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Effect of shrubs on soil saturated hydraulic conductivity depends on the grazing regime in a semi-arid shrub-encroached grassland

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ABSTRACT

Encroachment of woody plants has a positive effect on hydrological functions (e.g., infiltration), but few studies have examined the effects of shrub patches on infiltration under different grazing scenarios. We examined differences in characteristics of plants and soils and saturated hydraulic conductivity between shrubs and their associated interspaces in two grazing regimes at three sites in a semi-arid grassland encroached by *Caragana microphylla*, a leguminous N-fixing shrub. The results showed that the shrub patches had greater plant height, cover, and biomass compared to interspaces, and the shrubs positively affected the characteristics of soils such as porosity and water holding capacity, whereas grazing had a strong opposite effect. The effect of the relative interaction intensity (RII) of shrubs on the saturated hydraulic conductivity of the soil was greater under grazed (0.60) than ungrazed conditions (-0.01), and the negative effect of grazing was mainly achieved in interspaces. Generally, structural equation modeling revealed positive indirect effects of shrubs on saturated hydraulic conductivity via a greater root mass, with 3.5 times of that in interspaces and a lower bulk density (90% of that in interspaces) under conditions of overgrazing. Our findings highlight the critical role that shrubs play in maintaining infiltration under overgrazing conditions and suggest that they might partially offset the damaging effects of overgrazing on infiltration. Thus, shrub encroachment might be an adaptive mechanism of grassland ecosystems to encounter intensive human induced disturbance such as overgrazing.

1. Introduction

The encroachment of woody plants in grasslands has become a global issue (Archer and Predick, 2014; Eldridge et al., 2011). Woody encroachment is commonly considered to be a form of landscape degradation since it is typically associated with a reduction in herbaceous plant biomass, consequently the carrying capacity for livestock (Archer and Predick, 2014). The varied effects of encroachment range from the alteration in soil infiltration and species diversity of plants, reduction in productivity of herbaceous plants, and increase in heterogeneity of soil nutrients (Archer, 2010; Ward et al., 2018). Overgrazing associated with encroachment can also contribute to land degradation (Schlesinger et al., 1990). Encroachment has been found to influence hydrological functions (e.g., infiltration). Infiltration is a critical function in drylands since water is the key driver of productivity, and infiltration is the main route by that water enters the soil (Wang et al., 2012).

Enhanced infiltration associated to individual woody plants or aggregated plant patches, particularly shrubs, has been widely reported in the literature (Bhark and Small, 2003; Niemeyer et al., 2014; Li et al., 2013). However, relatively little is known about changes in soil infiltration associated with shrub patches disturbed by human activities, including livestock-related overstocking. Existing studies suggest that shrubs usually positively affect infiltration, partially offsetting the adverse impacts of overstocking on infiltration, along with their effects on hydrology, which are enhanced with plant size to some extent (Bhark and Small, 2003; Dunkerley, 2000; Eldridge et al., 2015a; Marquart et al., 2019), whereas overgrazing has an opposite effect. There are few studies examining the effects of shrub patches on infiltration experiencing long-term grazing to varying degrees. It is of the utmost importance to evaluate the effects of shrubs on infiltration under different grazing scenarios since it can help to understand the mechanism contributing to stability in ecosystem function under different degrees of disturbance caused by human induced activity.

Overgrazing in Eurasian steppe grasslands reduces organic matter

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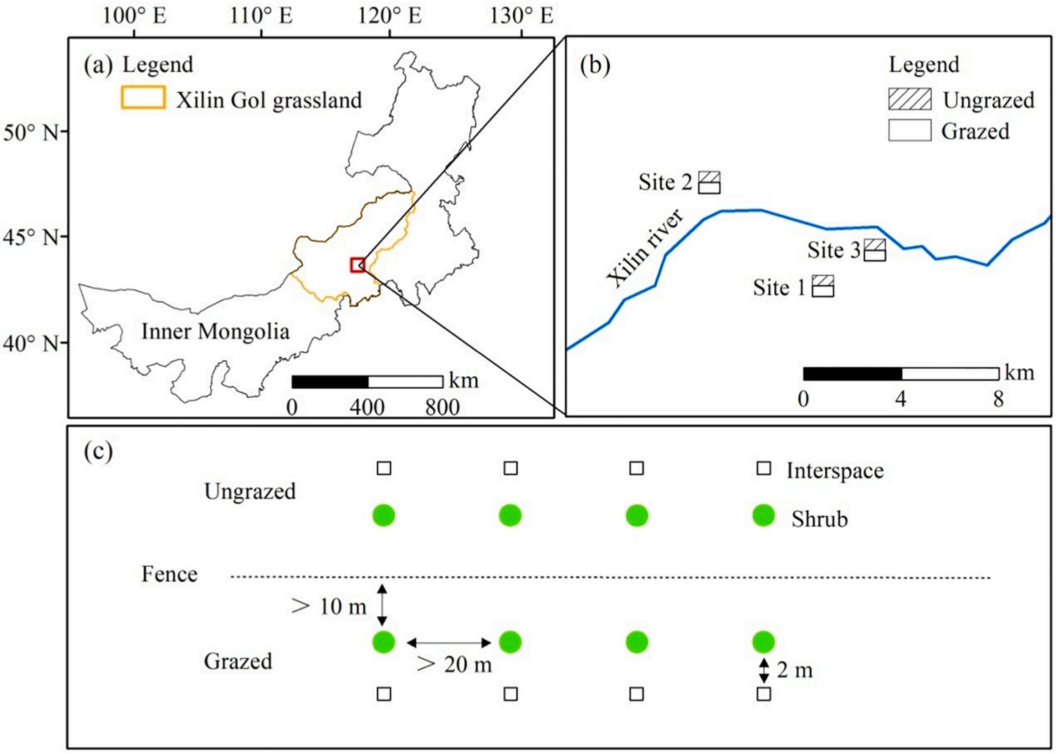

Fig. 1. Study area map (a), locations for grazed and ungrazed treatments at three study sites (b) and schematic diagram of sampling points of three sites (c).

inputs to the soil and reduces soil aggregate stability; thus, increasing soil compaction and reducing infiltration (Cai et al., 2020; Li et al., 2013). Moreover, grazing-induced degradation of grasslands result in a decrease in root density, further suppressing infiltration (Bai et al., 2015). However, substantial degradation of grasslands caused by overgrazing in many areas is associated with the encroachment of woody plants and therefore increasing infiltration. In encroached grasslands in Inner Mongolia, for example, the encroachment of thorny shrubs such as *Caragana microphylla* Lam. (Yan et al., 2019) might result from historical practices of overgrazing. Encroachment has been shown to increase root density and therefore affect infiltration pathways, resulting in higher infiltration capacity beneath shrub canopies (Hu et al., 2015; Li et al., 2013). Thus, the encroachment of shrubs may provide opportunities to partially reverse those adverse impacts of livestock grazing on infiltration rates.

In this study, we carried out a study to explore how grazing and shrubs, along with the related interspaces, affect water infiltration. We hypothesized that continuous overgrazing by livestock would suppress saturated soil hydraulic conductivity. Specifically, it is speculated that such beneficial roles of shrubs in maintaining saturated hydraulic conductivity should be intensified with increasing grazing intensity by livestock, and both plant and soil characteristics in interspaces would be significantly negatively affected compared with those in shrubs. For example, this might occur if a shrub restricted access for livestock animals, thereby avoiding herbivores and preventing soil compaction under the corresponding canopies. We tested this hypothesis in a shrub-encroached grassland using replicated paired grazed and ungrazed treatments. Biomass samples of above- and below-ground plant parts were collected, and soil saturated hydraulic conductivity and soil physical properties were evaluated to determine the alterations caused by grazing.

2. Methods

2.1. Site description

The present study was carried out at the Baiyinxile Pasture, Xilingele grasslands, Inner Mongolia of China (43.7°N, 116.07°E), at about 1,200 m a.s.l. This area is dominated by a typical continental temperate climate, and the average annual rainfall is 285 mm, of which approximately 75% occurs between June and September, with the average annual evaporation of 1,600–1,800 mm. There are strong winds between March and May, and the monthly mean wind speed is 4.9 $m\ s^{-1}$. The mean temperatures in the hottest (June) and coldest (January) months are 18.8 °C and –22.3 °C, respectively, and the frost-free season lasts about 100 days.

With regard to the soil type, this area is dominated by the calcic and chestnut chernozems, which are equivalent to the Mollisols Soil Order in USDA Soil Taxonomy. Soil parent materials are formed in Basalt plateaus, and sandy topsoil is formed due to obvious deposition and wind erosion (Yan et al., 2011). The contents of clay, silt, and sand in the soil in the grazed pasture were 0.96%, 12.14%, and 86.90%, respectively (Yan et al., 2015). Soil organic carbon content beneath shrubs was about 0.88%-1.23% and that in interspaces was 0.55%-0.65% in grazed conditions (Cai et al., 2020). The soil pH of the experimental area ranged from 6.67 to 6.93, and the soil water content was 7.55%-10.92% during the experiment. *Artemisia frigida* Willd., *Stipa grandis* P., *Leymus chinensis* Trin., and *Cleistogenes squarrosa* Trin. are the major species of the dominant local plants (Yan et al., 2019). Due to the overstocking to varying degrees, serious grassland (vegetation) degradation was observed; at certain places, the encroachment of *Caragana microphylla,* an N-fixing shrub, was distinctive (Yan et al., 2019). Shrub coverage was about 8.38% under grazed conditions, and 17.14% under ungrazed treatments in our study (Fig. S1).

To examine how grazing and the presence of shrubs affected the saturated hydraulic conductivity, we selected three sites with similar topographical conditions, with each site, including ungrazed and

Table 1
The mean (±SE) values of shrub size, plant height, and plant cover in relation to grazing and microsite types at three sites. G: grazed; UG: ungrazed; the figures specified after UG represent different fencing years. na = not applicable. The total represents the average values of parameters at all sites.

Site	Grazing scenario	Microsite	Shrub size (m^2)		Plant height (cm)			Plant cover (%)		
			Mean	SE	Mean	SE	*P*-value	Mean	SE	*P*-value
Site 1	G	Shrub	5.99	1.82	47.33	5.49	<0.01	75.67	8.09	>0.05
		Interspace	na	na	9.09	0.73		56.67	4.41	
	UG36	Shrub	6.05	0.37	59.17	5.55	<0.01	83.75	3.15	>0.05
		Interspace	na	na	28.22	2.31		77.00	3.14	
Site 2	G	Shrub	6.39	1.19	31.00	2.04	<0.01	51.50	3.84	<0.05
		Interspace	na	na	9.45	0.67		36.00	2.43	
	UG20	Shrub	5.95	1.00	55.97	8.82	<0.01	73.60	4.95	>0.05
		Interspace	na	na	22.91	3.39		78.33	6.76	
Site 3	G	Shrub	4.41	1.16	29.70	3.45	<0.01	48.00	6.40	>0.05
		Interspace	na	na	10.02	0.90		38.71	2.59	
	UG2	Shrub	3.27	0.81	28.11	2.80	<0.01	55.00	0.00	>0.05
		Interspace	na	na	13.45	0.68		56.33	5.55	
Total	G	Shrub	5.56	0.94	35.37	2.86	<0.01	57.94	3.53	<0.05
		Interspace	na	na	10.17	2.73		45.02	3.53	
	UG	Shrub	5.24	0.76	48.99	2.65	<0.01	67.57	3.42	>0.05
		Interspace	na	na	20.52	2.65		71.34	3.42	

adjacent grazed rangelands (Fig. 1). The ungrazed areas with grazing restrictions at three sites were fenced at different times for further research into the basic ecological restoration (Yan et al., 2015; Cai et al., 2020). However, the original status of grazing was maintained in the areas around the fences, with the mean stock density of about 2 sheep units per ha. The three sites were located within 6 km of one another, with the distance between the two sites>1 km. Each site was>20 ha. Specific descriptions of the three sites are as follows: Site 1, ungrazed for 36 years (UG36) and adjacent grazing treatment (G); Site 2, ungrazed for 20 years (UG20) and adjacent grazing treatment (G); Site 3, ungrazed for two years (UG2) and adjacent grazing treatment (G).

2.2. Plant community attributes

The grazed and ungrazed areas at each site were separated by fences. Therefore, we considered the fence as the center and selected four shrubs at symmetrical positions inside and outside the fence (>10 m away from the fence) (Fig. 1). All shrubs were similar in size (Table 1), and every two adjacent shrubs were placed at a distance of>20 m from each other, ensuring that shrubs were measured independently. Hence, a total of 24 shrubs (3 sites × 2 treatments × 4 replications) were selected. We then assessed the properties of the plants growing beneath the shrubs and at their corresponding interspaces within a 1 m^2 quadrat. The quadrats were placed directly beneath the canopy of each shrub, approximately 2 m away from the canopy edge of any shrub (interspace). We used a point frame within each quadrat to measure the plant cover using a grid constituting 100 crosshairs, and then the mean heights of 5 plants randomly selected from every species within the quadrat were measured. In addition, the shrub size was determined by measuring the long axis and short axis of one shrub patch, and shrub height were measured by ruler. Shrub and non-shrub plants within each quadrat were cut at ground level and separated according to their species; all litter within each quadrat was collected. The biomass was collected and dried in an oven at 65 °C for 48 h, and subsequently, the weight was measured to calculate the above-ground and litter biomass using an analytical electronic balance with an accuracy of 0.01 g.

2.3. Field measurements of saturated hydraulic conductivity

To determine how patch types (interspaces or shrubs), as well as the status of grazing (grazed or ungrazed), affected the infiltration, we measured the saturated hydraulic conductivity of the soil in all shrub patches and their paired interspaces ($n = 48$) at the same measurement positions as in the plant community survey. We used the pressure infiltrometer (DualHead Infiltrometer, Decagon, USA) in this experiment, maintaining a constant water level of 5 cm depth and creating two different pressure loads using air pressure. Besides, this infiltrometer also maintained the automatic water level while using three complete pressure cycles to measure infiltration rate. There were two periods in one cycle, with one period at which high pressure was kept and another with low pressure. The infiltration rate of this device ranges from 0.038 to 1,150 mm h^{-1}, with an accuracy of ± 5% and a resolution of 0.038 mm h^{-1} (infiltrometer' operator manual).

Before infiltration measurements, litter was removed from the soil surface at both microsites. A 15-cm diameter ring was then gently hammered into the soil to a depth of 5 cm, ensuring minimal disturbance. For all measurements, we used the following infiltration parameters: head with 5 cm low and 10 cm high pressure, soaking time of 15 min, and three cycles of 15 min holding time for each pressure head. The measurements were carried out for a total of 105 min, and the data were downloaded and analyzed. The water depth and pressure head, as well as the water flux per minute, were recorded. During each infiltration experiment, the infiltrometer head was periodically checked to ensure that the seal was intact. In case of any leakage or lateral flow from near-surface horizons, the test was aborted.

The final K_{fs} value is the average infiltration rate for both cycles of pressure head. With modifications to the original analytical equation, the dependence of the results of K_{fs} from the final field on soil characteristics was eliminated, and only the data on pressure head and infiltration rates were used for the calculation (Reynolds and Elrick, 1990) as follows:

$$k_{fs} = \frac{\Delta(i_1 - i_2)}{D_1 - D_2}$$

where K_{fs} is the saturated hydraulic conductivity (mm h^{-1}); Δ is the infiltrometer geometry constant; moreover, i represents the infiltration rate with the corresponding pressure head, and D represents the pressure head; the values are the averages of each of the pressure cycles.

2.4. Soil sampling and analysis

After the measurement of saturated hydraulic conductivity of the soil, roots were sampled by excavating the topsoil (20 cm) layer of a 20 × 20 cm soil column at each position. Roots were removed from the soil, transported to the laboratory, washed, dried in an oven for 72 h at 65 °C, and weighed to quantify the root biomass using an analytical electronic balance with an accuracy of 0.01 g. A 100-cm^3 steel corer was used to measure the bulk density of soil in the surface layer of soil (20 cm). Two samples were selected from each of 50 measurement locations. The saturated soil water content was measured using the water suction

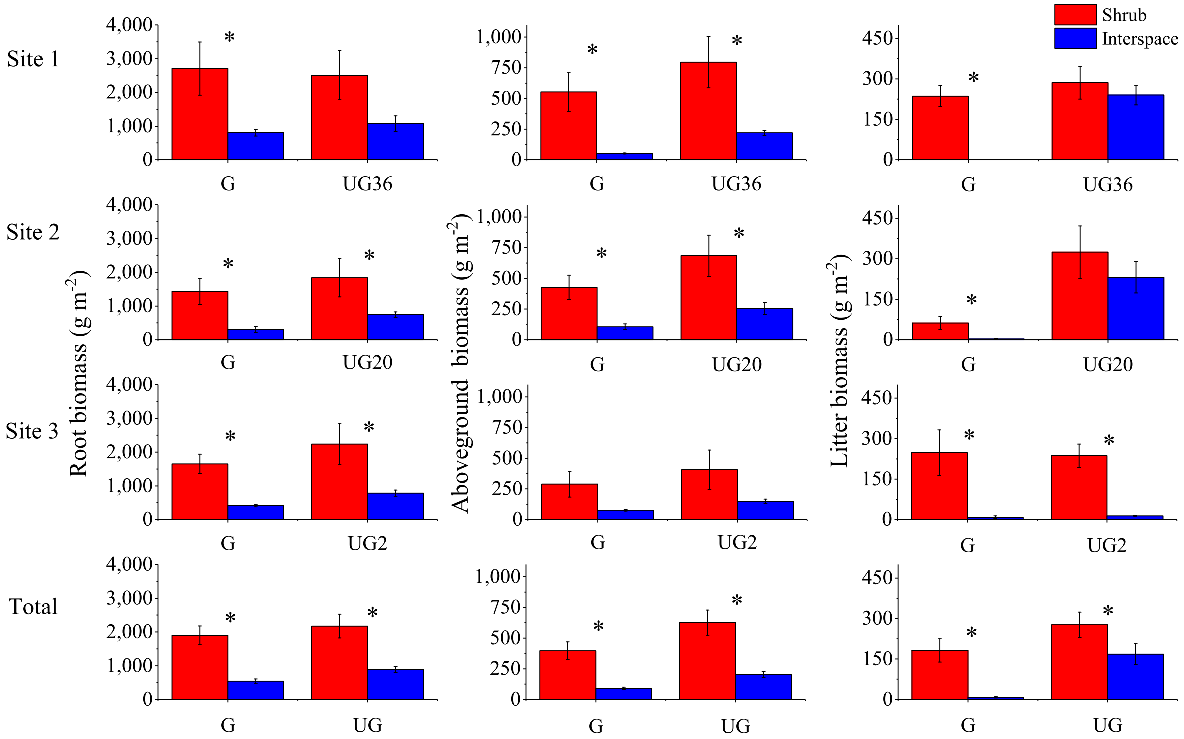

Fig. 2. The mean (±SE) values of root biomass (g m^{-2}), above-ground biomass (g m^{-2}), and litter biomass (g m^{-2}) for two microsite types across grazing regimes at three sites. G: grazed; UG: ungrazed; the figures specified after UG represent different fencing years. The asterisks for a specific grazing pattern indicate significant differences ($P < 0.05$) between shrubs and interspaces. The total represents the average values of parameters at all sites.

method (Bao, 2000). The steel corers were placed in a large plastic container with sufficient water to ensure that the water was just below the top of the corer. The soil corers were placed in water for approximately 24 h until a constant weight was obtained. The samples were oven-dried for 72 h at 104 °C to measure gravimetric soil water content.

2.5. Statistical analysis

Relative interaction intensity (RII; Armas et al., 2004) was used in the present study to determine how the shrub patch affected the above-ground and root biomass, saturated hydraulic conductivity, saturated water content, and bulk density. The following equation was used to determine RII.

$\mathrm{RII} = (X_{\mathrm{Shrub\ patch}}\text{-}X_{\mathrm{Interspace}})/(X_{\mathrm{Shrub\ patch}} + X_{\mathrm{Interspace}})$.

In this equation, X represents an attribute value, like the soil saturated hydraulic conductivity. The value of RII was within the range of $[-1-1]$, and the value of > 0 indicated large shrub patches compared with interspaces.

Before analysis, the normal distribution and homogeneity of error variance in residuals of data were tested using Levene's test (Eldridge et al. 2015a). We used the General Linear Model procedure (Proc GLM) was used to compare for differences in the effects of the two microsite types (shrub, interspace) in relation to the two grazing regimes (grazed, ungrazed) on vegetation characteristics, soil bulk density, saturated hydraulic conductivity, saturated water content, and the corresponding RII values at each of the three sites as well as the total (average values of three sites). Our analytical structure resembled a split-plot analysis. The first stratum represented site effects, grazing effects, and their interaction. The grazing-by-site interaction was used as the residual term to test the grazing effect. The second stratum was used to examine the effects of microsites and their corresponding associations with grazing. Statistical analyses were performed using SPSS software ver. 22.0 (SPSS for Windows, Version 22.0, Chicago, Illinois). Descriptive results were reported as the means ± standard error.

To explore the relationships between soil saturated hydraulic conductivity and bulk density, root biomass, grazing, and microsites (shrub and interspace), a congenital causal model was built and analyzed by structural equation modeling (SEM) (Grace, 2006). The proposed model facilitated the simultaneous analysis of the associations of several related variables with the saturated hydraulic conductivity. The as-constructed congenital model estimated that shrubs exerted powerful favorable impacts, whereas grazing had an indirect adverse impact on saturated hydraulic conductivity by changing root biomass and bulk density. During the process of the measurement of saturated hydraulic conductivity, above-ground vegetation and litter were removed to offset their effects on the hydraulic conductivity. SEM images were then obtained to partition the indirect impact of a variable on another direct counterpart and predict the extent of such multi-effects. In theory, SEM analysis is similar to path analysis, with the former involving certain advanced technologies to evaluate the goodness-of-fit of the given model compared with the observation results. To improve normality, these variables (*z*-transformation) were standardized before analysis. The goodness-of-fit index (GFI) of the model was evaluated by the Chi-square GFI statistics along with the corresponding *P*-value. Therefore, based on the values with greater probabilities, such models reflect rigid rhetorical causal structures related to the observed associations. The model showing the highest goodness-of-fit (such as high GFI, low χ^2, and high normal fit index [NFI]), was suggested to be the best fit for our data. Path coefficients similar to partial correlation coefficients were used to indicate the association and its strength across different variables (Grace, 2006). All SEM models were constructed and analyzed using AMOS 20 software (SPSS Inc. 2009).

3. Results

3.1. Plant community characteristics in relation to microsites and grazing treatments

The mean values of plant height, root biomass, and above-ground and litter biomass were greater in shrub microsites than in interspaces

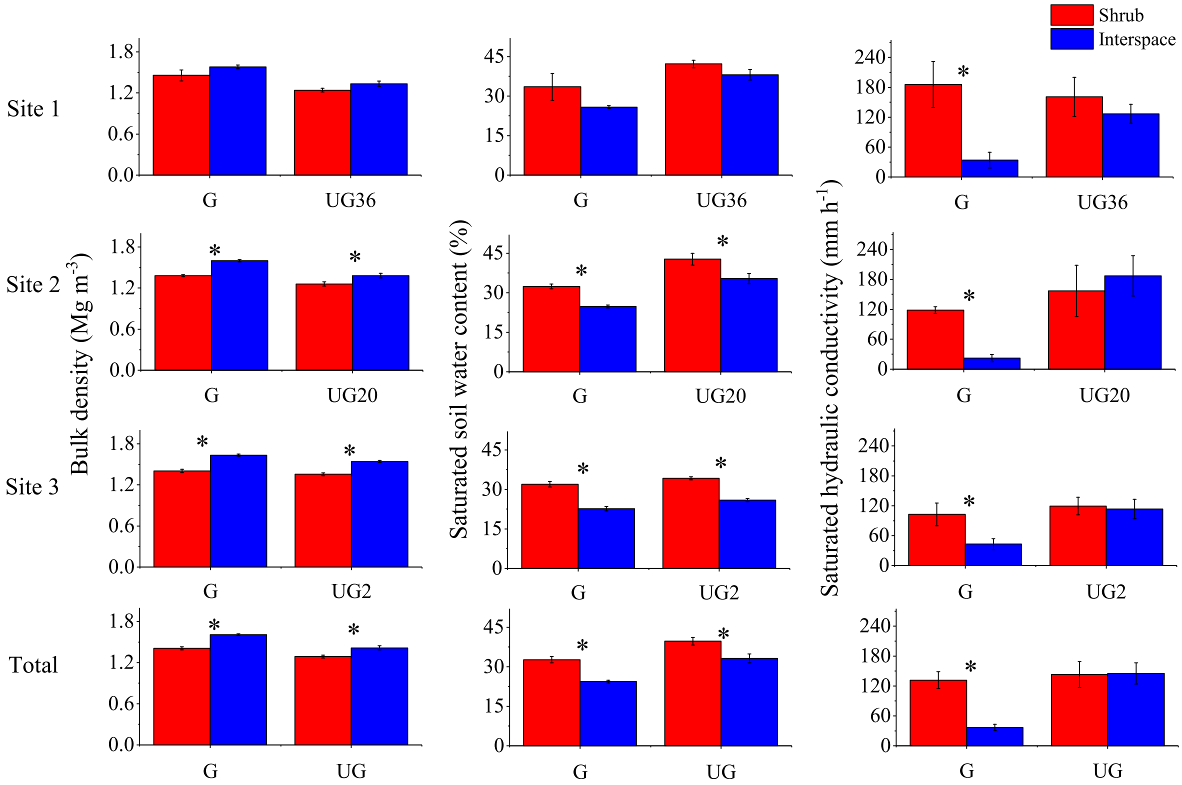

Fig. 3. Mean (±SE) values of bulk density (Mg m^{-3}), saturated soil water content (%), and saturated hydraulic conductivity (mm h^{-1}) for two microsite types across grazing regimes at three sites. G: grazed; UG: ungrazed; the figures specified after UG represent different fencing years. The asterisks for a specific grazing pattern indicate significant differences ($P < 0.05$) between shrubs and interspaces. The total represents the average values of parameters at all sites.

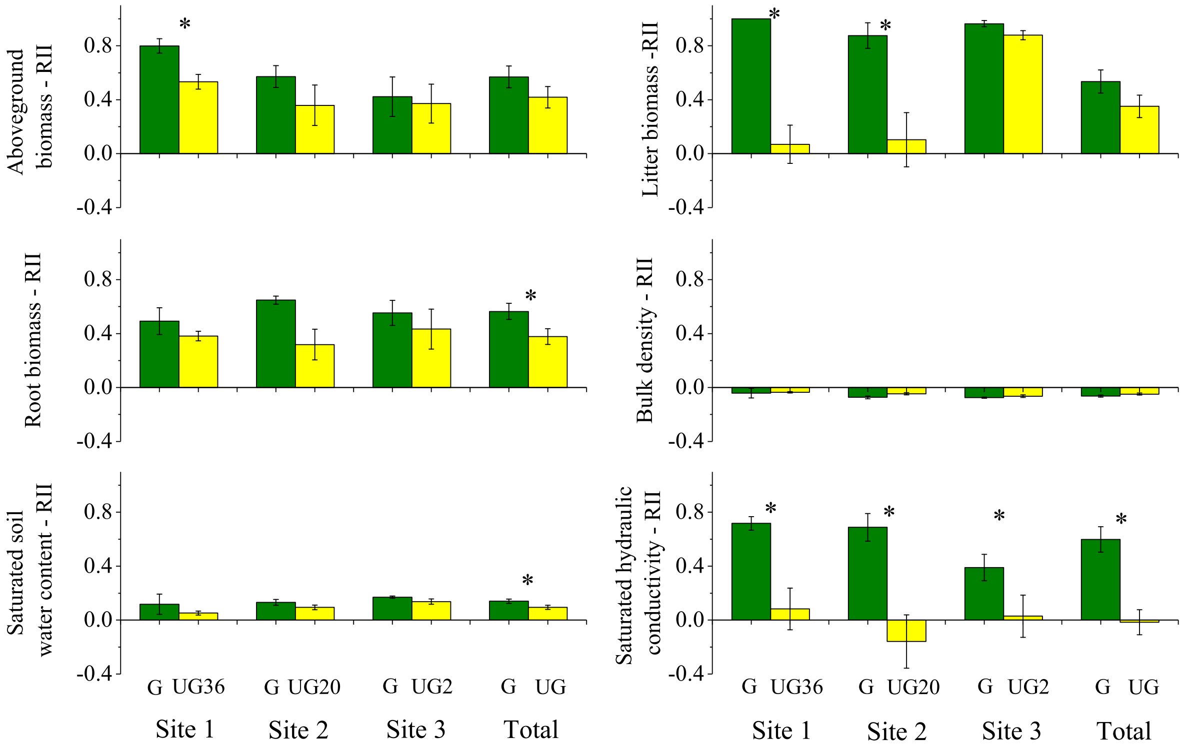

Fig. 4. Mean (±SE) values of relative interaction intensity (RII) for above-ground, litter, and root biomass, bulk density, saturated soil water content, and saturated hydraulic conductivity across grazing regimes at three sites. G: grazed; UG: ungrazed; the figures specified after UG represent different fencing years. The asterisks for a specific site indicate significant differences ($P < 0.05$) between grazed and ungrazed treatments.

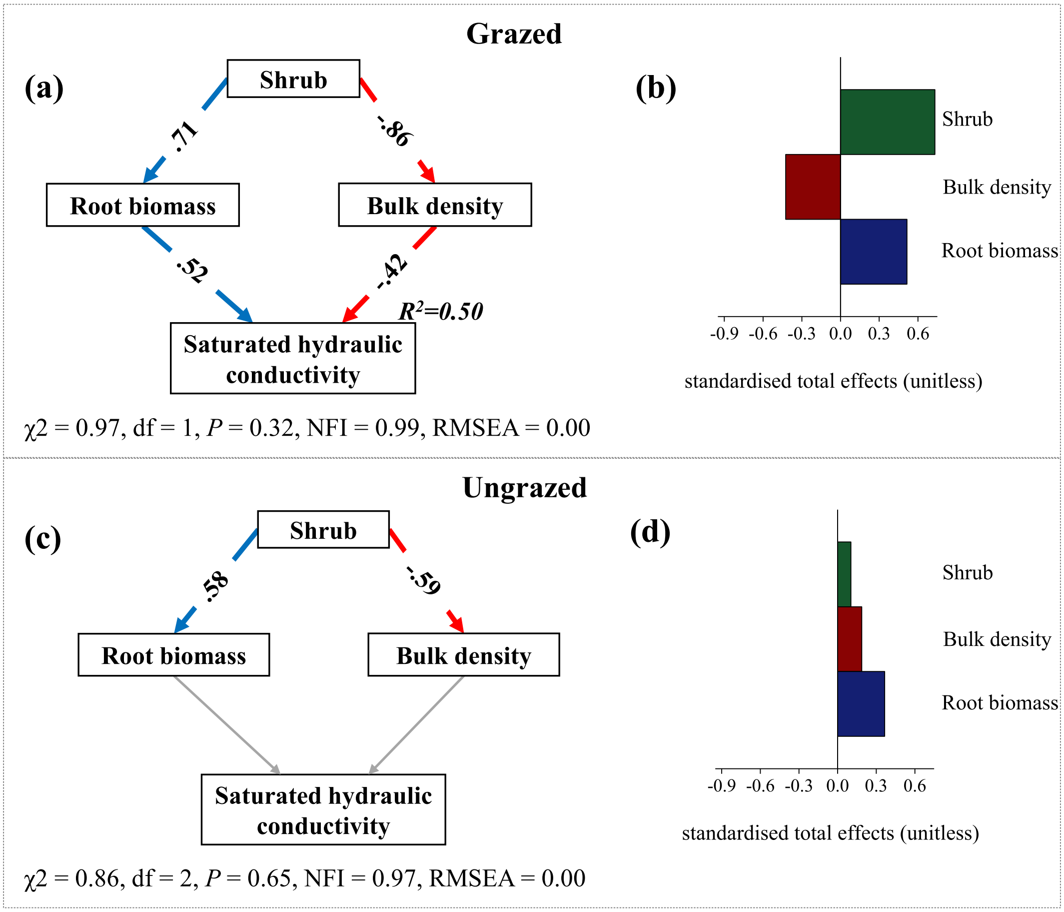

Fig. 5. Structural equation modeling shows the impacts of different driving factors (shrubs, bulk density, and root biomass) on soil saturated hydraulic conductivity across the two grazing regimes. Arrows indicate the effect direction, while nearby figures (path coefficients, either positive or negative, marked in blue and red, respectively) approximate the partial correlation pattern, which specifies the effect size of the association. Solid lines indicate significant ($P < 0.05$) pathways that show the proportion of variability (R^2) in the soil infiltration capacity function. The charcoal grey lines represent the pathways that are not significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

under both grazed and ungrazed conditions at all sites, and there was a significant difference ($P < 0.05$) between shrub patches and interspaces considering the average values of all three sites together (Table 1; Fig. 2). The values of the root, above-ground, and litter biomass did not differ in relation to grazing in shrub patches but were significantly lower in grazed than in ungrazed conditions in interspaces at all sites in most cases (Fig. S2). The RII values of root biomass in shrubs vs. interspaces did not significantly differ between the grazed and ungrazed treatments at all three sites but were greater ($P < 0.05$) in the grazing treatment when all three sites were considered together (Fig. 4). The difference in above-ground biomass or litter biomass in relation to grazing was not significant when all three sites were considered together (Fig. 4).

3.2. Saturated hydraulic conductivity in relation to microsites and grazing treatments

The interspaces had markedly higher bulk density but lower saturated water content of the soil, irrespective of grazing at sites 2 and 3 when all three sites were considered together (Fig. 3). We also found that the saturated hydraulic conductivity of the soil was similar for shrub patches and interspaces in ungrazed conditions at all sites, but a significantly higher value ($P < 0.05$) of saturated hydraulic conductivity beneath shrub was found under grazed conditions (Fig. 3). For both microsite types, the soil bulk density was lower, whereas the saturated water content was higher under ungrazed than under grazed conditions at all sites (Fig. S3). The saturated hydraulic conductivity in interspaces significantly differed between grazed and ungrazed areas at all sites, while there was no difference in shrub patches between the two grazing treatments (Fig. S3). There was no significant difference in soil bulk density beneath shrubs under grazed treatment compared with the ungrazed treatment at each site, but the values of water content and hydraulic conductivity were greater ($P < 0.05$) under grazed conditions when considering all three sites together (Fig. 4).

3.3. Quantitative models of saturated hydraulic conductivity

The results of the analysis of our standardized SEM showed that the effects of shrubs on saturated hydraulic conductivity were indirect due to an enhancement of the positive impact of root biomass and the reduction in the negative effect of bulk density on hydraulic conductivity under grazed conditions, while there was no such significant effect under ungrazed conditions (Fig. 5). We also found an indirect negative effect of grazing by increasing the negative impact of bulk density on hydraulic conductivity in interspaces, while grazing did not play a role in shrub microsites (Fig. 6).

4. Discussion

We found three major effects of shrubs and grazing on hydraulic conductivity in an arid shrubland system. First, the soil beneath shrubs had a lower bulk density, a higher soil water content, and greater plant biomass than in interspaces, while grazing had a strong negative effect

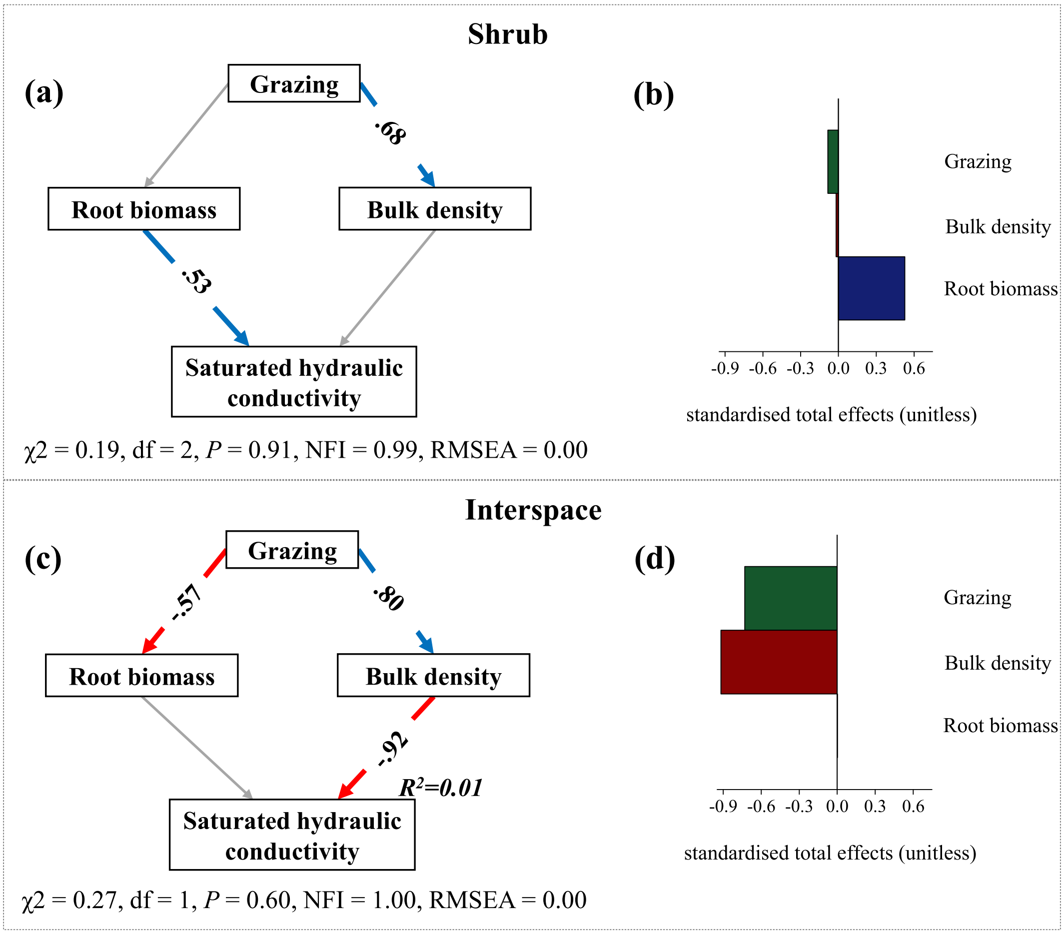

Fig. 6. Structural equation modeling that shows the impacts of different driving factors (root biomass, grazing, and bulk density) on soil saturated hydraulic conductivity for two microsite types. Arrows indicate the effect direction, while nearby figures (path coefficients, either positive or negative, marked in blue and red, respectively) approximate the partial correlation pattern, which specifies the effect size of the association. Solid lines indicate significant ($P < 0.05$) pathways that show the proportion of variability (R^2) in the soil infiltration capacity function. The charcoal grey lines represent the pathways that are not significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on plant biomass, porosity and soil water. Second, we found clear evidence that shrubs had more favorable impacts on hydraulic conductivity in grazed areas than in ungrazed areas, while grazing reduced the saturated hydraulic conductivity only in interspaces. Third, our SEM analysis showed the indirect impacts of grazing and shrubs on the saturated hydraulic conductivity by changes in root biomass and bulk density. Overall, our study strongly supports the notion that shrub patches could maintain a relatively larger infiltration capacity under grazed conditions, probably through a self-resistance mechanism of the response of the ecosystem to intense human induced activities (e.g., overgrazing).

4.1. Shrub patches maintain crucial plant and soil functions compared to interspaces

The encroachment of shrubs into grasslands is found to be a distinctive pattern of grassland degradation, largely due to the competition of shrubs for space and nutrients resources with grasses and forbs, as well as the reduction in livestock carrying capacity (Eldridge et al., 2011; Tews et al., 2006). Typically, shrub encroachment is frequently accompanied by increased grazing density, as well as aggravated land degradation (Chang et al., 2014; Chen et al., 2014), further exacerbating the loss of soil productive potential for many ecosystem functions and services provided by grasslands (Zhou et al., 2019; Daryanto et al., 2019). In our study, we found that shrubs had mostly positive effects on plant properties such as height, cover, and above-ground, below-ground, and litter biomass and soil characteristics, including bulk density and saturated water content as compared to adjacent interspaces. It is well known that shrubs enhance soil and plant functions based on studies conducted in a range of dryland environments worldwide. For example, shrubs enhance the deposition of litter and are known as crucial factors contributing to the development of forb and grass species (Howard et al., 2012), whose decomposition facilitates the release of nutrients into the soil beneath shrub patches (Han et al., 2008), resulting in the feedforward for the physiochemical characteristics of the soil. As a result of water and wind erosion along with litter mobility, the nutrients transported by wind, as well as the fine sediments, are accumulated under shrub canopies (Field et al., 2012; Yan et al., 2019). Regions located under shrub canopies usually have relatively low surface evapotranspiration and temperature, low erosion level, and high organic matter contents compared to those in interspaces (Schlesinger et al., 1996). These self-reinforcing effects of shrub patches as a result of woody encroachment might act as an adaptation mechanism in response to human-induced landscape disturbance and climate change (Yan et al., 2019; García Criado et al., 2020).

4.2. The enhanced infiltration under shrub canopies is associated with grazing

The prevailing view on shrub patches is that they enhance infiltration beneath their canopies (Bhark and Small, 2003; Wilcox et al., 2003). For example, Marquart et al. (2019) reported significantly higher sorptivity and steady-state infiltration rate beneath shrubs in an arid shrubland. Unlike studies showing higher hydraulic conductivity beneath shrubs (Eldridge et al., 2015b; Niemeyer et al., 2014), we found no significant difference in hydraulic conductivity between shrub patches and interspaces under ungrazed conditions, while grazing decreased the hydraulic conductivity only in interspaces. There are several plausible but not exclusive explanations for this observation. First, livestock trampling greatly affects the extent of the pore structure, and causes surface soil compaction, consequently affecting the hydraulic conductivity (Eldridge et al., 2016). Under grazing, shrubs could prevent livestock from entering shrub patches due to some characteristics, such as thorns and spikes (Smit et al., 2006) and protect them against herbivores (e.g., *Caragana microphylla*), resulting in less trampling (Wiesmeier et al., 2009). In contrast, overgrazing is likely to reduce soil hydraulic conductivity in interspaces by preventing plant covering and decreasing organic matter inputs, as well as enhancing the effects of trampling (Pavão et al., 2019; Li et al. 2013); thus, enhancing the differences between shrubs and their associated interspaces. Second, shrub patches exhibit higher macroporosity, soil organic matter content etc. also, greater root density beneath shrubs, and therefore more macropores (Cai et al., 2020; Li et al., 2013), and decaying root systems beneath shrubs act as preferential flow channels (Wu et al. 2020). These findings are consistent with the results of our SEM analysis, which showed that shrubs were associated with an increase in favorable impacts of roots along with the reduced adverse impacts of bulk density on hydrologic conductivity under grazing (Fig. 5).

The lack of difference under ungrazed conditions could be due to the optimum soil conditions in the interspaces, suggesting that grazing exclusion might be an effective technique that can be used to restore the infiltration capacity. In addition, ungrazed sites are also likely to support a greater density of shrubs simply due to the lack of animal activity. The average shrub coverage in ungrazed sites in our study was 17.1%, ranging from 4.5 to 29.8%, significantly higher than 8.4%, ranging from 5.6 to 11.6% observed in the grazed treatment (Fig. S1). Thus, in the absence of grazing, the interspaces are likely to be smaller, with shrubs having a greater influence on interspace conditions since their influences extend well beyond the edge of the canopy (Dunkerley, 2000; Throop and Archer, 2008).

Overall, the findings of the present study emphasize that shrubs play a vital role in the maintenance of soil infiltration capacity, particularly under grazed conditions. They also indicate that the shrub encroachment might be a response to grazing-induced disturbance, which leads to the increased resource concentrations in patches with shrub at the expense of large grasslands; the presence of shrubs also provides a means to maintain infiltration capacity. This finding provided evidence from the perspective of the maintaining infiltration capacity to support the notion that shrub encroachment should be taken as the response of a self-resistance or self-adapting mechanism of a grassland ecosystem that has been subjected to a human induced disturbance as overgrazing.

Author's contribution

Y. Y. designed the experiment; Y.C., Y.Y., and C.W. conducted the field work. Y.C., Y.Y. and D.J.E. performed the data analyses and wrote the manuscript, and all authors provided comments on the manuscript and the revisions and approved the final version.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105680.

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