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Understanding the effects of a new grazing policy: the impact of seasonal grazing on shrub demography in the Inner Mongolian steppe

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Summary

1. Grazing by livestock is a common land use in arid and semi-arid areas. Developing sustainable grazing regimes that conserve vegetation and maintain productivity is therefore important in these ecosystems. To solve environmental problems induced by overgrazing in Chinese semi-arid regions, the Chinese government has recently implemented a new policy of seasonal grazing, with no grazing from April to July. While this policy has been implemented in huge areas, its consequences for grazed plant populations have not been assessed so far.

2. We evaluated the demographic consequences of seasonal grazing for *Caragana intermedia*, a long-lived dominant shrub serving as a main food source for livestock in Inner Mongolia, China. Controlled seasonally grazed and ungrazed populations were monitored during 2007–2009, and their vital rates were compared. We then constructed integral projection models (IPMs) to analyse the effects of seasonal grazing on population dynamics.

3. Seasonal grazing negatively affected two vital rates: seedling survival and seedling recruitment were 25–71% and 69–91% lower in the seasonally grazed treatment than in the ungrazed situation, respectively. Seasonal grazing had a minimal effect on adult survival and growth, but improved juvenile survival by 8–31%.

4. Despite its effects on several vital rates, seasonal grazing did not significantly affect long-term population growth rates (λ), which remained close to unity in both grazed and ungrazed areas based on deterministic and stochastic analyses. An elasticity analysis showed that population growth rate was mainly governed by the high survival of large adults. Results of Life Table Response Experiments (LTREs) revealed that variation in population growth rates across treatments and years was more strongly governed by temporal differences than by grazing.

5. *Synthesis and applications*. Our study showed that the relatively large changes in vital rates induced by seasonal grazing did not affect population growth rates. *Caragana intermedia* populations can be sustained under the seasonal grazing regime probably because the grazing intensity is moderate and because this species has a high probability of adult survival under grazing. Plant species with similar life-history traits to *C. intermedia* are likely to offer good opportunities for sustainable seasonal grazing regimes in arid and semi-arid inland ecosystems.

Key-words: *Caragana intermedia*, elasticity, grazing, integral projection model, Life Table Response Experiments, semi-arid sandland, shrub demography, stochasticity

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Introduction

Arid and semi-arid areas throughout the world are commonly used as pastoral land for livestock (Fynn & O'Connor 2000; Watkinson & Ormerod 2001). Annual precipitation in these ecosystems is generally low and varies greatly between years (Mandujano *et al.* 2001; Salguero-Gomez *et al.* 2012). Vegetation cover is usually low and may easily get destroyed by improper grazing practices (Curtin 2002; Sasaki *et al.* 2008), especially in dry years. Vegetation loss may further lead to desertification and sand storms (Bisigato *et al.* 2005; Jiang, Han & Wu 2006). Therefore, designing sustainable grazing regimes is important for practical management in arid and semi-arid ecosystems. In northern China, livestock grazing is common in the extensive arid and semi-arid areas that cover over a quarter of the country's land area (Chen & Tang 2005). Over the past decades, China has been suffering from grazing-induced desertification and more frequent sand storms, which are causing severe economic losses in northern China (Chen & Tang 2005; Jiang, Han & Wu 2006). To solve these problems and stimulate sustainable pasture land management, new grazing policies have been put into practice by the Chinese government since 2003, which include a seasonal grazing policy (no grazing in late spring and early summer) and the complete cessation of grazing. Seasonal grazing and the complete cessation of grazing have each been applied to over 19 million hectares of pastoral land (Gan, Xu & Yi 2011), which have increased vegetation cover, plant height and above-ground biomass (Jiang, Han & Wu 2006).

While these landscape-level effects of the new grazing policies have been quantified, nothing is known about the effects of seasonal grazing on grazed plant species and the viability of grazed populations. Insights into the responses of semi-desert plants to grazing are crucial to understand vegetation changes at the landscape level and to provide advice on adaptation of grazing policies (Hunt 2001; Lennartsson & Oostermeijer 2001). Grazing can affect plant performance in complex ways. It directly affects plants by removing vegetative and reproductive tissues (Bastrenta 1991; Hunt 2001) and indirectly through trampling-induced physical damage and soil compaction (Bastrenta 1991; Hunt 2001; Heckel *et al.* 2010). However, plants may also benefit from grazing as soil nutrition, light use efficiency and photosynthetic capacity may increase (Hunt 2001; Augustine & McNaughton 2006). The responses of plants of different sizes to grazing often vary, imposing different effects on population dynamics (Hunt 2001; Hegland, Jongejans & Rydgren 2010; Kolb 2012). The analysis of grazing effects on plant populations requires an integrated approach including individuals of all sizes and all vital rates (Hegland, Jongejans & Rydgren 2010; Hunt 2010). Demographic models are an appropriate tool to evaluate the integrated effects of grazing on plant populations (Hunt 2001; Hegland, Jongejans & Rydgren 2010; Kolb 2012).

Here we evaluate the effects of restricted (seasonal) grazing on population dynamics of a dominant shrub, *Caragana intermedia*, in Mu Us Sandland, Inner Mongolia, China (Zhang 1994). This species is one of the main food sources for livestock in the region and plays important roles in sand fixation. Because of these advantages, it has been planted in large areas in the dry ecosystems in northern China (Zhang 1994). We performed a controlled grazing experiment and evaluated the demographic effects of grazing using integral projection models (IPMs). Specifically, we addressed: (i) How does seasonal grazing affect the vital rates (survival, growth and reproduction) of *C. intermedia*? (ii) How does seasonal grazing affect population growth? (iii) Which demographic rates play critical roles in population growth under seasonally grazed and ungrazed conditions? We discuss the implications of our findings for the current grazing policy and provide recommendations for sustainable grazing.

Materials and methods

STUDY SPECIES

Caragana intermedia Kuang et H. C. Fu (Leguminosae) is a long-lived shrub with multiple stems bearing thorns and compound leaves. The species can grow over 2 m tall, and its crown diameter can reach over 10 m. Flowering occurs in May and lasts about 20 days. Seeds ripen in July, and seed germination is triggered by summer rainfall. Shoots usually grow out at the end of the flowering period. *Caragana intermedia* is widely distributed in semi-fixed and fixed dunes in Inner Mongolia, China, where domestic animals feed on its shoot tips, leaves, flowers and pods (Zhang 1994; Fang *et al.* 2006).

STUDY SITES

The study was conducted during 2007–2009 on a farm at Chahan Aobao (39°18′434″N, 108°38′611″E) located in Etuoke Banner in the Mu Us Sandland in Inner Mongolia, China. This is a semi-arid area with an average summer temperature of 20–28 °C and a mean annual precipitation of 260–450 mm that is concentrated in summer, following a prolonged spring drought (Zhang 1994). Our first study period 2007–2008 (hereafter 'a standard year') represented average climate conditions at the site, with the annual rainfall close to the long-term average calculated from the precipitation records available for 1986–2012 (data from KNMI Climate Explorer, http://climexp.knmi.nl). The second study period 2008–2009 was drier (hereafter 'a dry year'), with the annual rainfall and growing season rainfall being 11% and 24% lower than the average, respectively. Most plant species in the area are forbs and grasses, but a few woody species, for example, *C. intermedia*, *Artemisia ordosica*, *Hedysarum laeve* and *Salix psammophila,* often dominate plant communities (Li *et al.* 2011).

In our study region, grazing is widespread, has a long history and has caused serious vegetation degradation (Zhang 1994). Since 2001, two grazing policies have been implemented in most of the region: (i) seasonal grazing, that is, grazing is allowed nine months per year, with a 3-month interruption from April 1 to July 1, and (ii) the complete cessation of grazing.

We conducted our study in a pasture area where seasonal grazing was applied to a total area of approximately 250 ha, while ungrazed areas covered approximately 10 ha. These grazed and ungrazed sites were adjacent, but separated by wire fences. Both sites had undergone free grazing for over half a century, while the current practices of seasonal grazing and no grazing were implemented for the first time in 2001, 6 years before the onset of our study. At the seasonally grazed site, there were approximately 2·3 goats per ha during the 9-month grazing period, which is a moderate grazing level in this region (Liu *et al.* 2007).

SAMPLING DESIGN AND FIELD MEASUREMENTS

We established three 100 × 100 m permanent plots at the seasonally grazed site and three others at the ungrazed site. We note that treatments (ungrazing and seasonal grazing) were not replicated as we were unable to find other sites that were large enough for demographic studies and had comparable grazing history and grazing intensity. Such replication problems are unfortunately rather common among applied ecological and conservation studies (Ramage *et al.* 2013). To ease data collection, each plot was divided into 100 subplots of 10 × 10 m by permanently marking the four corners of each subplot with woody sticks. The distance between plots within site was > 100 m and sites were >1 km apart. Censuses were conducted in August 2007, 2008 and 2009, resulting in data from 1036 and 2083 individuals at the ungrazed and grazed site, respectively. At the first census, plant height was measured for each individual. For small individuals (crown diameter < 2 m), we measured the two largest perpendicular diameters and marked the positions of their ends and their crossing point at the central crown with bamboo sticks in the soil to ensure that subsequent measurements were taken in the same direction. For large individuals (crown diameter ≥ 2 m), we measured four crown diameters that all crossed the central point in the crown, and any two adjacent radii were 45° away from each other. We measured the eight corresponding radii from the central point of the crown and again marked the ends of crown radii and the central point of the crown with bamboo sticks. Since we measured the crown growth from multiple directions, it gave a good description of the actual growth that would not be biased by a large increase or shrinkage of one or few radii. Crown area was estimated by adding the section areas defined by the four or eight radii, each of which was approximated by the area of a triangle. Crown volume was estimated by multiplying plant height with the total crown area. Reproductive status (flowering or not) was recorded for each individual.

Upon the first measurement, all plants were labelled and their coordinates were recorded. In 2008 and 2009, the survival of the labelled plants was checked; survived plants were remeasured in the same directions and their reproductive status was recorded. In addition, new recruits were searched, labelled and measured. Because adult individuals of *C. intermedia* usually produce a huge amount of pods, especially in the ungrazed plots, it proved impossible to quantify the number of pods (and seeds) for each individual. We therefore assumed that the number of pods produced by an individual was linearly related to its crown volume (x) and estimated the number of seedlings produced per individual (p_e) as $p_e = x(n/\mathrm{sum}(x))$, where n is the number of established seedlings in the plot.

STATISTICAL ANALYSES

To examine differences in vital rates between plots within treatments, we conducted a variance composition analysis with plot as a random factor using the lmer function in R for growth and glmer function for survival and flowering probability. Since variances in vital rates between plots generally accounted for little (<10%) of the overall variances, with the exception of survival and flowering probability under the seasonally grazed treatment (variance 16·4–31·1%), we pooled the data across plots within treatments.

To test for temporal differences in vital rates within seasonally grazed and ungrazed treatments, we used paired t-tests for individual growth ($\mathrm{size}_{t+1}-\mathrm{size}_t$) and generalized linear models for survival and flowering probability with census period as a factor. As models with crown volume (ln-transformed) yielded higher R^2 values than models based on other size measures (plant height, crown area), we used crown volume to characterize plant size. We found differences between census periods for all three vital rates examined within each treatment ($P \leq 0{\cdot}03$ in all cases) and therefore fitted statistical models for each period separately.

We used linear models to examine the effects of seasonal grazing and current plant size (x, at t) on future plant size (μ, at $t+1$, that is, growth) and the variance of growth (σ^2). Generalized linear models were used to examine the effects on survival and flowering probability. The future plant size ($\mu(x)$) and variance of growth ($\sigma^2(x)$) were fitted with linear regressions, and the probability of survival $s(x)$ and flowering $p_f(x)$ was fitted by logistic regressions, with plant size at t and treatment as explanatory variables.

INTEGRAL PROJECTION MODELS

We constructed IPMs to evaluate how the effects of seasonal grazing on individuals translated into the population dynamics of *C. intermedia*. An IPM describes how a continuously size-structured population changes in discrete time (Easterling, Ellner & Dixon 2000). It yields a similar output to matrix models, in which the dominant eigenvalue is equivalent to the population growth rate, and the stable population structure is the right eigenvector (Easterling, Ellner & Dixon 2000). In contrast to matrix models, IPMs require fewer demographic parameters and explicitly incorporate growth variation between individuals (Easterling, Ellner & Dixon 2000; Salguero-Gomez & de Kroon 2010; Zuidema *et al.* 2010). In an IPM, the state of the population at time t is described by a distribution function $n(x, t)$, where $\mathrm{n}(x, t)$ dx represents the number of individuals with size in the range [x, x + dx]. The population dynamics are then described as follows:

$$n(y, t+1) \int_{L}^{U} [p(y, x) + f(y, x)]\, n(x, t)\mathrm{d}x,$$

where [L,U] is the range of all possible sizes x or y, $p(y, x)$ represents survival and growth from size x to size y, and $f(y, x)$ represents the number of recruits of size y produced by parents of size x. $p(y, x)$ was calculated as $p(y, x) = s(x)\,g(y, x)$, where $s(x)$ is survival and $g(y, x)$ is a normal probability density function with mean future plant size ($\mu(x)$) and growth variance ($\sigma^2(x)$). To avoid the annual survival probability of large adults reaching the unrealistic value of 100%, we bounded survival to ≤99·9%. $f(y, x)$ was calculated as $f(y, x) = pf(x)\ pe\ fd(y)$, where $pf(x)$ is flowering probability, pe is the mean number of seedlings produced per size-specific adult plant, and $fd(y)$ is the truncated normal size distribution of seedlings. We did not include a seed bank because most seeds germinate in the year after dispersal (Wang & Liang 1995). Then, the kernel $K(y, x)$ was calculated as $K(y, x) = p(y, x) + f(y, x)$. We applied the mid-point rule to convert the kernel into a large transition matrix with 400 mesh points (Easterling, Ellner & Dixon 2000). Because we found significant differences in vital rates between census periods and treatments, we constructed IPMs for each combination of period and treatment, resulting in four IPMs. For each IPM, we calculated the deterministic population growth rate (λ) with confidence intervals using bootstrapping (Jongejans *et al.* 2010). For each bootstrap estimate, we resampled individuals with replacement from the data sets (n = 2083 and 1036 in seasonally grazed and ungrazed treatments, respectively), recalculated regression coefficients, constructed the kernel and calculated λ. This was repeated 5000 times, and the 95% confidence intervals for λ were obtained from the frequency distribution of these values. The damping ratio, which measures how rapidly a population returns from a disturbed state to the stable dynamic equilibrium, was calculated as the ratio of the dominant eigenvalue to the subdominant eigenvalue.

We also calculated stochastic population growth rates (λ_s) for both treatments by selecting either a dry-year or standard-year kernel with the probability of 33% and 67% for each of 10 000 model iterations. These probabilities were chosen based on the long-term climate records during 1986–2012, in which the growing season rainfall was equal to or lower than that in our dry year in nine out of 27 years (data from KNMI Climate Explorer). We then calculated the geometric means of the obtained annual growth rates after excluding the first 200 transient iterations (Tuljapurkar, Horvitz & Pascarella 2003) and obtained 95% confidence intervals for λ_s from its frequency distribution.

To examine whether the observed plant size distribution deviated from the expected one, we compared the observed population structures (mean of the three annual censuses) to the stable structures resulting from deterministic and stochastic IPMs for both ungrazed and seasonally grazed conditions.

To examine the relative importance of each vital rate to λ, we conducted an elasticity analysis, in which we separated survival from growth and shrinkage (Zuidema & Franco 2001; Li *et al.* 2011). Elasticity quantifies the impact of a proportional change in a vital rate on the proportional change of λ and can be used to guide management (de Kroon, van Groenendael & Ehrlén 2000; Caswell 2001). To explore whether very high adult survival probability will lead to unrealistic elasticity results, we conducted an elasticity analysis with the maximum survival set to either 99·9% or 95·0%. As these analyses resulted in qualitatively very similar elasticities (the absolute changes in elasticity values <0·01 in all vital rates across treatments and periods), we only presented elasticities based on 99·9% survival.

The analysis of Life Table Response Experiments (LTREs) allows quantifying the contribution of each vital rate to the observed difference in population growth rate (Caswell 2001). In the case where differences in the values of λ are very small or absent, an LTRE analysis may still reveal to what extent population dynamics differ as in this case a positive contribution of one vital rate may be outweighed by negative contributions of other vital rates (Yamada *et al.* 2007). We conducted a fixed design of two-factor LTRE on vital rates to evaluate the contributions of variation in vital rates to differences in population growth rates (see Appendix S1, Supporting Information for details).

All analyses were performed with the software R 2.10.0 (R Development Core Team 2010).

Results

VITAL RATES IN RELATION TO CENSUS PERIOD AND GRAZING REGIME

In the first census period (2007–2008), survival probability of newly recruited *C. intermedia* seedlings [with ln(crown volume in cm^3) of 1·8–3·6] was low, but increased rapidly in juvenile plants [with ln(crown volume in cm^3) of 3·6–10], and no mortality was observed in reproductive adults [with ln(crown volume in cm^3) >10; Table 1, Fig. 1a]. Survival probability was higher for seedlings and lower for juveniles in the second, drier census period (2008–2009) than in the first census period (Table 1, Fig. 1a,b). Survival probabilities differed between seasonally grazed and ungrazed treatments (Fig. 1a,b), and seasonal grazing reduced seedling survival by 25–71% and increased juvenile survival by 8–31% depending on the census period (data not shown).

Growth generally decreased with plant size, as indicated by the regression slopes of <1 (Table 1). Seasonal grazing only slightly increased seedling growth in the first period in seasonally grazed plots (Fig. 1c). Both positive growth and shrinkage were observed for individuals in grazed and ungrazed plots (Fig. 1c,d). The proportion of individuals that shrunk was higher in grazed (62%) than in ungrazed plots (51%), but the average magnitude of shrinkage was the same (22–23% of crown volume; data not shown).

Flowering probability increased with plant size (Table 1), and individuals generally started to reproduce at the size of ln(crown volume in cm^3) > 10. Flowering probability was not affected by seasonal grazing in either of the census periods (Table 1, Fig. 1e,f). The number of newly recruited seedlings greatly differed between treatments. Compared to ungrazed populations, 69% and 91% fewer seedlings were produced in seasonally grazed populations during the first and second census periods, respectively (Table 1), suggesting a drastic effect of grazing on population recruitment.

SEASONAL GRAZING EFFECTS ON POPULATION GROWTH RATES AND STABLE STRUCTURES

Deterministic and stochastic models produced similar estimates of population growth rates for grazed and ungrazed populations, with all estimates being close to 1 and the 95% confidence intervals always including the value of 1 (Table 2). This suggests that population growth remained unaffected by seasonal grazing and that grazed populations could be sustained over time given the current grazing regime and environmental conditions. The damping ratios were very similar in both treatments (1·081 and

1·083 in ungrazed and seasonally grazed populations, respectively). The observed and expected stable (deterministic and stochastic) population structures under seasonally grazed conditions were dominated by large adults with a smaller proportion of seedlings and juveniles compared to the structure in ungrazed populations (Fig. 2). The observed population structure deviated from the expected stable size distributions in both ungrazed and seasonally grazed populations (Fig. 2), indicating that the study populations have experienced strong changes and/or that vital rates observed during the study differ from those in the past. The similarity between the observed and the stochastic structure was a bit lower in ungrazed than in seasonally grazed populations (Fig. 2), which is consistent with what would be expected if population structure would have changed more in ungrazed than in seasonally grazed areas in recent years.

ELASTICITY ANALYSES

Vital rate elasticity analyses revealed that population growth of *C. intermedia* was most sensitive to changes in the survival of larger individuals, whereas changes in the other vital rates (growth, fecundity and shrinkage) would have a minor effect on population growth (Fig. 3). The distribution of survival elasticities over size categories shifted to relatively larger adults in the second, drier period (Fig. 3c,d). Ungrazed (Fig. 3a,c) and seasonally grazed treatments (Fig. 3b,d) showed a similar distribution of elasticity values over vital rates.

LIFE TABLE RESPONSE EXPERIMENTS

Life Table Response Experiments (LTREs) showed that grazing treatment contributed less to the variation in λ than census period or the interaction between treatment and period (Table 3). The LTRE analysis revealed that the differences in λ between grazing treatments were mainly caused by slightly higher adult survival and considerably lower fecundity in grazed plots (Fig. 4a,b). The faster growth and lower survival during the second, drier year were the main contributors to the differences in population growth rates between years (Fig. 4c,d).

Discussion

EFFECTS OF SEASONAL GRAZING ON VITAL RATES

Seasonal grazing affected several vital rates of *C. intermedia* in different life stages. It greatly reduced seedling

Table 1. Statistical models and parameter estimates used to construct the kernels for the integral projection models of *Caragana intermedia* in Mu Us Sandland during 2007–2008 (period 1) and 2008–2009 (period 2). The models are functions of plant size (x; natural log scale of crown volume, originally measured in cm^3), treatment (seasonal grazing) and interactions between size and treatment, using the ungrazed treatment as a reference. Functions for seasonally grazed treatment and ungrazed control were written separately whenever they were significantly different from each other. R^2 for survival and flowering is Nagelkerke R^2

Demographic process	Period	Model
Survival probability (s)	1	Ungrazed: $\text{logit}(s) = -6{\cdot}08 + 1{\cdot}42x$ Seasonally grazed: $\text{logit}(s) = -8{\cdot}99 + 2{\cdot}60x$ $n = 2813$, $R^2 = 0{\cdot}84$, $P < 0{\cdot}0001$
	2	Ungrazed: $\text{logit}(s) = -2{\cdot}54 + 0{\cdot}63x$ Seasonally grazed: $\text{logit}(s) = -5{\cdot}25 + 1{\cdot}01x$ $n = 1694$, $R^2 = 0{\cdot}67$, $P < 0{\cdot}0001$
Flowering probability (p_f)	1	Ungrazed and seasonally grazed: $\text{logit}\ (p_f) = -15{\cdot}97 + 1{\cdot}30x$ $n = 2813$, $R^2 = 0{\cdot}87$, $P < 0{\cdot}0001$
	2	Ungrazed and seasonally grazed: $\text{logit}\ (p_f) = -19{\cdot}00 + 1{\cdot}58x$ $n = 1694$, $R^2 = 0{\cdot}85$, $P < 0{\cdot}0001$
Future size (growth, μ)	1	Ungrazed: $\mu = 0{\cdot}37 + 0{\cdot}96x$ Seasonally grazed: $\mu = 0{\cdot}77 + 0{\cdot}93x$ $n = 1614$, $R^2 = 0{\cdot}98$, $P < 0{\cdot}0001$
	2	Ungrazed and seasonally grazed: $\mu = 1{\cdot}24 + 0{\cdot}92x$ $n = 1480$, $R^2 = 0{\cdot}98$, $P < 0{\cdot}0001$
Variance of growth (σ^2)	1	Ungrazed: $\sigma^2 = 0{\cdot}57 - 0{\cdot}03x$ Seasonally grazed: $\sigma^2 = 0{\cdot}90 - 0{\cdot}053x$ $n = 1614$, $\mathrm{R}^2 = 0{\cdot}16$, $P < 0{\cdot}0001$
	2	Ungrazed and seasonally grazed: $\sigma^2 = 0{\cdot}89 - 0{\cdot}05x$ $n = 1480$, $\mathrm{R}^2 = 0{\cdot}24$, $P < 0{\cdot}0001$
Seedling establishment per size-specific adult (p_e)	1	Ungrazed: $p_e = x(61/\text{sum}(x))$, $n = 393$ Seasonally grazed: $p_e = x(19/\text{sum}(x))$, $n = 629$
	2	Ungrazed: $p_e = x(195/\text{sum}(x))$, $n = 396$ Seasonally grazed: $p_e = x(18/\text{sum}(x))$, $n = 638$
Seedling size distribution (f_d)	1	Ungrazed: Gaussian with mean = 3·13, variance = 0·27, $n = 61$ Seasonally grazed: Gaussian with mean = 3·54, variance = 0·13, $n = 19$
	2	Ungrazed: Gaussian with mean = 2·68, variance = 0·53, $n = 195$ Seasonally grazed: Gaussian with mean = 1·80, variance = 0·05, $n = 18$

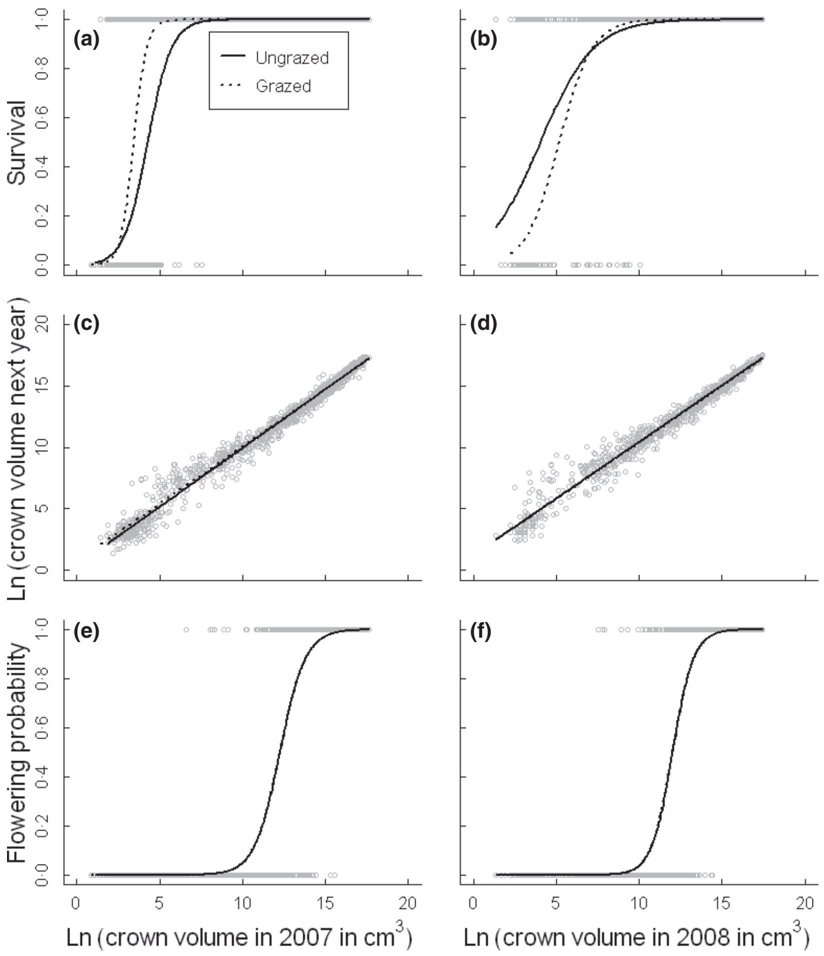

Fig. 1. Relations of vital rates with crown volume for *Caragana intermedia* in Mu Us Sandland during 2007–2008 (a, c, e) and 2008–2009 (b, d, f) in ungrazed and seasonally grazed treatments. Regression functions are described in Table 1.

Table 2. Population growth rates of *Caragana intermedia* in Mu Us Sandland in ungrazed and seasonally grazed treatments during the two study periods. Values in brackets refer to 95% confidence intervals

Treatment	Deterministic (λ)		Stochastic (λs)
	2007–2008	2008–2009	
Ungrazed	0·991 [0·982, 1·082]	1·011 [0·970, 1·028]	0·996 [0·924, 1·059]
Seasonally grazed	0·999 [0·999, 1·001]	0·999 [0·999, 1·000]	0·999 [0·995, 1·001]

survival and recruitment, considerably increased juvenile survival, but did not affect adult survival. High seedling mortality was likely caused by direct grazing and/or trampling by livestock (Ehrlén 1995a; Warner & Cushman 2002; Gomez 2005; Heckel *et al.* 2010). Adult mortality is commonly low in long-lived woody species and not greatly affected by grazing (Watson, Westoby & Holm 1997; Warner & Cushman 2002; Sanchez-Velasquez & Pineda-Lopez 2010). Juveniles could have benefited from grazing due to reduced density-dependent mortality (Toft & Fraizer 2003; Sanchez-Velasquez & Pineda-Lopez 2010) as desert shrubs at young stages are often strongly aggregated (Toft & Fraizer 2003), and this was also observed for *C. intermedia* (S.-L. Li Personal observation). In arid and semi-arid areas, aggregation can induce strong intraspecific competition for water, especially when deep roots have not yet developed (Toft & Fraizer 2003). Higher seedling mortality rates in grazed populations probably led to reduced juvenile densities and lower competition between individuals. Thus, it appears that direct and indirect effects of grazing interactively shaped the responses of *C. intermedia* to seasonal grazing.

The growth of adult *C. intermedia* individuals was hardly affected by seasonal grazing. This tolerance to grazing is probably related to its high capacity for compensatory growth. Species with a high capacity of resprouting can often recover from herbivory (Gomez 2005; Fang *et al.* 2006). Fang *et al.* (2006) found that a closely related species, *C. korshinskii*, had a high compensatory growth after experimental clipping due to increased investment in the growth of current year shoots. Furthermore, nutrients released from goat faeces could also contribute to high compensatory growth (Heckel *et al.* 2010), especially in nutrient-poor areas such as in Mu Us

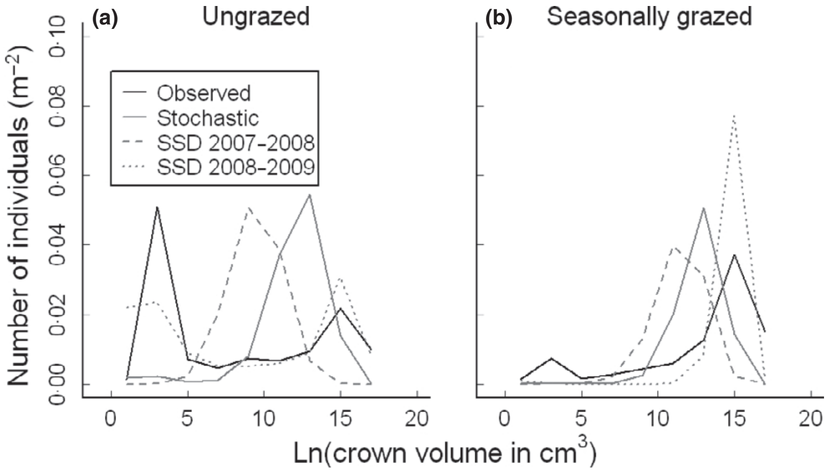

Fig. 2. Population size structures of *Caragana intermedia* in Mu Us Sandland at ungrazed (a) and seasonally grazed sites (b). Observed population structure (Observed), stable size structure (SSD) resulting from deterministic integral projection models for 2007–2008 and 2008–2009 and stochastic size structure from a stochastic integral projection model.

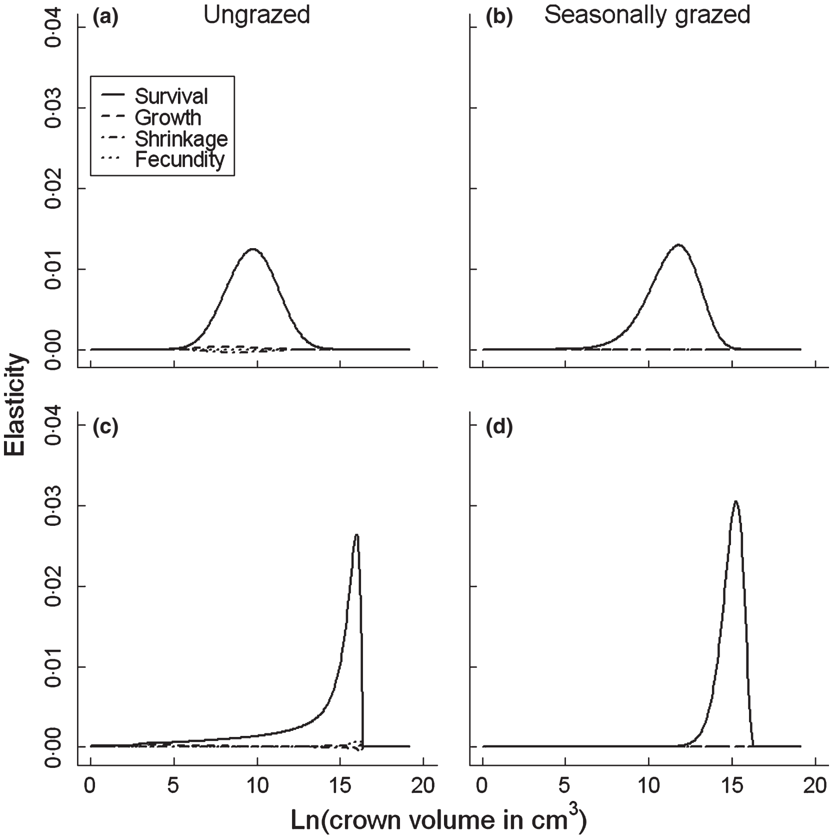

Fig. 3. Vital rate elasticity for *Caragana intermedia* in Mu Us Sandland during 2007–2008 (a, b) and 2008–2009 (c, d) in ungrazed (a, c) and seasonally grazed treatments (b, d).

Sandland. In our study, the N and P contents in the top 10 cm of soil in the seasonally grazed plots were indeed higher, which were 1·5 and 1·7 times those in the ungrazed plots (S.-L. Li unpubl. data).

Seasonal grazing did not affect the flowering probability of *C. intermedia*, but greatly reduced the number of seedlings recruited in the population. In the study area, grazing was ceased from April 1 to July 1. After July 1, a large proportion of the pods were still attached to the plants, many of which are likely consumed by goats, potentially leading to reduced seedling recruitments. The low seedling recruitment in seasonally grazed plots could also be caused by increased soil compaction by livestock trampling (Gomez 2005; Heckel *et al.* 2010). Another cause for the reduced recruitment may be a shift in biomass allocation to vegetative growth as a result of leaf loss (Bastrenta 1991). Although it was impossible to count the number of seeds produced in the present study, our impression is that considerably fewer pods were produced in seasonally grazed than in ungrazed plots. At least the closely related *C. microphylla* produced more seeds in ungrazed than in grazed areas (He & Huang 2010), but seed germination was not influenced by grazing (Zhang & Wang 2011). Therefore, the low seedling

Table 3. Contributions of treatment and temporal effects to variation in population growth rate (λ) of *Caragana intermedia* based on the Life Table Response Experiment (LTRE). The mean and standard deviations of the absolute values of all levels within an LTRE effect are also given

LTRE effect	
Treatment	
Ungrazed	−0·0003
Seasonally grazed	0·0001
Mean ± SD of $\lvert\alpha^{m}\rvert$	0·0002 ± 0·0001
Period	
2007–2008	−0·0019
2008–2009	0·0039
Mean ± SD of $\lvert\beta^{n}\rvert$	0·0029 ± 0·0014
Interactions between treatment and census period	
Ungrazed × 2007–2008	0·0017
Seasonally grazed × 2007–2008	0·0066
Ungrazed × 2008–2009	0·0071
Seasonally grazed × 2008–2009	−0·0083
Mean ± SD of $\lvert\alpha\beta^{mn}\rvert$	0·0059 ± 0·0029

establishment of *C. intermedia* in seasonally grazed plots was probably caused by reduced seed production rather than reduced seed germination. Reproduction in perennial plants is often affected by herbivory (Bastrenta 1991; Ehrlén 1995a; Knight, Caswell & Kalisz 2009), and frequent grazing and trampling can greatly reduce or even completely block their seed production (Bastrenta 1991; Ehrlén 1995a,b; Gomez 2005; Knight, Caswell & Kalisz 2009).

EFFECTS OF SEASONAL GRAZING ON POPULATION DYNAMICS

According to IPMs, both seasonally grazed and ungrazed populations would maintain their current size over time. This suggests that the population growth of *C. intermedia* is not affected by the currently applied grazing regime with a grazing period of 9 months per year and a grazing intensity of 2·3 goats per hectare. This result is consistent with the findings from other long-lived woody species in arid zones that have been shown to be highly tolerant to grazing due to their high compensatory growth (Watson, Westoby & Holm 1997; Sanchez-Velasquez & Pineda-Lopez 2010). Besides grazing, other sources of spatial variation such as water availability, nutrient amount and vegetation composition may also account for the observed differences in population growth rates between the grazed and ungrazed sites. As grazing in our study was not spatially replicated, we were unable to unambiguously distinguish the differences caused by the grazing treatments from those caused by other sources of spatial variation (Ramage *et al.* 2013). However, the grazed and ungrazed sites in our study were adjacent, were geographically very similar and experienced the same grazing pressure for decades before the new grazing policy was implemented. Since the present study is based on demographic data over two census intervals, it captures only a part of the environmental variation. Increased environmental variation usually tends to reduce population growth rate (e.g.

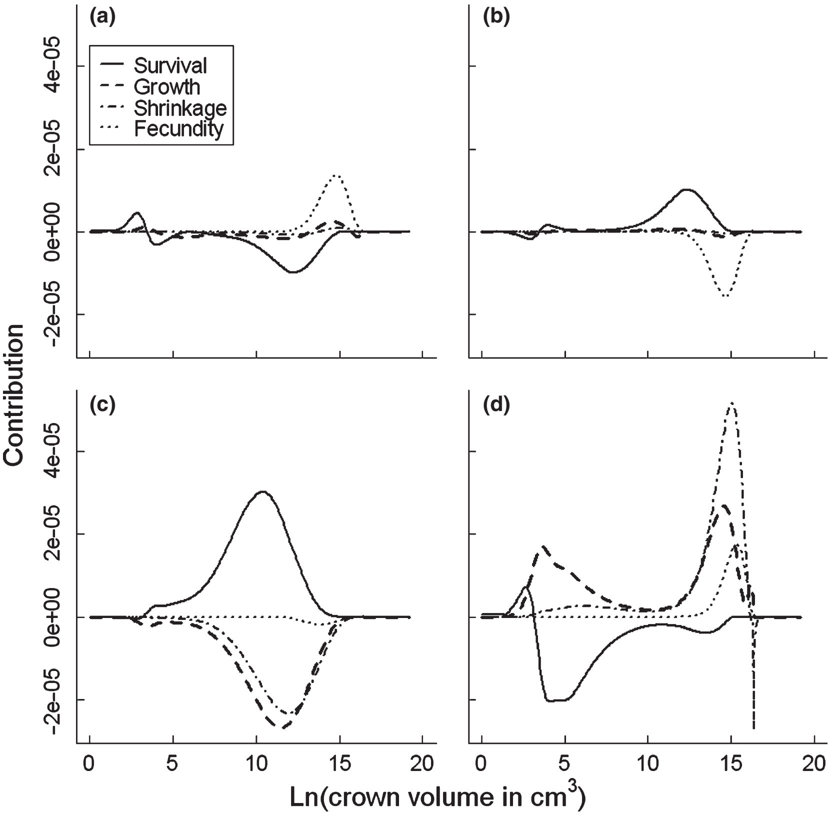

Fig. 4. Results of analyses of Life Table Response Experiments (LTREs) for *Caragana intermedia* in Mu Us Sandland. The contributions of vital rates to population growth variation in ungrazed (a) and seasonally grazed treatments (b) and contributions to temporal variation in population growth for 2007–2008 (c) and 2008–2009 (d).

Boyce 1992; Higgins, Pickett & Bond 2000), meaning that extremely dry years that were not observed during the current study may result in declining populations, particularly in the grazed site. On the other hand, the occurrence of an extremely favourable year with high recruitment may also increase population growth for perennial plant species exhibiting high adult survival (Higgins, Pickett & Bond 2000). As population growth rate could be potentially much higher or lower during extreme years than observed here, our grazing recommendations should be confirmed by longer-term studies.

How are populations of *C. intermedia* maintained under seasonally grazed conditions? Elasticity analysis revealed that the population growth was governed in similar ways with and without grazing. The survival of large adults was most important for population growth, which is typical for long-lived woody species (Franco & Silvertown 2004; Sanchez-Velasquez & Pineda-Lopez 2010) and is an important feature in arid areas where rainfall varies over time. This apparent importance of adult survival for population maintenance points to the need to maximize adult survival in grazed populations (Hunt 2001). Even when similar population growth rates are found across treatments, strong differences in population dynamics may still occur between such treatments if the positive and negative effects of vital rates cancel each other out (Yamada *et al.* 2007). This was not the case in our study: the LTRE analysis revealed that all vital rates made minor contributions to the differences in population growth between treatments, suggesting that the seasonal grazing regime had little effect on the population dynamics of *C. intermedia*. In fact, population growth varied more strongly between census periods than between treatments, indicating that climatic variability had a stronger impact on the population dynamics of our study species than grazing. The similar damping ratios in seasonally grazed and ungrazed treatments suggest that grazed populations have equal resistance to environmental disturbances and can bounce back to their stable dynamics with a similar speed to ungrazed populations.

MANAGEMENT IMPLICATIONS

We found that grazing effects strongly differed across the life stages and vital rates of the shrub *C. intermedia*, in which recruitment was strongly affected by grazing, whereas adult survival remained unaffected. The effects of grazing on population dynamics ultimately depend on how sensitive population growth rate is to changes in given vital rates. In our case, the strong reduction in recruitment did not translate into changes in population growth because of the low sensitivity to changes in fecundity. On the other hand, a small effect of grazing on adult survival could cause a strong demographic impact as population growth is highly sensitive to adult survival. However, adult plants seem highly tolerant to grazing in our case. Management recommendations can be based on vital rates that are mostly affected by grazing and those that are most important for population growth.

The most affected vital rate by grazing in the present study, seedling recruitment, did not cause strong population-level changes. Yet, its drastic reduction under seasonal grazing and great fluctuations between years could potentially reduce population growth, for example, in very dry years. Protecting parts of populations from being grazed during such years would allow continued recruitment and the maintenance of viable populations. We therefore recommend retaining parts of *C. intermedia* populations without grazing, either at all times or during particularly dry years. One option would be to allow undisturbed recruitment in a rotational system, in which a different area of the population is left without grazing in each time.

Although the most important vital rate for population maintenance, adult survival, was not affected by grazing in the present study, any negative effects would have major implications for population growth. For long-lived shrub species in arid areas, it usually takes a long time to grow into large adults and only a proportion of seedlings reach that stage. For *C. intermedia*, we estimated that large individuals with the size of 80% of the maximum observed size in our population are 72–140 years old (passage time; Metcalf *et al.* 2013). For instance, a 5% decrease in adult survival would convert the currently stable populations under seasonal grazing into declining ones, with λ dropping to 0·963 [0·954, 0·982] and 0·949 [0·949, 0·950] in the first and second census periods, respectively. Thus, to maintain viable *C. intermedia* populations, grazing intensity should be controlled to a level that does not threaten the survival of adults. Adult survival is easy to assess, and monitoring the proportion of dead plants would be a good indicator of the sustainability of grazing regimes.

Arid inland dunes, in which the precipitation fluctuates between years in an unpredictable way, impose a great challenge on population maintenance of dune plants. Therefore, species that are able to survive in dry dune environments and retain stable population growth under fluctuating annual rainfall conditions should be preferred for sustainable grazing in inland dune areas. Our first demographic study on *C. intermedia* under a recently implemented seasonal grazing policy at one site over two census periods suggests that this particular species is rather resilient to the current grazing regime and can sustain viable populations in years with both normal and reduced rainfall. Future studies that are replicated in space and conducted over longer periods of time are necessary for providing firm recommendation for grazing policies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Analysis of Life Table Response Experiment.