

## Article

# Sexual Reproduction Is Not Responsible for *Caragana* Shrub Encroachment in Grasslands

Lina Xie <sup>1</sup>, Yuchen Li <sup>2</sup>, Mingyan Lin <sup>1</sup>, Hongyu Guo <sup>1</sup> , Yue Wang <sup>1</sup>, Lihong Wang <sup>1</sup> and Chengcang Ma <sup>1,\*</sup> 

<sup>1</sup> Tianjin Key Laboratory of Animal and Plant Resistance, College of Life Sciences, Tianjin Normal University, Tianjin 300387, China; xielina1989@163.com (L.X.); mia200001@163.com (M.L.); hongyuguo88@163.com (H.G.); wangyue5182023@163.com (Y.W.); wanglihong5182023@163.com (L.W.)

<sup>2</sup> College of Life Sciences, Nankai University, Tianjin 300071, China; 2120211142@mail.nankai.edu.cn

\* Correspondence: machengcang@163.com

**Abstract:** Shrubs tended to increase their abundance as climatic aridity and grazing intensity increased in the Inner Mongolian grassland. Increasing shrub abundance was believed to be due to enhanced reproduction. However, the effects of climatic aridity and grazing on the sexual reproduction of shrubs in grassland remain largely unclear. In this study, we conducted field experiments with *Caragana microphylla* to examine the variation of sexual reproduction aspects (seed production, seed vigor, and sapling establishment) along a climatic aridity gradient (subhumid, semiarid, arid, and dry arid zones) and a grazing intensity gradient (fenced, mildly grazed, and severely grazed). We then quantified the population growth rate based on seed production and sapling establishment rates. Our objective was to evaluate whether sexual reproduction is the main mechanism for *Caragana* encroachment into grasslands. We found that climatic aridity decreased seed quantity and seed vigor but increased the sapling establishment rate of *Caragana* shrubs. Under ungrazed conditions, climatic aridity did not affect population growth rates, while under grazing conditions, increased aridity stresses reduced population growth rates. Grazing reduced seed production, sapling establishment, and population growth rates. Climatic aridity enhanced the negative effects of grazing on sexual reproduction, while grazing intensified the negative effects of aridity on the population growth of *Caragana* shrubs. In conclusion, climatic aridity, grazing, and their combined effects had negative effects on the sexual reproduction of *Caragana* shrubs. Therefore, sexual reproduction could not fully explain the increased abundance of shrubs with increasing aridity and grazing. Clonal reproduction might be of considerable importance for understanding the mechanism of shrub encroachment in grasslands.

**Keywords:** shrub encroachment; population growth; sexual reproduction; grazing; climatic aridity gradient



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## 1. Introduction

Woody encroachment is occurring in grasslands worldwide [1]. Alterations in the density of woody plants have been mainly attributed to environmental factors and the characteristics of encroaching shrubs. It is suggested that long-term overgrazing and climatic aridity led to grassland vegetation degradation with reductions in species richness, abundance, and cover, resulting in reductions in fire frequency and heterogeneous distributions of vegetation and soil resources, as well as land desertification. These conditions would favor woody plants over grasses [2–4]. It is also suggested that strong grazing resistance [2] and drought adaptability [5–8] of shrubs can confer on their adult plants a survival advantage under constant overgrazing and intensive climatic aridity. All of these characteristics are likely to alter the competition between grass and woody plants under biotic and abiotic stress. Generally, increasing shrub abundance was believed to be due to increased reproduction. So far, the role of reproduction in shrub encroachment is still unclear.

*Caragana* shrubs are the dominant native perennial woody plants in the Inner Mongolian grassland ecosystem. This region has a strong aridity gradient from the northeast to the southwest, along which their climatic aridity conditions range from subhumid, semi-arid, arid, dry arid, and intensively arid. Livestock grazing is the most important and pervasive anthropogenic disturbance in grasslands. Our previous studies documented that shrub encroachment by *Caragana* in the Inner Mongolian grassland had two characteristics [6,9]. First, *Caragana* shrubs tended to increase their encroachment as climatic aridity increased. Second, shrub encroachment became more serious as grazing intensity increased as well. Given that such a direct increase in abundance is attributed to an increase in reproduction, we hypothesized that climatic aridity and grazing would promote *Caragana* shrub reproduction, which would be responsible for the current shrub encroachment in the Inner Mongolian grassland.

There are few grasslands on earth with natural aridity gradients, so very few studies have been conducted to examine how the sexual reproduction of grassland plants varies across aridity gradients. Studies have shown that seed yield [10] and seed vigor [11–13] of herbaceous plants in grasslands decreased with increasing aridity. However, studies also showed that seed production was significantly greater in a semi-arid environment than in a comparable Mediterranean environment [14], and there were no clear trends in seed or pod-related traits along the aridity gradient from arid to humid zones [15]. Similarly, drought also affected seedling establishment and population growth rates. For example, drought severely limited tree regeneration, increased population mortality rates [16–18], and decreased seedling survival rates [19]. Other studies found that seed germination and seedling recruitment of grass were not strongly impacted by an increasing water deficit in the Patagonian steppe [20]. However, how seed production, sapling recruitment, and population growth of shrub species vary along a climatic aridity gradient remain largely unknown.

Contrary to climatic aridity effects, many studies offered insights into the effect of grazing on the sexual reproduction of grassland plants. First, grazing influences seed production for different plant species in grasslands in different ways. For example, grazing decreased seed production of *Atriplex vesicaria* [21], *Ruellia humilis* and *Amorpha canescens* [22], *Stipa grandis*, *Agropyron cristatum*, and *Cleistogenes squarrosa* [23], and decreased flower and fruit numbers of *Agrostis vinealis* and *Ranunculus bulbosussome* [24]. Whereas the reverse was also true for some unpalatable plant species, such as *Agrostis capillaris*, *Dianthus deltoides* [24], and *Ligularia narynensis* [25]. While grazing did not affect the reproduction of *Festuca gracillima* [26] and *Artemisia tridentata* [27]. Second, grazing directly affected the seedling establishment process. For example, grazing had a negative effect on plant recruitment and population growth [28–31] by decreasing seedling survival rate and increasing seedling mortality rate, thereby decreasing seedling number [32–35]. However, other studies found that grazing facilitated seedling establishment, especially for legume plants and non-grass herbs that are unpalatable [36,37]; moderate grazing increased the number of newborn seedlings [38], and the number of sexual offspring increased with increasing grazing intensity in grasslands [39,40]. Moreover, in a few cases, grazing did not affect seedling establishment in herbaceous and shrub species [41,42]. Given the above divergent observations, an improved understanding of how the sexual reproduction of shrubs varies along the grazing gradient would help predict the pattern of shrub encroachment.

Moreover, the joint effects of climatic aridity and grazing stress on population growth have rarely been addressed [43–45], even though these two stressors commonly co-occur in natural ecosystems and play important roles in shaping plant communities. Consequently, empirical studies are necessary to test their joint effects on the population growth of shrubs, which would advance our understanding of shrub encroachment into grasslands.

In this study, we conducted field experiments to test the sexual reproduction (seed production, seed vigor, and sapling establishment) of *Caragana microphylla* along a climatic aridity gradient (subhumid, semiarid, arid, and dry arid zones) and a grazing intensity gradient (fenced, mildly grazed, and severely grazed) in the Inner Mongolian grassland.

We then quantified population growth based on seed production and sapling establishment rates. Our objective was to evaluate whether sexual reproduction is the main factor in *Caragana* shrub encroachment into grasslands.

## 2. Study Area and Methods

### 2.1. Study Area and Grazing Treatment

We conducted the field experiment at four study sites in the Inner Mongolian Steppe in northern China. The study sites were distributed in a wide range of aridity gradients, including (1) the Xiwu site in the subhumid zone; (2) the Abaga site in the semiarid zone; (3) the Suniteyou site in the arid zone; and (4) the Siziwang site in the dry arid zone (Table 1). The mean annual precipitation (MAP) and mean annual temperature (MAT) of this region ranged from 210 mm to 354 mm and from 1.87 °C to 3.60 °C, respectively (Table 1). We obtained the MAP and MAT data from the ERA5-Land dataset (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land-monthly-means?tab=overview>; accessed on 7 January 2023). The aridity level of each site was quantified as the Aridity Index (AI) = MAP/(10 + MAT), where a higher AI value indicates that a site is more mesic (less arid). The vegetation of the study sites is dominated by the shrub species *C. microphylla*.

**Table 1.** Location and environmental data of the study sites.

Site	Longitude (°E)	Latitude (°N)	Altitude (m)	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)	Aridity Index	Aridity Type
Xiwu	117°38'53"	44°36'50"	1024	354	2.42	28.51	Subhumid
Abaga	114°58'02"	44°04'00"	1126	245	1.87	20.64	Semi-arid
Suniteyou	112°56'39"	42°21'00"	1144	220	3.09	16.81	Arid
Siziwang	111°53'22"	41°47'28"	1492	210	3.60	15.44	Dry arid

We established three levels of grazing treatment within each site: fenced (F), mild grazing (MG), and severe grazing (SG). The grazing intensities were as follows: (1) 1.2 sheep/ha (MG), 2.5 sheep/ha (SG) at the Xiwu site; (2) 1.1 sheep/ha (MG), 2.2 sheep/ha (SG) at the Abaga and Suniteyou sites; (3) 1.0 sheep/ha (MG), 2.0 sheep/ha (SG) at the Siziwang site. Since vegetation cover decreases gradually with the increase in climatic aridity stress from the subhumid zone to the dry arid zone, the grazing intensity at each site was set according to the local vegetation condition for logistical reasons. The four study sites were all under long-term grazing treatments (over 14 years). Considering interannual climate variation, the experiments were conducted twice (seed production in 2017 and 2018; sapling establishment in 2018–2019 and 2019–2020).

### 2.2. Seed Production Experiment

In each grazing treatment, we established four subplots (the area of each subplot was more than 1 ha). During the pod ripening seasons in July–August 2017 and 2018, we first randomly chose 10 shrubs within each subplot. Then we collected three branches from each shrub, counted the number of mature pods and seeds on branches, and calculated the number of seeds/dry biomass (g) after drying the branches at 80 °C for 72 h.

### 2.3. Seed Vigor Experiment

In July–August 2017 and 2018, a large number of seeds were collected from each subplot, air dried, and stored at 4 °C. Then we conducted a seed germination experiment in November of the same year. 100 randomly selected seeds from each subplot were surface sterilized with a 1% NaClO solution for 10 min, followed by rinsing with distilled water several times. Sterilized seeds were placed in an incubator with 12 h light and 12 h dark cycles and a temperature of 25 °C under light conditions/15 °C under dark conditions. A seed with a germ length of 1 mm was defined as a germinated seed. We recorded

the number of germinated seeds per day during the germination test until there was no seed germination for 5 consecutive days. Then, we calculated the seed germination index  $GI = \sum Gt/Dt$ , where  $Gt$  is the number of germinated seeds on day  $t$  and  $Dt$  is the time corresponding to  $Gt$  in days.

#### 2.4. Sapling Establishment Experiment

The field-sowing experiments were conducted during 2018–2019 and 2019–2020, respectively. At the beginning of the growing season in 2018 and 2019, we established a transect of 100 m in each subplot and placed  $1 \times 1 \text{ m}^2$  quadrats at intervals of 10 m along each transect (in total, 10 quadrats per subplot). We sowed 100 *C. microphylla* seeds in each quadrat. The seeds sown at each site were collected from the same site the previous year. At the end of the growing season in the next year (18 months after sowing), we recorded the sapling number in each quadrat and then calculated the sapling establishment rate for each quadrat using the formula: sapling establishment rate = sapling number/100.

#### 2.5. Population Growth Rate

We quantified the population growth rate by sexual recruitment using the formula: population growth rate = seed number (seed/g dry biomass)  $\times$  sapling establishment rate (sapling/seed).

#### 2.6. Statistical Analysis

We performed data analyses using GLMMs, with sampling shrubs within subplots and subplots within grazing treatments as random variables (sampling shrubs ( $n = 20$ ) were nested in each subplot; subplots ( $n = 4$ ) were nested in each grazing treatment) in order to examine the differences in seed production among climatic aridity zones and grazing intensities. We performed ANOVAs to analyze the differences in means of germination index and population growth rate among climatic aridity zones and grazing intensities. We used Tukey HSD post-hoc tests to identify the differences among individual treatments. We also performed GLMMs with quadrats within subplots and subplots within grazing treatments as random variables (sampling quadrats ( $n = 20$ ) were nested in each subplot, and subplots ( $n = 4$ ) were nested in each grazing treatment) in order to examine the differences in sapling establishment among climatic aridity zones and grazing intensities.

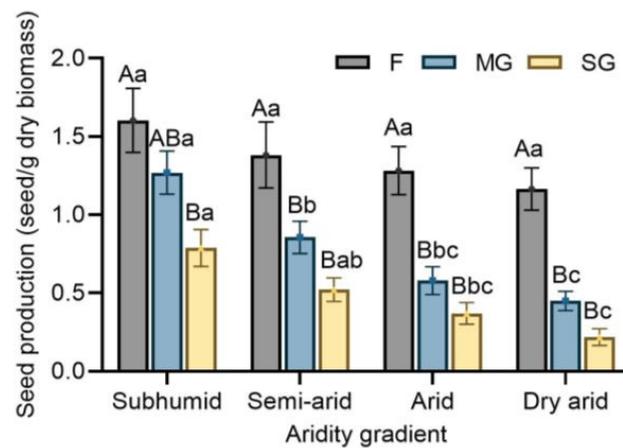
### 3. Results

#### 3.1. Effects of Climatic Aridity and Grazing on Seed Production

*C. microphylla* shrubs at the wettest end of the arid gradient produced more seeds, and seed production gradually decreased as climatic aridity increased ( $F_{3, 948} = 17.45$ ,  $p < 0.01$ ). There was a 64.6% decrease in seed production in the MG treatment across the aridity gradient, with the average seed production ranging from 1.27 seeds at the least arid site to 0.45 seeds at the most arid site. We also noticed that seed production in the F treatment did not change significantly along the aridity gradient (Figure 1).

We observed a similar trend along the grazing intensity, with a sharp decrease in seed production as grazing intensity increased ( $F_{2, 948} = 67.45$ ,  $p < 0.01$ ). In the dry arid zone, seed production in the MG and SG treatments was 61.2% and 81% less than that in the F treatment, respectively (Figure 1).

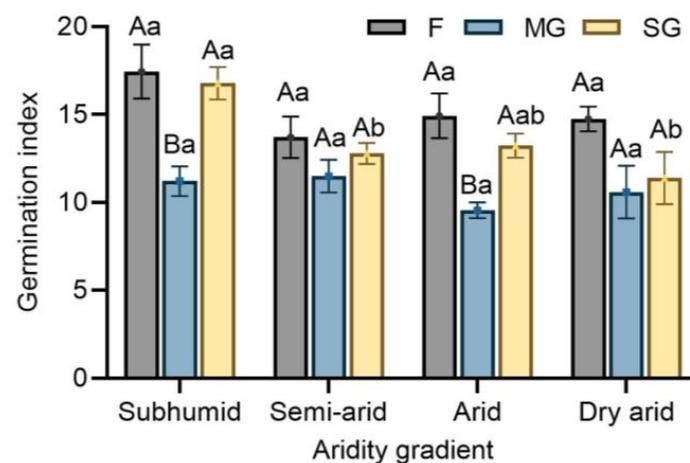
As climatic aridity stress increased, the negative effect of grazing on seed production gradually increased, although the interaction effect between climatic aridity and grazing was not significant ( $F_{6, 948} = 0.717$ ,  $p = 0.64$ ). Compared with the F treatment, seed production in the SG treatment decreased by 51% in the subhumid zone, 62% in the semiarid zone, 71% in the arid zone, and 81% in the dry arid zone, respectively (Figure 1).



**Figure 1.** Effects of climatic aridity and grazing on seed production of *Caragana microphylla*. Error bars indicate standard errors. F, fenced; MG, mild grazing; SG, severe grazing. For the same climatic aridity, different uppercase letters indicate significant differences between grazing intensities; and for the same grazing intensity, different lowercase letters indicate significant differences between climatic aridity zones.

### 3.2. Effects of Climatic Aridity and Grazing on Seed Vigor

Seed germination indexes of *C. microphylla* showed a decreasing trend as climatic aridity stress increased ( $F_{3, 84} = 4.70, p < 0.01$ ), ranging from 17.5 in the subhumid zone to 14.8 in the dry arid zone in the fenced plots (Figure 2). Grazing had a significant effect on the seed germination index of *C. microphylla* ( $F_{2, 84} = 18.01, p < 0.01$ ), with the highest value in the F treatment and the lowest value in the MG treatment. Germination indexes in the arid zone were 63.0% lower in the MG treatment and 11.4% lower in the SG treatment, compared with those in the F treatment (Figure 2). The interaction between climatic aridity and grazing had no significant effects on the seed germination index of *C. microphylla* ( $F_{6, 84} = 1.37, p = 0.24$ ; Figure 2).

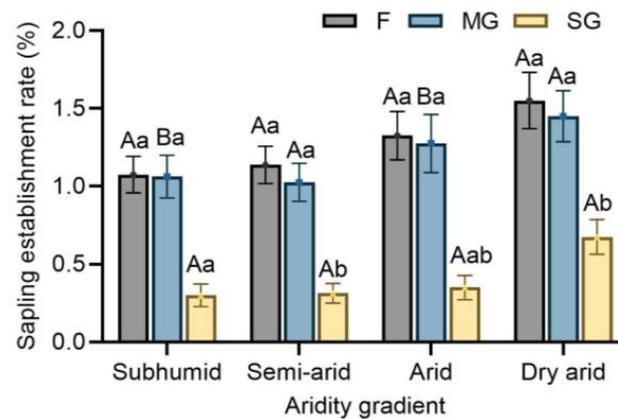


**Figure 2.** Effects of climatic aridity and grazing on seed germination index of *Caragana microphylla*. Error bars indicate standard errors. F, fenced; MG, mild grazing; SG, severe grazing. For the same climatic aridity, different uppercase letters indicate significant differences between grazing intensities; and for the same grazing intensity, different lowercase letters indicate significant differences between climatic aridity zones.

### 3.3. Effects of Climatic Aridity and Grazing on Sapling Establishment

The increase in the sapling establishment rate of *C. microphylla* was found from the subhumid zone to the dry arid zone ( $F_{3, 948} = 6.66, p < 0.01$ ). In the fenced plots, the sapling establishment rates in the semi-arid, arid, and dry arid zones were 5.3%, 18.8%, and 30.3%

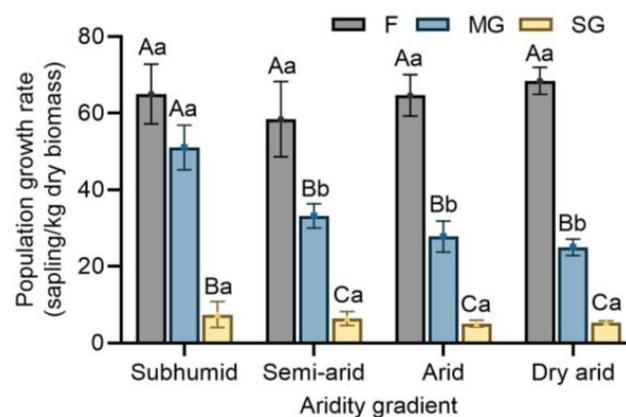
higher than those in the subhumid zone, respectively (Figure 3). Sapling establishment rate decreased as grazing intensity increased ( $F_{2, 948} = 55.28, p < 0.01$ ), and as a result, this rate was 56.5–73.6% lower in the SG treatment than that in the F treatment (Figure 3). The interaction between climatic aridity and grazing had no significant effect on the sapling establishment rate of *C. microphylla* ( $F_{6, 948} = 0.18, p = 0.98$ ; Figure 3).



**Figure 3.** Effects of climatic aridity and grazing on sapling establishment rate of *Caragana microphylla*. Error bars indicate standard errors. F, fenced; MG, mild grazing; SG, severe grazing. For the same climatic aridity, different uppercase letters indicate significant differences between grazing intensities; and for the same grazing intensity, different lowercase letters indicate significant differences between climatic aridity zones.

### 3.4. Effects of Climatic Aridity and Grazing on Population Growth

The population growth rate of *C. microphylla* in the F treatment did not change significantly along the aridity gradient, whereas there was a strong decreasing trend of population growth rate in the MG treatment with increasing aridity. The population growth rate in the MG treatment was 50.1 saplings in the subhumid zone, 33.2 saplings in the semi-arid zone, 27.8 saplings in the arid zone, and 25.0 saplings in the dry arid zone, respectively. Thus, there was a significant interaction between climatic aridity and grazing, as grazing intensified the negative effect of climate aridity on the population growth rate of *C. microphylla* ( $F_{6, 84} = 2.19, p = 0.05$ ; Figure 4).



**Figure 4.** Effects of climatic aridity and grazing on population growth rate of *Caragana microphylla*. Error bars indicate standard errors. F, fenced; MG, mild grazing; SG, severe grazing. For the same climatic aridity, different uppercase letters indicate significant differences between grazing intensities; and for the same grazing intensity, different lowercase letters indicate significant differences between climatic aridity zones.

There was a sharp decrease in the population growth rate of *C. microphylla* as grazing intensity increased ( $F_{2,84} = 145.12, p < 0.01$ ). In the semi-arid zone, the population growth rate was 43.2% and 89.1% less in the MG and SG treatments than that in the F treatment (Figure 4).

## 4. Discussion

### 4.1. Effect of Climatic Aridity on Sexual Reproduction

Seed production of *C. microphylla* decreased across all four aridity levels. Patterns for seed production were consistent with those of some herbaceous plants and desert shrubs, in which plant populations from the most arid locations produced fewer seeds [46–49]. This was likely due to a reduced capacity to take up nutrients under aridity stresses [50], which would lead to a decrease in biomass allocation to sexual reproduction and thus decrease the fecundity of shrubs. In addition, aridity stress may cause the abortion of flowers and early fruit drops [51], which may account for hindering the seed development process. These results were contrary to patterns found for *C. stenophylla*, another shrub species of the same *Caragana* genus, whose seed number gradually increased from the semi-arid zone to the very arid zone [44].

The seed vigor of *C. microphylla* decreased with increasing aridity. Reduced seed vigor under the most arid conditions was also reported for herbs [11–13]. These may also be due to nutrient shortages caused by water deficit stress, which were not able to allow the production of more vigorous seeds [13,52]. This suggests that aridity could act as a selective pressure, unfavoring seed vigor. However, some other studies on seed germination showed that there were no significant differences in seed vigor for seeds from different arid zones [45].

Many studies have shown that aridity reduces seedling establishment in herbs [16–18] and shrubs [19,45]. In our study, the sapling establishment rate of *C. microphylla* increased from the subhumid zone to the dry arid zone. Such a response might enable *C. microphylla* to be more adaptive to arid conditions at seed germination and the seedling stage. This could be one of the important factors facilitating shrub encroachment into grasslands.

Under ungrazed conditions, the seed production and population growth rate of *C. microphylla* did not change significantly along the aridity gradient. This was probably due to the stronger drought adaptability of *Caragana* shrubs [6–8]. Moreover, *Caragana* shrubs are leguminous with nitrogen-fixing capability. In general, nitrogen-fixing plants would have higher water use efficiency and a stronger competitive advantage in more arid environments [53,54], which might enable them to survive, grow, and develop during prolonged periods of drought. In addition, leguminous plants tend to have higher levels of nitrogen-fixing capability in more arid areas (Armstrong 2019; Doctoral dissertation, San Jose State University), which would greatly increase soil nitrogen content in these areas [55]. Such increased soil nutrition conditions would also offset the negative effects of aridity stress on the sexual reproduction of *Caragana* shrubs. In contrast, under grazing conditions, increasing aridity stress resulted in a greater reduction in the population growth rate. This suggests that the strong drought tolerance of *C. microphylla* is insufficient for maintaining a relatively high population growth rate under hyper aridity conditions.

No consensus has been reached on whether sexual reproduction is the main factor in shrub encroachment into grasslands. The results of our study suggested that this is indeed possible. For example, we showed that shrub sapling establishment increased as climatic aridity stress increased. However, our study found no evidence that sexual reproduction could fully explain the phenomenon of a higher abundance of shrubs with increasing aridity. This could be attributed to the reduction in seed production along the aridity gradient, which led to no increase (under ungrazed conditions) and even a substantial decrease (under grazing conditions) in population growth rate with increasing aridity.

#### 4.2. Effect of Grazing Intensity on Sexual Reproduction

Studies suggest that grazing has negative effects on seed production [56–59], sapling establishment [32–35], sexual recruitment [33,60,61], and thus population growth [28–31,62,63] of grassland plants. Indeed, our experiment showed that seed production and sapling establishment of *C. microphylla* were greatly reduced with the increase in grazing intensity, which reduced the population growth of this shrub plant. This could be explained by three potential mechanisms. First, many of the young shoots and leaves are prone to being consumed by livestock in grasslands under long-term grazing, potentially leading to reduced fertility in *Caragana* shrubs. There were studies on other plant species in arid steppes showing that grazing strongly reduced spike biomass, biomass allocation for sexual reproduction [64,65], and pollination efficiency [66]. The second potential mechanism is that livestock trampling could greatly increase soil compaction [67,68], resulting in reduced water retention and nutrient availability. The third potential mechanism could be that reproductive organs, flowers, fruits, seeds, and seedlings might be directly consumed by ungulates [67–69]. However, there were also some other studies showing that grazing did not affect fruit numbers [70] or even that grazing could promote seed production [25] and sapling establishment [36–38], indicating that grazing had no significant effect on population growth [33].

In our study, the seed vigor in the severe grazing plots was significantly higher than that in the mild grazing and fenced plots. This was probably because the increased grazing intensity significantly decreased the pod abundance of *C. microphylla* (Figure 1). *Caragana* has generally large and compact cushion-like canopies. Such shrub morphology could provide a shield for pods from herbivores, and thus only the pods hidden in shrub canopies could survive in the severe grazing plots, resulting in only a few mature *Caragana* pods. Specifically, the seed abundance in the severe grazing plots was 18.7–49.1% of that in the fenced plots. Thus, greater resources should be allocated to the survival seeds under severe grazing conditions, resulting in more vigorous seeds.

We found that *Caragana* population growth drastically decreased under long-term grazing, which did not support our hypothesis. Thus, sexual reproduction cannot fully explain the higher abundance of shrubs under increased grazing intensity. Whereas we noticed that the effect of grazing on *Caragana* shrubs would also vary with the duration of grazing. Under short-term grazing, livestock would mainly feed on palatable herbaceous plants rather than thorny *Caragana* shrubs, thereby reducing the competition intensity of herbaceous plants with shrubs, thus benefiting the growth and reproduction of *Caragana* shrubs [2,3], and facilitating shrub encroachment in grasslands. In contrast, under long-term grazing (as in the situation in this study), herbaceous plant populations would decline substantially, and livestock would mainly feed on less palatable *Caragana* shrubs, which would negatively affect the growth and reproduction of shrubs.

#### 4.3. Interactive Effects between Climatic Aridity and Grazing on Sexual Reproduction

Our results showed that as climatic aridity increased, the negative effects of grazing on seed production of *Caragana* shrubs gradually increased. Herbaceous plants predominate at more mesic sites. Under such conditions, herbivores naturally prefer to feed on grasses rather than *Caragana* shrubs. Thus, *Caragana* shrubs were not significantly affected by grazing. However, increasing aridity would increase the cover of woody plants, potentially leading to an increase in the ratio of woody to herbaceous cover. Under such conditions, herbivores switched from a preference for grasses to a diet based mainly on *Caragana* plants [45]. Consequently, grazing has the strongest negative effects on the seed production of *Caragana* shrubs in the dry arid zone. These results suggested that grassland ecosystems would become more sensitive to grazing disturbance as aridity stress increased from the subhumid zone to the dry arid zone.

We also found that grazing intensified the negative effect of climatic aridity on the population growth rate of *Caragana*. This was probably due to the fact that young shoots,

leaves, flowers, pods, seeds, and saplings of shrubs are likely consumed more by livestock under drier conditions.

Overall, our study demonstrated that the joint effect of climatic aridity and grazing stress greatly suppressed the sexual population growth of *Caragana* shrubs, suggesting that these two stress factors did not promote shrub encroachment through sexual reproduction. Thus, shrub encroachment may not be realized through sexual reproduction. Other forms of reproduction, such as clonal reproduction, may deserve further investigation for a better understanding of the mechanisms underlying shrub encroachment in grasslands.

## 5. Conclusions

Climatic aridity decreased seed quantity and seed vigor of *Caragana* shrubs, increased the sapling establishment rate, and reduced the population growth rate at the grazing sites, but did not affect the population growth rate at the ungrazed sites. Long-term grazing reduced seed production, sapling establishment, and population growth rates. Climatic aridity stress enhanced the negative effects of grazing on the sexual reproduction of *Caragana* shrubs while grazing intensified the negative effect of climatic aridity on the population growth rate of *Caragana* shrubs. Climatic aridity, grazing, and their combined effects had a negative influence on the sexual reproduction of *Caragana* shrubs. Sexual reproduction could not fully explain the increased abundance of *Caragana* shrubs with increasing aridity and grazing intensity. Clonal reproduction may be of considerable importance for understanding the mechanism of shrub encroachment in grasslands.

**Author Contributions:** Conceptualization, L.X. and C.M.; methodology, L.X.; formal analysis, Y.L. and M.L.; investigation, L.X., Y.L., Y.W. and L.W.; data curation, L.X.; writing—original draft preparation, L.X., H.G. and C.M.; writing—review and editing, H.G. and C.M.; visualization, L.X. and C.M. All authors have read and agreed to the published version of the manuscript.

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