



Original Research

Effects of Grazing on Population Growth Characteristics of *Caragana stenophylla* Along a Climatic Aridity Gradient[☆]



Li-Na Xie^{a,b}, Hong-Yu Guo^b, Wei-Zhong Chen^b, Zhe Liu^b, Song Gu^a, Cheng-Cang Ma^{b,*}

^a College of Life Sciences, Nankai University

^b Tianjin Key Laboratory of Animal and Plant Resistance, College of Life Sciences, Tianjin Normal University, Tianjin, China

ARTICLE INFO

Article history:

Received 29 March 2017

Received in revised form 28 June 2017

Accepted 10 July 2017

Key Words:

drought
forage legumes
grassland ecology
grazing management
pasture growth
seed production

ABSTRACT

Shrubs are important plant species in grassland ecosystems worldwide, and their density and cover have been gradually increasing globally. However, the interaction effect of grazing and aridity on population recruitment and population growth of shrub species in grasslands has not been examined explicitly. We examined sapling establishment, sexual recruitment, population mortality, and population growth of *Caragana stenophylla* along a climatic aridity gradient and a grazing intensity gradient in the Inner Mongolia Steppe, using manipulative field experiments. Sapling establishment, sapling height, and sexual recruitment of *C. stenophylla* decreased as climatic aridity and grazing intensity increased. The negative effects of grazing on sapling establishment and sexual recruitment gradually increased as climatic aridity increased. The effect of climatic aridity and grazing on population mortality was influenced by sexual recruitment. In the combined treatments of climatic aridity and grazing, population mortality was relatively high when sexual recruitment was relatively high, while population mortality increased as climatic aridity and grazing increased when sexual recruitment was relatively low. *C. stenophylla* population increased under relatively low drought stress and mild grazing but declined under strong drought stress and/or severe grazing. Our results suggested that to maintain viable *Caragana* populations, appropriate grazing policies must be made according to climate aridity gradient.

© 2017 The Society for Range Management. Published by Elsevier Inc. All rights reserved.

Introduction

Population growth is basically determined by recruitment and mortality (Li et al., 2013). Sapling establishment is a critical step for recruitment because of the relatively high mortality rate during this stage. Sapling establishment is affected by biotic factors, such as seed addition (Moles and Westoby, 2002), interspecific competition (Carón et al., 2015b), below-ground competition (Haugo et al., 2013), plant size (Li et al., 2013), clonal integration (Yu et al., 2004), interspecific facilitation (Holl, 2002; Castro et al., 2004b; Caldeira et al., 2014), and grazing (Buckley et al., 2010; Osem et al., 2015). Sapling establishment is also affected by abiotic factors, such as soil origin (prairie vs. forest) (Haugo et al., 2013), sand burial (Zhao et al., 2007; Li et al., 2010), denudation (Li et al., 2010), drought (Noumi et al., 2015; Carón et al., 2015a), and precipitation (Carón et al., 2015b). The mortality rate is also influenced by biotic factors and abiotic factors, such as interspecific competition

(Ehrlén et al., 2005; Hamre et al., 2010), grazing (Hunt, 2010), drought (Faust et al., 2011), soil nutrients and water availability (de Campos Franci et al., 2016), sand burial (Li et al., 2010), and precipitation and soil sand content (Fortunel et al., 2016).

Climatic aridity and grazing are two widespread, often co-occurring factors affecting sapling establishment, population mortality, and population growth of plant species in the Inner Mongolia Steppe (Fynn and O'Connor, 2000; Chen and Tang, 2005). Previous studies in other areas showed that drought severely limited regeneration of trees and increased population mortality rate (Traveset et al., 2003; Castro et al., 2004a, 2005). But how sapling recruitment and the consequent population growth changes along a climatic aridity gradient remain unclear (Cipriotti et al., 2008). Grazing can influence plant recruitment by decreasing seedling numbers (Macias et al., 2014; Smit et al., 2015), restraining seedling height (Osem et al., 2015), and increasing seedling mortality rate. Therefore, grazing has negative effects on population growth (Farrington et al., 2009; Hegland et al., 2010; Mandle and Ticktin, 2012; Mandle et al., 2015). However, few studies explicitly examined the combined effects of climatic aridity and grazing on the population growth (Hunt, 2010; Faust et al., 2011). Understanding the combined effects of climatic aridity and grazing on the population growth of plant species is critical for appropriate grazing management of grasslands under different climatic regimes.

[☆] This study was supported by the National Natural Science Foundation of China (31570453, 31170381).

* Correspondence: Cheng-Cang Ma, College of Life Sciences, Tianjin Normal University, Tianjin 300387, China.

E-mail address: machengcang@163.com (C.-C. Ma).

Shrubs are important plant species in grassland ecosystems worldwide, and their density and cover have been gradually increasing globally. *Caragana* species are widespread and dominant shrub species in the Inner Mongolia Steppe, China (Xiong et al., 2002). In grasslands, *Caragana* species have not only economic values as important fodder, green manure, and honey resource but also environmental protection values for wind-erosion attenuation, sand fixation, and water and soil conservation. *Caragana* species play increasingly important roles in mediating grassland ecosystem functions and services. Therefore, understanding the population growth characteristics of *Caragana* species was critical for maintaining the sustainability of grassland ecosystem functions and services.

There are 16 *Caragana* species distributed in the Inner Mongolia Steppe, and *Caragana stenophylla* is one of the most important plant species with its widespread distribution, forage value, and other ecological functions in the region (Xie et al., 2014). Therefore, we selected *C. stenophylla* as the target plant species to examine the population growth characteristics of *Caragana* species under the combined influences of climatic aridity and grazing gradients in the Inner Mongolia Steppe.

Seed production and seedling establishment are two critical processes of sexual recruitment for plant populations. We previously reported the seed production characteristics of *C. stenophylla* under the combined influences of climatic aridity and grazing gradients in the Inner Mongolia Steppe (Xie et al., 2016). In this study, we examined the sapling establishment of *C. stenophylla* along a climatic aridity gradient (across semiarid, arid, very arid, and intensively arid zones) and a grazing intensity gradient (fenced, mildly and severely grazed) using manipulative field experiments in the Inner Mongolia Steppe. Moreover, we calculated the annual sexual recruitment (the annual number of saplings produced by each plant) of *C. stenophylla* based on annual seed production (Xie et al., 2016) and sapling establishment rate. Meanwhile, we investigated the annual population mortality along this climate gradient and grazing intensity using population demography. On the basis of the annual sexual recruitment and annual population mortality, we quantified the annual population growth of *C. stenophylla*. We aimed to answer the following questions: 1) What are the effects of the interactions between climatic aridity and grazing on the sapling establishment of *C. stenophylla*, and 2) What are the combined effects of climatic aridity and grazing on the population growth of *C. stenophylla*? Our study provides the scientific basis for appropriate grazing management along climatic aridity gradients in grassland ecosystems.

Methods

Study Sites and Study Material

The Inner Mongolia Steppe, located in the northern China, spans an extensive area ($\sim 1183 \times 10^3 \text{ km}^2$), ranging from $97^\circ 12' \text{E}$ to $126^\circ 04' \text{E}$ in longitude (a distance of $\sim 2500 \text{ km}$) and $37^\circ 24' \text{N}$ to $53^\circ 23' \text{N}$ in latitude (a distance of $\sim 1700 \text{ km}$), and is one of the largest steppes in the world. There is a strong gradient of increasing climatic aridity from the northeast to the southwest (across humid, subhumid, semiarid, arid, very arid, intensively arid, and extremely arid zones). Grazing by livestock is a common land use form in the Inner Mongolia Steppe. Therefore, the Inner Mongolia Steppe provides an ideal system to study plant population growth under combined influences of climatic aridity gradient and grazing.

C. stenophylla is a leguminous, xeromorphic, deciduous dwarf-shrub with a spinose stem, which is distributed across a large geographic range in the Inner Mongolia Steppe, predominately from the semiarid zone to the intensively arid zone (Ma et al., 2013; Xie et al., 2015). *C. stenophylla* has both sexual and clonal reproduction.

Experimental Design

We conducted the field study at 4 sites: 1) Xilinhaote in the semiarid zone, 2) Siziwang in the arid zone, 3) Etuoke in the very arid zone, and

4) Alashanzuo in the intensively arid zone of the Inner Mongolia Steppe. Geographical locations and environmental data of these study sites are shown in Figure 1 and Table 1.

At each study site, we selected three plots for fenced, mildly grazed and severely grazed management. And each plot was more than 500 ha. Within each plot, we demarcated four subplots ($\sim 3 \text{ ha}$ each subplot) with distances of $\sim 800 \text{ m}$ between subplots. Because vegetation coverage decreased gradually as the climatic drought stress increased from the semiarid zone to the intensively arid zone, the grazing intensity was set according to local vegetation conditions for logistic reasons. At each study site, the grazing intensity in the severely grazed plot was about twice as high as that in the mildly grazed plot. The grazing intensity at each study site was mildly grazed, Xilinhaote (in the semiarid zone) 1.2 sheep per ha; Siziwang (in the arid zone) 1.0 sheep per ha; Etuoke (in the very arid zone) 0.8 sheep per ha; Alashanzuo (in the intensively arid zone) 0.4 sheep per ha; severely grazed, Xilinhaote 2.8 sheep per ha, Siziwang 1.9 sheep per ha; Etuoke 1.5 sheep per ha; and Alashanzuo 0.8 sheep per ha. The grazing treatments at each study site have been established for $> 5 \text{ yr}$.

Seed Vigor Measurements

During June–July in 2012 and 2013, we collected and air-dried healthy *C. stenophylla* seeds from each of four study sites, respectively. We put the seeds in the field for the winter and measured seed vigor in the next March. We did not consider the effect of grazing intensities on seed vigor measurements because there were very few or no seeds in the severely grazed plots (Xie et al., 2016); thus, we did not include the factor of grazing intensity when collecting seeds from each aridity zone. Germination rate and germination index values (averages) were calculated on 2 yr of germination data. Germination rate and germination index were calculated using following formulas:

$$\text{Germination rate} = \left(\frac{\text{the number of germinated seeds}}{\text{the total number of experimental seeds}} \right) \times 100\%$$

$$\text{Germination index} = \sum \frac{G_t}{D_t} \quad (G_t \text{ represents the number of germinated seeds on day } t, D_t \text{ represents corresponding germination days})$$

Seedling or Sapling Establishment

The twice–field-sowing experiments were conducted during 2013–2014 and 2014–2015, respectively. At the beginning of the growing season in 2013 and 2014, we sowed *C. stenophylla* seeds within plots. The seeds sowed to each site were collected from the same site in the previous year. The beginning time of growing season varies among the four study sites, so we sowed the seeds on different dates at different sites according to the timing of the local growing season. Sowing dates were April 20 at Alashanzuo site, April 26 at Etuoke site, May 1 at Siziwang site, and May 8 at Xilinhaote site.

In each subplot, we established two transects of 90 m in each subplot and placed $1 \times 1 \text{ m}$ quadrats at intervals of 10 m along each transect (in total 18 quadrats per subplot), and the quadrats were under/in *C. stenophylla* shrubs, grasses, or open areas. We sowed 100 seeds in each quadrat (1800 seeds per subplot, 7200 seeds per plot, and in total 21600 seeds per site). Our previous study has investigated the seed densities of *C. stenophylla* in soils (semiarid zone: 4 seeds/m²; arid zone: 2 seeds/m²; very arid zone: 1 seed/m²; intensively arid zone: 0.5 seed/m²) (Xie et al., 2015). Thus, when sowing seeds, we deducted the number of preexisting seeds in soil. Six mo after sowing (at the end of the growing season in current year) and 18 mo after sowing (at the end of the growing season in the next year), we recorded seedling (6 mo old) or sapling (18 mo old) number in each quadrat and then calculated seedling or sapling establishment rate for each quadrat (18 quadrats per subplot) using the following formula: seedling or sapling establishment rate = seedling

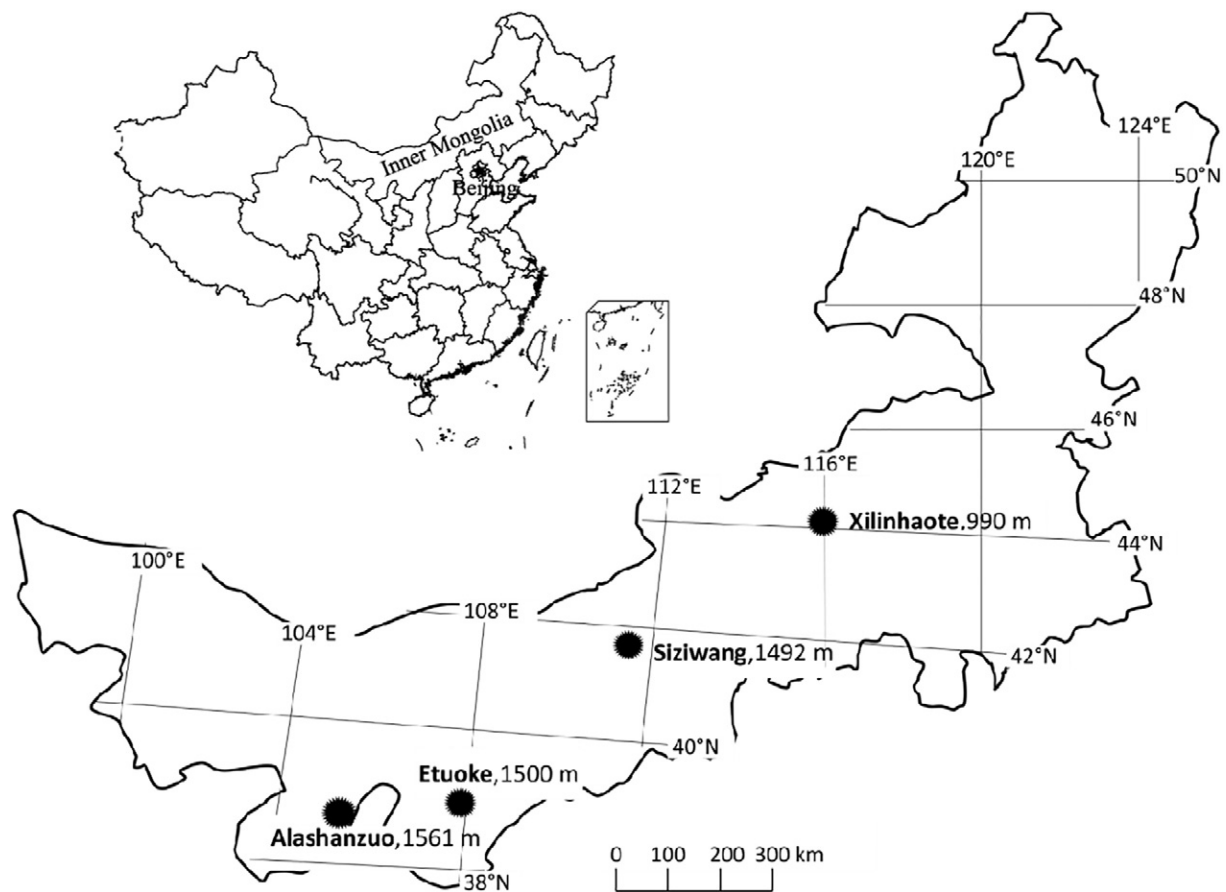


Figure 1. Map of Inner Mongolia region with the study sites. ●study site; digit is altitude.

or sapling number/100. We calculated the average seedling or sapling establishment rate for each subplot (based on data from the 18 quadrats). At 18 mo after sowing, we measured sapling height for the survival saplings.

Annual Sexual Recruitment, Annual Population Mortality, and Annual Population Growth

In each subplot, we selected five shrubs randomly, harvested all the reproductive branches, measured dry biomass (dried at 80°C for 72 hr), and calculated the average values of reproductive branch biomass per shrub for each subplot. On the basis of the annual number of seeds per g shrub biomass (Xie et al., 2016), reproductive branch biomass (g) per shrub and sapling establishment rate, we quantified the annual sexual recruitment of *C. stenophylla* using the following formula: Annual sexual recruitment (sapling/100 shrubs) = seed number (seed/g biomass) × reproductive branch biomass per shrub (g) × sapling establishment rate (sapling/seed) × 100 shrubs, where seed number represents the annual number of seeds per g brush biomass. The seed number was the average of 2012 and 2013 in corresponding subplot (data were from our previous study, Xie et al., 2016).

Shrub mortality was investigated twice (2013–2014, 2014–2015). In each subplot, we established a 100 × 100 m quadrat. In the first year (September 2013 and September 2014), we labeled all *C. stenophylla* and investigated the total number of individuals (in total > 150 shrubs in all quadrat). In the next year (September 2014 and September 2015), all the labeled plants were checked and the dead individuals were recorded. Annual population mortality (mortality/100 shrubs) = (dead individuals/total number of individuals) × 100. And we calculated the average of the data from the two investigations for each subplot.

On the basis of the annual sexual recruitment and annual population mortality, we calculated annual population growth using the following formula: Annual population growth (individuals/100 shrubs) = annual sexual recruitment – annual population mortality

Data Analysis

We conducted analysis of variance to examine the difference in means of seed germination rate, germination index, seedling and sapling establishment rate, sapling height, annual sexual recruitment, annual population mortality, and annual population growth among climate zones and grazing intensities, as well as to evaluate the

Table 1
Environmental data of the 4 field sites in the Inner Mongolia Steppe

Site	Mean annual precipitation (mm)	Annual mean temperature (°C)	Sunshine duration (h/yr)	Aridity index (I_{dm})	Moisture classification	Vegetation classification
Xilinhaote	281	2.35	2932	22.75	Semiarid	Steppe
Siziwang	240	3.40	3065	17.91	Arid	Desertification steppe
Etuoque	210	6.40	3050	12.80	Very arid	Steppe desert
Alashanzuo	110	7.80	3200	6.18	Intensively arid	Desert

I_{dm} was calculated according to the de Martonne method (Meng and Zhi, 2004), I_{dm} = annual average precipitation/(annual average temperature + 10).

interactive effects of climate gradient and grazing intensity. We performed Tukey HSD post-hoc tests or Student's *t*-tests to identify differences between treatments. All analyses were performed using SPSS 17.0.

Results

Seed Germination Rate and Germination Index

The germination rates of *C. stenophylla* seed were 91%–93%. Both the germination rate and germination index were not different significantly among different climatic aridity zones (Fig. 2, Table 2).

Seedling/Sapling Establishment Rate and Sapling Height

Seedling/sapling establishment rate of *C. stenophylla* drastically decreased from the semiarid zone to the intensively arid zone. In the fenced plots, seedling establishment rate was 1.38 seedlings/100 seeds for the semiarid zone, 0.69 seedling/100 seeds for the arid zone, 0.21 seedling/100 seeds for the very arid zone, and 0.18 seedling/100 seeds for the intensively arid zone, respectively. And sapling establishment rates for the four zones were 0.79, 0.32, 0.15, and 0.08 sapling/100 seeds, respectively (Fig. 3a–3b; see Table 2).

There was a sharp decrease in the establishment rate as grazing intensity increased for both seedling and sapling. No sapling survived in plots subjected to severe grazing in the intensively arid zone (see Fig. 3a–3b; Table 2).

The seedling establishment rate of *C. stenophylla* from seed to 6-mo seedling was lower than 2%, and sapling establishment rate from 6-mo seedling to 18-mo sapling was about 50–60% (see Fig. 3a–3b).

The interaction between climate gradient and grazing intensity had highly significant effects on the seedling/sapling establishment rate of *C. stenophylla*. As climatic drought stress increased, the effects of grazing on seedling/sapling establishment rate gradually increased. Compared with the fenced treatment, severe grazed treatment decreased seedling establishment rate by 77% in the semiarid zone, 72% in the arid zone, 73% in the very arid zone, and 100% in the intensively arid zone, respectively (see Fig. 3a–3b; Table 2).

Sapling height decreased as climatic drought stress increased. For example, under mildly grazed treatment, sapling height in the semiarid, arid, very arid, and intensively arid zones was 15.42 cm, 15.16 cm, 14.33 cm, and 13.14 cm, respectively. Sapling height tended to decrease as grazing intensity increased. The interaction

between climate gradient and grazing intensity had no significant effects on sapling height of *C. stenophylla* (see Fig. 3c; Table 2).

Annual Sexual Recruitment and Annual Population Mortality

Annual sexual recruitment of *C. stenophylla* sharply decreased as climatic drought stress increased. For example, under fenced treatment, annual sexual recruitment of *C. stenophylla* in the semiarid zone was 1.74 times as high as that in the arid zone, 2.53 times as high as that in the very arid zone, and 39.63 times as high as that in the intensively arid zone, respectively (see Fig. 3d; Table 2).

Annual sexual recruitment of *C. stenophylla* sharply decreased as grazing intensity increased. For example, in the semiarid zone, the annual sexual recruitment under fenced treatment was 2.90 times as high as that under the mildly grazed treatment and 12.52 times as high as that under the severe grazed treatment (see Fig. 3d; Table 2).

The interaction between climate gradient and grazing intensity had highly significant effects on annual sexual recruitment of *C. stenophylla*. As climatic drought stress increased, the negative effects of grazing on sexual recruitment gradually increased. Within the same climatic zone, compared with the fenced treatments, the annual sexual recruitment of *C. stenophylla* in plots with mild grazing decreased by 65.6% in the semiarid zone, by 79.5% in the arid zone, by 90.2% in the very arid zone, and by 89.7% in the intensively arid zone (see Fig. 3d; Table 2).

Annual population mortality of *C. stenophylla* decreased as climatic drought stress increased under fenced and mildly grazed treatments. There was an increasing trend as climatic drought stress increased under severely grazed treatment (see Fig. 3e; Table 2).

Annual population mortality of *C. stenophylla* decreased as grazing intensity increased in the semiarid and arid zones but increased as grazing intensity increased in the intensively arid zone. There was no clear relationship between annual population mortality of *C. stenophylla* and grazing intensity in the very arid zone (see Fig. 3e; Table 2).

Annual Population Growth

Annual population growth of *C. stenophylla* decreased as climatic drought stress and grazing intensity increased (see Fig. 3f; Table 2). In the semiarid, arid, and very arid zones under fenced treatments, and in the semiarid and arid zones under mildly grazed treatments, sexual recruitment of *C. stenophylla* was greater than mortality rates, and thus annual population growth was positive. While under the other treatments, sexual recruitment of *C. stenophylla* was less than mortality rate, and thus annual population growth was negative (see Fig. 3d–f).

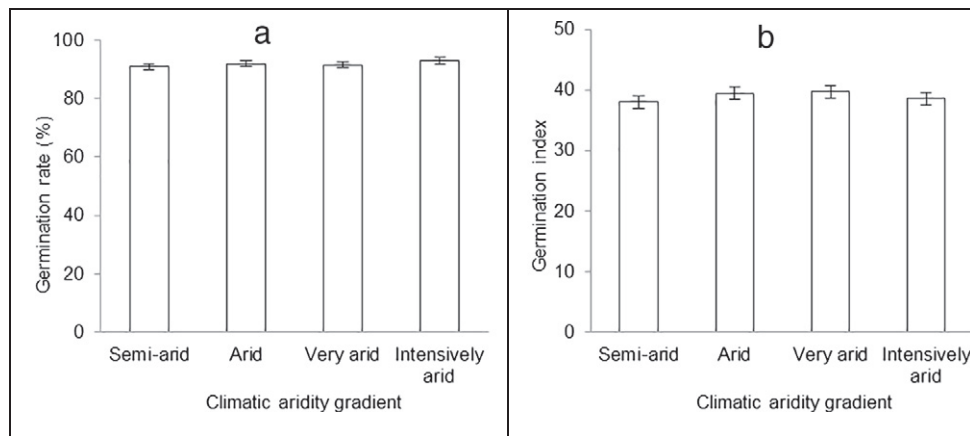


Figure 2. (a and b) Germination rate and germination index of *Caragana stenophylla* seeds in the four climatic aridity zones.

Table 2
Summary of analyses of variances examining the effects of climatic aridity zones, grazing intensities, and interactive effects between climate zone and grazing intensity on variables

Variables	Climatic aridity zones	Gazing intensities	Climatic aridity × gazing
Seed germination rate	$F_{3,23} = 0.16, P = 0.93$		
Seed germination index	$F_{3,23} = 0.10, P = 0.96$		
Seedling establishment rate	$F_{3,36} = 145.92, P < 0.01$	$F_{2,36} = 117.18, P < 0.01$	$F_{6,36} = 23.64, P < 0.01$
Sapling establishment rate	$F_{3,36} = 140.93, P < 0.01$	$F_{2,36} = 84.38, P < 0.01$	$F_{6,36} = 18.91, P < 0.01$
Sapling height	$F_{3,31} = 8.80, P < 0.01$	$F_{2,31} = 2.65, P = 0.087$	$F_{5,31} = 0.16, P = 0.977$
Annual sexual recruitment	$F_{3,36} = 79.28, P < 0.01$	$F_{2,36} = 194.39, P < 0.01$	$F_{6,36} = 30.57, P < 0.01$
Annual population mortality			
Fenced	$F_{3,15} = 13.48, P < 0.01$		
Mildly grazed	$F_{3,15} = 17.04, P < 0.01$		
Severely grazed	$F_{3,15} = 2.08, P = 0.16$		
Semiarid zone		$F_{2,11} = 10.98, P < 0.01$	
Arid zone		$F_{2,11} = 2.10, P = 0.18$	
Intensively arid zone		$F_{2,11} = 5.40, P < 0.01$	
Annual population growth	$F_{3,36} = 64.21, P < 0.01$	$F_{2,36} = 196.22, P < 0.01$	

Discussion

Sapling Establishment Under the Influence of Climate Aridity and Grazing Gradient

Water shortage and grazing by domestic livestock are the major ecological constraints in woody plant seedling establishment in grasslands (Rousset and Lepart, 2000; Castro et al., 2004a, 2005). As climatic drought stress increased, the negative effects of grazing on seedling/sapling establishment of *C. stenophylla* gradually increased (see Fig. 3a–3b). In the semiarid zone, the relative benign environment led to higher plant cover including herbaceous plant and shrub, which then protected *C. stenophylla* seedling/sapling from grazing by ungulates. However, as climatic drought stress gradually increased from the semiarid zone to the intensively arid zone, herbaceous plant and shrub cover gradually decreased, which would provide less protection to *C. stenophylla* seedlings and sapling, and thus more seedlings and sapling would be consumed by ungulates. Besides these, drought can increase foliar nutrient concentration and reduce plant defenses (White, 1984; Huberty and Denno, 2004), leading to an increased chance of being grazed by ungulates.

Seedling/sapling establishment of *C. stenophylla* decreased as drought stress increases from the semiarid zone to the intensively arid zone (see Fig. 3a–3b). This was mainly due to climatic drought, which resulted in low seed germination, as well as low survival rate of saplings (Clark et al., 1998). Additionally, increasing climatic aridity and poorer soil resources (Ekrtova and Kosnar, 2012; Guan et al., 2016) from the semiarid zone to the intensively arid zone commonly led to decreased sapling height (see Fig. 3c).

Seedling/sapling establishment of *C. stenophylla* sharply decreased as grazing intensity increased (see Fig. 3a–3b). This was consistent with the general findings of many previous experimental studies, in which grazing tended to have negative influence on sapling establishment, as grazing would decrease woody species seedling survival rate (Li et al., 2013; Smit et al., 2015) and sapling height (Van Uytvanck et al., 2010; Osem et al., 2015). The decrease in sapling establishment of *C. stenophylla* might be due to the direct grazing by ungulates (Warner and Cushman, 2002; Gómez, 2005; Heckel et al., 2010). Additionally, the low sapling establishment in grazed plots could also be due to increased soil compaction by livestock trampling (Gómez, 2005; Heckel et al., 2010).

The seedling establishment percentage of *C. stenophylla* from seed to 6-mo seedling was < 2%. And survival rates of *C. stenophylla* from 6-mo seedling to 18-mo sapling were about 50–60%. This was probably due to seed loss, seedlings/saplings mortality caused by drought, and/or consumption by livestock. Low seedling or sapling establishment percentage of *C. stenophylla* might also be attributable to poor resource availability in arid areas, as limited resource is usually taken by adult shrubs, which tend to have stronger absorbing ability. This

phenomenon is commonly observed in arid areas (Li et al., 2013). These results suggested that the seed-to-seedling life stage was a bottleneck for the success of sexual reproduction of *C. stenophylla* in the Inner Mongolia Steppe, which was suffering from both grazing and drought stress.

Sexual Recruitment and Mortality Under the Influence of Climate Aridity and Grazing Gradient

The negative effects of grazing on sexual recruitment gradually increased as climatic drought stress increased (see Fig. 3d). This was probably because increasing climatic aridity enhanced the suppression effect of grazing on seed production (Xie et al., 2016) and seedling/sapling establishment of *C. stenophylla* (see Fig. 3a–3b).

Sexual recruitment of *C. stenophylla* sharply decreased as climatic drought stress increased from the semiarid zone to the intensively arid zone (see Fig. 3d). This was probably due to decrease in seed production (Xie et al., 2016) and seedling/sapling establishment of *C. stenophylla* (see Fig. 3a–3b) as climatic drought stress increased. There were many sapling recruits in the semiarid zone (41.86 saplings/100 shrubs, see Fig. 3d) under fenced treatments, which supported the finding in our previous studies that higher proportion of sexual individuals in the zone (Ma et al., 2013; Xie et al., 2015). However, in the intensively arid zone, no single young individual was observed (Ma et al., 2013; Xie et al., 2015) due to the fact that there were few sapling recruits in the zone (1.05 saplings/100 shrubs; see Fig. 3d).

Sexual recruitment of *C. stenophylla* sharply decreased as grazing intensity increased, and a similar pattern was also observed for *Pinus sylvestris*, *Pinus nigra* (Boulant et al., 2008), *Caragana intermedia* (Li et al., 2013), and *Quercus agrifolia* (López-Sánchez et al., 2014). This was probably because of decreases in seed production (Xie et al., 2016) and seedling/sapling establishment (see Fig. 3a–3b) as grazing intensity increased. This study also showed that under severely grazed treatment, sexual recruitment of *C. stenophylla* was rare (see Fig. 3d). These results suggested that overgrazing could decrease not only herbaceous recruitment (Azamivand et al., 2010) but also shrub recruitment, which could accelerate the degradation of grassland. Therefore, efforts should be taken to manage grazing in steppe appropriately.

Under fenced and mildly grazed treatments, there were many young *C. stenophylla* shrubs (a crown diameter of ~10–30 cm), and young shrubs were often more sensitive to drought than adult shrubs. Therefore, mortality was mainly due to the loss of young shrubs. The mortality of *C. stenophylla* under fenced and mildly grazed treatments decreased as climatic drought stress increased (see Fig. 3e). This was associated with decreases in numbers of young shrubs as climatic drought stress increased. However, under severely grazed treatment, there were few new recruited individuals (see Fig. 3d). Mortality was mainly due to adult shrubs, and as a result, mortality of *C. stenophylla* under severely grazed treatment was lower than that under fenced and mildly grazed

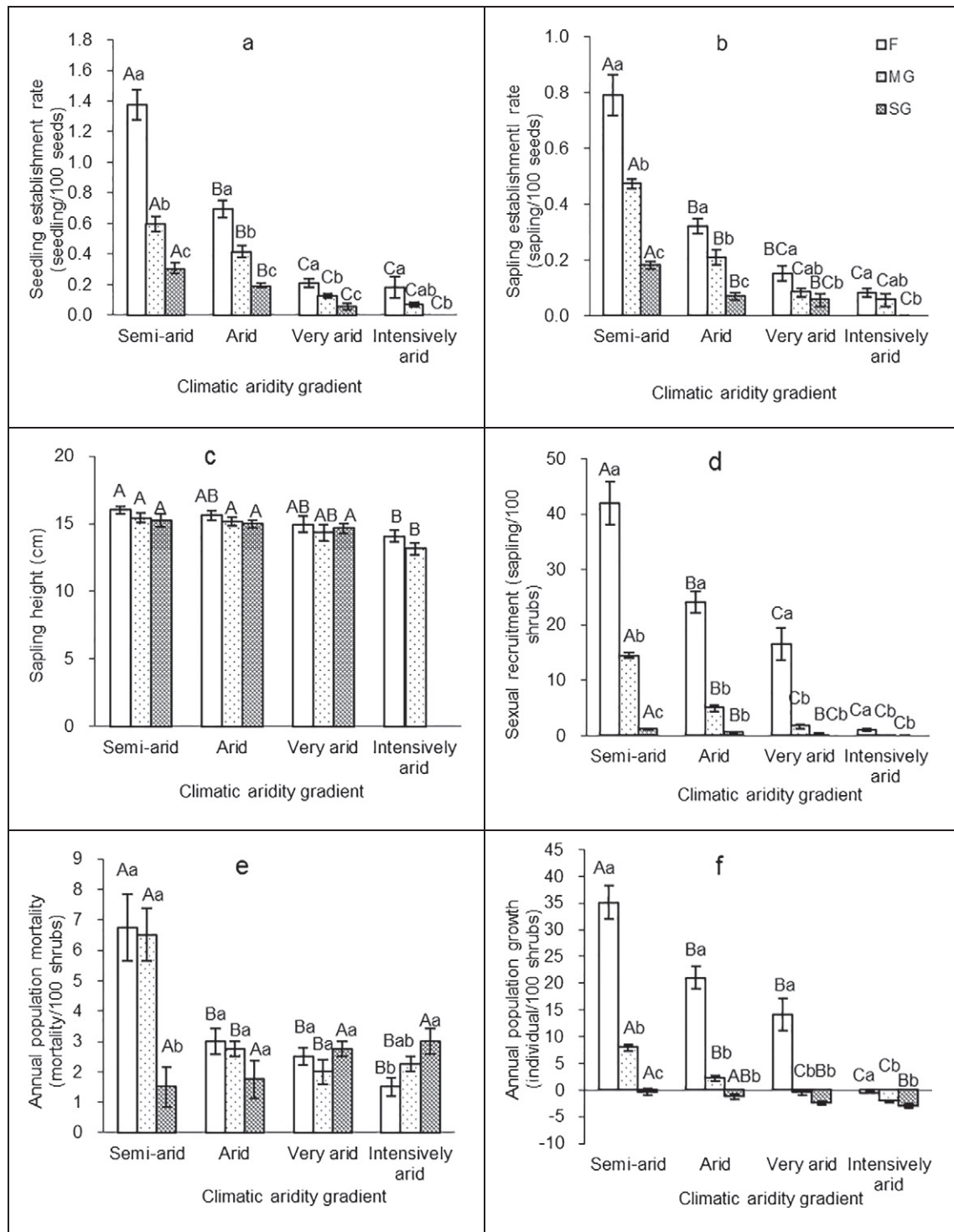


Figure 3. Seedlings establishment rate (a), sapling establishment rate (b), sapling height (c), annual sexual recruitment (d), annual population mortality (e), and annual population growth (f) of *Caragana stenophylla* in the four climatic aridity zones and three grazing intensities (mean \pm SE, $n = 4$). F, fenced; MG, mildly grazed; SG, severely grazed. For the same climate zone, different lowercase letters indicate significant differences between grazing intensities; and for the same grazing intensity, different uppercase letters indicate significant differences between climate zones (Tukey honestly significant difference tests, $P < 0.05$).

treatments. Moreover, mortality rate increased as climatic drought stress increased (see Fig. 3e).

Similarly, in the semiarid and arid zones, a large portion of *C. stenophylla* individuals are relative young shrubs, which could be prone to being consumed by ungulates, resulting in relatively higher mortality. The number of young shrubs sharply decreased as grazing intensity increased, which was likely the reason why mortality rate of *C. stenophylla* decreased as grazing intensity increased (see Fig. 3e). In

the intensively arid zone, mortality was mainly caused by loss of adult shrubs. While mortality is commonly low for long-lived woody species, and it is not greatly affected by grazing (Watson et al., 1997; Warner and Cushman, 2002; Sánchez-Velásquez and del Rosario Pineda-López, 2010; Li et al., 2013), mortality rate of *C. stenophylla* in the intensively arid zone was lower than that in the semiarid and arid zones (see Fig. 3e). In the intensively arid zone, mortality increased as grazing intensity increased (see Fig. 3e). This was likely caused by direct grazing

by livestock (Warner and Cushman, 2002; Gómez, 2005; Heckel et al., 2010). Our results also further demonstrated that mortality of adult shrubs would be low even under extreme drought or severe grazing conditions, and shrub mortality mainly occurred at the life stage of young shrubs, which is consistent with the previous findings for *Caragana intemedica* (Li et al., 2013).

Population Growth Under the Influence of Climate Aridity and Grazing Gradient

Our results showed that the highest population growth (35 individual/100 shrubs) of *C. stenophylla* occurred in the fenced treatment in the semi-arid zone (with low stress and rich in recourse), and the lowest population growth (−3 individuals/100 shrubs) occurred in the severely grazed treatment in the intensively arid zone (with high stress and poor in recourse). These results were due to the variation in the balance between population recruitment and mortality as climatic aridity and grazing intensity changed. Our results indicated that population growth under severe drought conditions was further suppressed under heavy grazing.

The population growth of *C. stenophylla* was negatively affected by grazing intensities (see Fig. 3f), which was consistent with the findings for other plant species, such as ginseng (Farrington et al., 2009), *Bromus tectorum* (Bradley, 2009; Concilio et al., 2013), and palm (Mandle et al., 2015). But this was in contrast to the findings of Li et al. (2013), which showed that seasonal grazing did not significantly affect long-term population growth rate (λ).

Our results showed that sexual recruitment of *C. stenophylla* decreased from the semiarid zone to the intensively arid zone (Fig. 3f), which contrasted with our previous observation showing that *Caragana* species abundant and canopy size increased along the same climatic aridity gradient. This was likely due to the associated increase in asexual reproduction via ramet from the semiarid zone to the intensively arid zone (Ma et al., 2013), which might, to some extent, compensate the decrease in sexual reproduction of *C. stenophylla*.

Management Implication

In areas with relative low drought stress and mild intensity of grazing, population growth of *C. stenophylla* was positive; therefore, *C. stenophylla* population increased. While under high drought stress and severe intensity of grazing conditions, population growth was negative, *C. stenophylla* population declined. Thus, to maintain viable *Caragana* populations, sustain grassland ecosystem structure and function, and further promote sustainable grassland management in the Inner Mongolia Steppe, appropriate grazing policies must be made according to the climate aridity gradient. On the basis of the results of this study, we suggested that there should be mild-intensity grazing and moderate-intensity grazing in the semiarid zone, mild-intensity grazing in the arid and very arid zones, and no grazing in the intensively arid zone due to the vulnerability of *Caragana* populations in this area.

References

Azarnivand, H., Farajollahi, A., Bandak, E., Pouzesh, H., 2010. Assessment of the effects of overgrazing on the soil physical characteristic and vegetation cover changes in rangelands of Hosainabad in Kurdistan province, Iran. *Journal of Rangeland Science* 1, 95–102.

Boulant, N., Kunstler, G., Rambal, S., Lepart, J., 2008. Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands. *Diversity & Distributions* 14, 862–874.

Bradley, B.A., 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Global Change Biology* 15, 196–208.

Buckley, Y.M., Ramula, S., Blomberg, S.P., Burns, J.H., Crone, E.E., Ehrlén, J., Knight, T.M., Pichancourt, J.B., Quested, H., Wardle, G.M., 2010. Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. *Ecology Letters* 13, 1182–1197.

Caldeira, M.C., Ibáñez, I., Nogueira, C., Bugalho, M.N., Lecomte, X., Moreira, A., Pereira, J.S., 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *Journal of Applied Ecology* 51, 349–358.

de Campos Franci, L., Nabe-Nielsen, J., Svenning, J.C., Martins, F.R., 2016. Short-term spatial variation in the demography of a common Neotropical liana is shaped by tree community structure and light availability. *Plant Ecology* 1–18.

Carón, M.M., De Frenne, P., Brunet, J., Chabrierie, O., Cousins, S.A., De Backer, L., Decocq, G., Diekmann, M., Heinken, T., Kolb, A., Naaf, T., Plue, J., Selvi, F., Strimbeck, G.R., Wulf, M., Verheyen, K., 2015a. Interacting effects of warming and drought on regeneration and early growth of *Acer Pseudoplatanus* and *A. Platanoides*. *Plant Biology* 17, 52–62.

Carón, M.M., Frenne, P.D., Brunet, J., Chabrierie, O., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Heinken, T., Kolb, A., 2015b. Divergent regeneration responses of two closely related tree species to direct abiotic and indirect biotic effects of climate change. *Forest Ecology & Management* 342, 21–29.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2004a. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology* 92, 266–277.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., Gómez-Aparicio, L., 2004b. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology* 12, 352–358.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2005. Alleviation of summer drought boosts establishment success of *Pinus sylvestris* in a Mediterranean mountain: an experimental approach. *Plant Ecology* 181, 191–202.

Chen, Y., Tang, H., 2005. Desertification in north China: background, anthropogenic impacts and failures in combating it. *Land Degradation & Development* 16, 367–376.

Cipriotti, P.A., Flombaum, P., Sala, O.E., Aguiar, M.R., 2008. Does drought control emergence and survival of grass seedlings in semi-arid rangelands? An example with a Patagonian species. *Journal of Arid Environments* 72, 162–174.

Clark, J.S., Macklin, E., Wood, L., 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68, 213–235.

Concilio, A.M., Loik, M.E., Belnap, J., 2013. Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. *Global Change Biology* 19, 161–172.

Ehrlén, J., Syrjänen, K., Leimu, R., Begona García, M., Lehtilä, K., 2005. Land use and population growth of *Primula veris*: an experimental demographic approach. *Journal of Applied Ecology* 42, 317–326.

Ekrtova, E., Kosnar, J., 2012. Habitat-related variation in seedling recruitment of *Gentiana Pannonica*. *Acta Oecologica* 45, 88–97.

Farrington, S.J., Muzika, R.M., Drees, D., Knight, T.M., 2009. Interactive effects of harvest and deer herbivory on the population dynamics of American ginseng. *Conservation Biology* 23, 719–728.

Faust, C., Süß, K., Storm, C., Schwabe, A., 2011. Threatened inland sand vegetation in the temperate zone under different types of abiotic and biotic disturbances during a ten-year period. *Flora-Morphology, Distribution, Functional Ecology of Plants* 206, 611–621.

Fortunel, C., Paine, C.E., Fine, P.V., Mesones, I., Goret, J.Y., Burban, B., Jocelyn, C., Baraloto, C., 2016. There's no place like home: seedling mortality contributes to the habitat specialisation of tree species across Amazonia. *Ecology Letters* 19, 1256–1266.

Fynn, R.W.S., O'Connor, T.G., 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology* 37, 491–507.

Gómez, J.M., 2005. Long-term effects of ungulates on performance, abundance, and spatial distribution of two montane herbs. *Ecological Monographs* 75, 231–258.

Guan, L.J., Mei, X.F., Zhang, Y.Y., Han, L., Li, Q.F., Ma, C.C., 2016. The temporal and spatial distribution of soil water and nutrient of *Caragana stenophylla* nabkha in the different habitats of the Inner Mongolia Plateau. *Arid Zone Research* 33, 253–259.

Hamre, L.N., Rydgren, K., Halvorsen, R., 2010. The effects of mulching and abandonment on the viability of the perennial grassland species *Plantago lanceolata*. *Plant Ecology* 211, 147–158.

Haugo, R.D., Bakker, J.D., Halpern, C.B., 2013. Role of biotic interactions in regulating conifer invasion of grasslands. *Forest Ecology & Management* 289, 175–182.

Heckel, C.D., Bourg, N.A., McShea, W.J., Kalisz, S., 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91, 319–326.

Hegland, S., Jongejans, E., Rydgren, K., 2010. Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models. *Oecologia* 163, 695–706.

Holl, K.D., 2002. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology* 90, 179–187.

Huberty, A.F., Denno, R.F., 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85, 1383–1398.

Hunt, L.P., 2010. Spatial variation in the demography and population dynamics of a perennial shrub (*Atriplex vesicaria*) under sheep grazing in semi-arid Australian rangelands. *Austral Ecology* 35, 794–805.

Li, S.L., Werger, M.J., Zuidema, P.A., Yu, F.H., Dong, M., 2010. Seedlings of the semi-shrub *Artemisia ordosica* are resistant to moderate wind denudation and sand burial in Mu Us sandland, China. *Trees* 24, 515–521.

Li, S.L., Yu, F.H., Werger, M.J., Dong, M., Ramula, S., Zuidema, P.A., 2013. Understanding the effects of a new grazing policy: the impact of seasonal grazing on shrub demography in the Inner Mongolian steppe. *Journal of Applied Ecology* 50, 1377–1386.

López-Sánchez, A., Schroeder, J., Roig, S., Sobral, M., Dirzo, R., 2014. Effects of cattle management on oak regeneration in northern Californian Mediterranean oak woodlands. *Plos One* 9, e105472.

Ma, C.C., Zhang, J.H., Guo, H.Y., Li, Q.F., Xie, L.N., Gao, Y.B., 2013. Alterations in canopy size and reproduction of *Caragana stenophylla* along a climate gradient on the Inner Mongolian Plateau. *Flora—Morphology, Distribution, Functional Ecology of Plants* 208, 97–103.

Macias, D., Mazia, N., Jacobo, E., 2014. Grazing and neighborhood interactions limit woody encroachment in wet subtropical savannas. *Basic & Applied Ecology* 15, 661–668.

Mandle, L., Ticktin, T., 2012. Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. *Journal of Ecology* 100, 997–1008.

- Mandle, L., Ticktin, T., Zuidema, P.A., 2015. Resilience of palm populations to disturbance is determined by interactive effects of fire, herbivory and harvest. *Journal of Ecology* 103, 1032–1043.
- Meng, M., Zhi, Z., 2004. Aridity index and its applications in geo-ecological study. *Acta Phytocologica Sinica* 28, 853–861.
- Moles, A.T., Westoby, M., 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99, 241–248.
- Noumi, Z., Chaieb, M., Michalet, R., Touzard, B., 2015. Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study. *Applied Vegetation Science* 18, 391–401.
- Osem, Y., Fogel, T., Moshe, Y., Brant, S., 2015. Managing cattle grazing and overstorey cover for the conversion of pine monocultures into mixed mediterranean woodlands. *Applied Vegetation Science* 18, 396–410.
- Rousset, O., Lepart, J., 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). *Journal of Ecology* 88, 401–412.
- Sánchez-Velásquez, L.R., del Rosario Pineda-López, M., 2010. Comparative demographic analysis in contrasting environments of *Magnolia dealbata*: an endangered species from Mexico. *Population Ecology* 52, 203–210.
- Smit, C., Ruifrok, J.L., van Klink, R., Olf, H., 2015. Rewilding with large herbivores: the importance of grazing refuges for sapling establishment and wood-pasture formation. *Biological Conservation* 182, 134–142.
- Traveset, A., Gullias, J., Riera, N., Mus, M., 2003. Transition probabilities from pollination to establishment in a rare dioecious shrub species (*Rhamnus ludovici-salvatoris*) in two habitats. *Journal of Ecology* 91, 427–437.
- Van Uytvanck, J., Van Noyen, A., Milotic, T., Decler, K., Hoffmann, M., 2010. Woodland regeneration on grazed former arable land: a question of tolerance, defence or protection? *Journal for Nature Conservation* 18, 206–214.
- Warner, P.J., Cushman, J.H., 2002. Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. *Oecologia* 132, 77–85.
- Watson, I.W., Westoby, M., McR, A., 1997. Demography of two shrub species from an arid grazed ecosystem in western Australia 1983–93. *Journal of Ecology* 85, 815.
- White, T.C.R., 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63, 90–105.
- Xie, L.N., Ma, C.C., Guo, H.Y., Li, Q.F., Gao, Y.B., 2014. Distribution pattern of *Caragana* species under the influence of climate gradient in the Inner Mongolia region, China. *Journal of Arid Land* 6, 311–323.
- Xie, L.N., Guo, H.Y., Gabler, C.A., Li, Q.F., Ma, C.C., 2015. Changes in spatial patterns of *Caragana stenophylla* along a climatic drought gradient on the Inner Mongolian Plateau. *Plos One* 10, e0121234.
- Xie, L.N., Chen, W.Z., Gabler, C.A., Han, L., Guo, H.Y., Chen, Q., Ma, C.C., Gu, S., 2016. Effects of grazing intensity on seed production of *Caragana stenophylla* along a climatic aridity gradient in the Inner Mongolia Steppe, China. *Journal of Arid Land* 890–898.
- Xiong, X.G., Han, X.G., Chen, Q.S., Pan, Q.M., 2002. Increased abundance of woody plants in grasslands and savannas. *Acta Ecologica Sinica* 23, 2436–2443.
- Yu, F.H., Dong, M., Krüsi, B., 2004. Clonal integration helps *Psammochloa villosa* survive sand burial in an inland dune. *New Phytologist* 162, 697–704.
- Zhao, W.Z., Li, Q.Y., Fang, H.Y., 2007. Effects of sand burial disturbance on seedling growth of *Nitraria sphaerocarpa*. *Plant and Soil* 295, 95–102.