Neighbouring grasses along the precipitation gradient were not always the same and environmental stress should select species that are more drought-tolerant. When both interacting species are stress-tolerant, facilitation can be expected at moderate stress while competition may occur at high-stress levels (Maestre & Cortina, 2004). This may lead to a collapse of facilitation at the extreme end of the stress gradient (Maestre, Callaway, Valladares, & Lortie, 2009). In addition, our experiment was carried out for only one single year; inter-annual fluctuations of precipitation might affect biomass production and shrub–grass interactions. Therefore, long-term investigations of plant interactions across several years are still needed.

5 | CONCLUSIONS

Our results show consistent and positive effects of leguminous shrub encroachment on soil C and N pools in temperate steppe of the Inner Mongolia and a strong dependence of these effects on precipitation. Leguminous shrub encroachment (*C. microphylla*) on more mesic sites promoted neighbour-plant N uptake and increased soil N pools but these effects were relatively weak for *C. stenophylla* on dry sites. Moreover, C. *microphylla* also promoted neighbour-plant biomass production while *C. stenophylla* only had little effects. Extending our results to the global scale, soil fertility (soil organic C and N) from leguminous shrub encroachment also showed a positive response to increasing precipitation, whereas this correlation did not exist for non-leguminous shrub encroachment. In other words, interactions mediated by soil nutrients and shrub characteristics (N-fixers and non-fixers) play important roles in determining aboveground plant–plant interactions and should be incorporated into the mechanisms included in conceptual frameworks of plant facilitation.

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AUTHORS' CONTRIBUTIONS

H.-Y.Z., X.-T.L. and X.-G.H. conceived and designed the experiments; H.-Y.Z. and X.-G.W. performed the experiments; H.-Y.Z., Q.Y., X.-T.L. analysed the data. All authors wrote the manuscript together.

DATA ACCESSIBILITY

Synthesized dataset are uploaded as online supporting information and have been placed in the Dryad Digital Repository https://doi.org/10.5061/dryad.537k1 (Zhang et al., 2017).

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