

## Article

# Sandy Habitats Play an Important Role in Shrub Encroachment in Grasslands

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**Abstract:** Shrub species have increased in density and cover in desertification areas, however, the role of sandy habitats in contributing to the expansion of shrubs is poorly understood. Although the effect of sandy habitats on plant growth and reproduction have been demonstrated, most existing studies lack either experimental demonstration or an integrated study during the whole shrub life cycle. We performed field and laboratory experiments to examine the responses of four stages in the life cycle of shrubs (seed germination, plant growth, seed reproduction, clonal reproduction) to sandy habitats (including sand substrate, sand burial and wind erosion) for *Caragana* shrubs. Results showed that both sand substrate and sand burial facilitated seed germination, seedling biomass, sapling establishment, plant growth, and root-shoot ratio of *Caragana*. Meanwhile, they both strongly increased seed number and seed preservation, and thus enhanced sexual reproduction. Sand burial favored clonal reproduction of *Caragana* by promoting the formation of branch-derived ramets, while wind erosion benefited clonal reproduction by facilitating the formation of root-derived ramets. These results suggested that sandy habitats facilitated seed germination, plant growth, sexual reproduction, and clonal reproduction of *Caragana*, which could explain why shrub abundance, shrub area and shrub height of *Caragana* in sandy areas was higher than in grasslands. Our study provided an experimental demonstration that sandy habitats promoted the population growth of *Caragana* shrubs during the whole life cycle and highlighted the significant role of sandy habitats in facilitating shrub encroachment in grasslands.

**Keywords:** sand burial; wind erosion; sand substrate; clonal reproduction; sexual reproduction; *Caragana* species



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## 1. Introduction

Desertification, resulting from climatic changes (such as elevated levels of CO<sub>2</sub> and parallel increase in temperature) and human activities (such as overgrazing), is considered as one of the most critical ecological and environmental issues in grasslands worldwide [1,2]. Arid and semi-arid regions of northern China, characterized by low precipitation, loose soil structure and frequent strong winds, are especially vulnerable to desertification. The local herbaceous species are easily degraded under certain extreme conditions (e.g., drought, burial and erosion). However, such harsh sandy conditions favored the growth of the woody plants, most of which are psammophytes shrubs, due to their high windbreak and sand-fixation capacities [3]. Therefore, a large and rapidly increasing number of shrub plants encroach into grasslands, resulting in thicket grasslands with shrub patches [4,5]. A large number of studies have focused on the causes and consequences of shrub encroachment into grasslands [2], and some attention has also been paid to how shrubs adapt to the harsh conditions [6,7]. However, the contribution of sandy habitats in the process of shrub encroachment is poorly understood.

The relative proportions of sand, silt and clay particles, also known as soil texture, has a major role in influencing plants' growth [8]. Usually, a sandy soil substrate is specialized

by a lower nutrient content and water retention capacity, but have a large overall volume of pore spaces and high permeability. Therefore, plants growing in sandy soil will allow their roots to extend more easily [9] and increase seed germination [10], but will reduce the cover and biomass of both shrubs and herbaceous species [11], and constrain the distribution of plants species [12]. Additionally, soils with high sand content would alter the relationship between mycorrhizal fungi and plants, thereby influencing plant biomass production in grasslands [13].

Sand burial and wind erosion are strong stresses for plants in sandy habitats. Previous studies have reported that sand burial or wind erosion affected the critical stages of plant life cycle. For example, sand burial affected seed germination [7,14–17], plant growth [18–20], clonal reproduction [21–23], and sexual reproduction [24], thus influencing community cover in sandy habitats [25]. Wind erosion also influenced seedling survival, plant growth [26,27], ramet numbers, survival rate and biomass [6,22,28], thereby influencing total community cover and ecosystem productivity [29].

Thus far, some studies have examined the effects of sandy habitats on plant growth and reproduction based on field observations [11,18–24]. However, such effects have never been examined by factor control experiments (except for seed germination) with psammophyte shrubs that commonly colonize and stabilize sandy land habitats. Moreover, studies assessing the effects of sandy habitats on shrub encroachment at population level, during the whole life cycle, are scarce.

Here, we conducted field and laboratory experiments to examine the response of four stages in the life cycle: seed germination, plant growth (plant height, plant biomass and root-shoot ratio), seed reproduction (reproduction effort and seed preservation), and clonal reproduction, in sandy habitats (including sand substrate, sand burial and wind erosion) for *Caragana* shrubs, which are the pioneer plants occurring naturally in the harsh, sandy conditions with frequent sand burial and wind erosion. It is the common observation that *Caragana* encroached into grassland in Inner Mongolia [4,5]. Previous studies have suggested that the causes of *Caragana* encroachment into grassland might be a result of their tolerance to drought and grazing [4,5]. However, limited empirical evidence exists on the role of sandy habitats in this ecological process. Therefore, the objective of this study was to examine the effects of sandy habitats on population growth of shrubs from the whole life cycle perspective, using *Caragana* as the model shrub, and to evaluate the role of sandy habitats in the process of shrub encroachment.

## 2. Materials and Methods

### 2.1. Study Species and Study Site

*Caragana* (Fabaceae) are xeromorphic, winter-deciduous shrubs with a high capability of trapping sand. They are widely distributed in sandy lands or in grasslands with high sand content. Therefore, *Caragana* shrubs are an ideal model for studying the value of sand context to the population growth of shrubs. There are 16 *Caragana* species distributed in the Inner Mongolia Steppe; *C. stenophylla* Pojark is one of the most important species due to its widespread distribution, forage value, and other ecological functions in the region [30]. *C. stenophylla* realizes population recruitment by both sexual and clonal reproduction. The clonal reproduction of *C. stenophylla* includes branch-derived and root-derived clonal reproduction. The branch-derived clonal reproduction produces adventitious roots from branches, forming new ramets. The root-derived clonal reproduction produces horizontal roots (spacers) from taproots of the mother plant or adult ramets; at the end or the middle of the horizontal roots, vertical roots grow deeper, and adventitious buds grow towards the soil surface, forming new ramets [31,32].

The Alxa region (37°24'~42°47' N, 97°10'~106°52' E; altitude ~1550 m; area ~270,000 km<sup>2</sup>) in Inner Mongolia, China, is a hyper-arid area. The whole Alxa region is enclosed by the Helan Mountains to the east, the Qilian Mountains to the south, and the north-eastern part of the Tibetan Plateau to the south-west. The region has three deserts: the Tengger (Tengri) Desert in the south, the Badain Jaran (Baden Dzareng or Batan Tsalang) in the west, and

the Ulan Buh (Wulanbuhe) in the northeast. We conducted the field study in the Alashan Left Banner, which is located in the northeast of the Tengger Desert (38°19' N, 105°41' E). In the study area, the mean annual precipitation is 110 mm; the mean annual temperature is 7.8 °C; the mean annual total sunshine time is 3200 h, with a mean daily solar radiation intensity of 1.71 kJ cm<sup>-2</sup> d<sup>-1</sup>. Driven by wind, sand burial with little vegetation cover (<20%) is dominated by xerophytic shrubs, such as the *Caragana* shrub species, accounting for ~60% of the total plant biomass.

### 2.2. *Caragana* Population Survey in Grassland and Sandy Land

In July 2019, we conducted a *Caragana* survey in two distinct microhabitats (sandy land and grassland). Here, we define “sandy land” as land covered by a sandy soil, with a vegetation cover of less than 5%, which includes areas of sandy desert [33]. Three plots were established on each of the two microhabitats. Each plot contained a 50 m × 50 m quadrat. For each quadrat, we first recorded the number of *C. stenophylla* shrubs in order to assess the shrub abundance (shrub/hectare). Then, we chose 10 shrubs at random, measured the length of the long axis and short axis of the shrub crown, the shrub height and nabkha height for each selected shrub, and calculated the shrub area (shrub area =  $\pi \times$  semi-long axis  $\times$  semi-short axis). Meanwhile, at the seed maturation stage, we cut three branches from each shrub, counted the number of seeds on branches, and calculated the reproductive effort (number of seeds/dry biomass (g)) after drying the branches at 60 °C for 72 h. Reproductive effort is traditionally defined as the proportion of total biomass allocation to seeds and other “obvious” reproductive structures [34].

### 2.3. Seed Preservation Experiment for Sand Burial Treatments

To assess the effect of sand burial on the preservation of the seeds, in July 2021, we performed seed preservation experiments in the three sandy land plots. In each plot, we established ten 50 cm × 50 cm quadrates, which were randomly assigned to two treatments: five quadrates for no sand burial treatment (seeds was totally exposed to the air, referred to “ground surface preservation” hereafter) and the other five quadrates for sand burial treatment (seeds was burial with 1 cm sandy soil, referred to “sand burial preservation” hereafter). We scattered 100 seeds, evenly, in each quadrate. We recorded the number of remaining seeds in each quadrate after 15 days.

### 2.4. Seed Germination Experiment for Burial Treatments

Washed, moist sand was placed in pots (10 cm deep × 20 cm diameter) with drainage holes on the bottom, to a depth of 3 cm; 100 *Caragana* seeds were placed in each of the pots and then assigned in the following treatments: buried by sand of 2 cm, 3 cm or 5 cm deep, or not buried (seeds lying on the sand surface). There were 5 replicates for each treatment. We conducted the germination trials in an incubator with 12 h light and dark cycles, and with temperature of 25 °C under light condition/15 °C under dark condition. Tap water was applied to keep the soil moist during the seed germination period. We recorded the number of seed germination after 30 days. All the seedlings were weighted after being oven-dried at 60 °C for 72 h. For the ungerminated seeds, we used 1% TTC stain to evaluate their vigor. If seeds showed viability but did not germinate, they were considered dormant seeds. If seeds showed no viability, they were considered dead seeds. We then calculated the seed germination rate and seed mortality rate.

### 2.5. Planting Experiment with Grassland Soil and Sandy Land Soil

Soils for this experiment were collected from the natural grassland (the soil is typical grey-brown desert soil, referred to hereafter as “grassland soil”) and the sandy land (referred to hereafter as “sandy soil”) in the field. After collection, soil was immediately sieved through a 5 mm mesh to remove stones and roots, thoroughly mixed, and brought back to the laboratory. A total of 15 plastic pots (17 cm diameter × 18 cm height) were used and divided into two treatments. Of these, 5 pots were randomly selected for the grass-

land soil treatment (G), and the remaining 10 pots were used for the sandy soil treatment (S). Each pot was filled with 3.5 kg of field soil and immediately watered with 100 mL Hoagland's solution; 50 *Caragana* seeds were sowed per pot at 2 cm burial depth. All pots were randomly kept in a greenhouse with a temperature regime of ~22 °C during daytime and ~18 °C during night and were watered regularly to keep the soil moist during the experiment. Forty-five days after sowing, we first calculated the sapling establishment rate (the number of saplings formed by 100 seeds). Then, we kept eight vigorous saplings in each pot and the others were removed. Five pots of S treatment were randomly selected for experimental sand burial treatment (SB) by artificially adding sand. Sand was added to each pot in the following 60 days with a total burial depth of 2 cm. The plant height, above and below ground biomass was measured 120 days after sowing, and the root-shoot ratio was calculated.

#### 2.6. Probability of Branches Forming Adventitious Roots under Buried or Not Buried Conditions

In August 2019, we selected 10 *Caragana* shrubs in each of the three plots in sandy land. For each selected shrub, we marked four branches, of which two branches were buried in sand from the base up to 2/3 of their heights, the other two was completely exposed to the air. In August 2020, we counted the number of branches forming adventitious roots, and calculated their percentage.

#### 2.7. The Number of Adventitious Buds on Horizontal Roots under Wind Eroded and Non-Wind Eroded Conditions

In August 2019, we selected five *Caragana* shrubs in each of the three plots in sandy land. For each selected shrub, we first carefully removed the sand dune and dug, 20 cm down from the surface, to expose the horizontal roots. Then, we chose two horizontal roots, one of which was buried in sand, and the other one was exposed to the air, with an exposure length of 100~120 cm. These selected roots were marked. In August 2020, we counted the number of adventitious buds on each horizontal root buried in sand and exposed to the air, respectively.

#### 2.8. Statistical Analyses

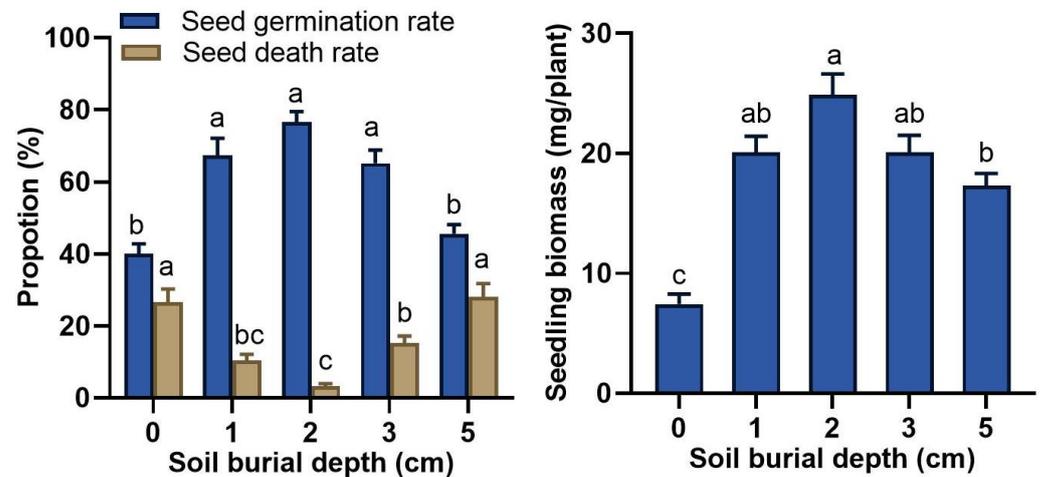
We performed one-way ANOVA to examine the differences in seed germination rate, seed death rate and seedling biomass among burial depth treatments. If ANOVA showed significant differences, post hoc tests (Tukey HSD) were performed to compare these indices among the burial depth treatments. We performed *t*-tests to examine the differences in reproduction effort between grassland and sandy land, the differences in seed preservation between sand burial and ground surface, the differences in sapling establish rate and plant growth between grassland soil and sandy land soil, the differences in plant growth between sandy land soil and sandy land soil + sand burial, the differences in percentage of branches forming adventitious roots between sand burial and control, the differences in ramet number on horizontal roots between wind erosion and control, and the differences in shrub abundance between grassland and sandy land. We performed analyses, using GLMMs, with sampling shrubs within plot and plots within landscape (grassland and sandy land) as random variables (sampling shrubs were nested in plot; plots were nested in landscape) in order to examine the differences in shrub height, shrub area and nabkha height between grassland and sandy land. All analyses were performed with SPSS 21.0 (IBM, Armonk, NY, USA) and the significant level was  $p < 0.05$ .

### 3. Results

#### 3.1. Effect of Sand Burial on Seed Germination

The burial depth significantly affected the seed germination rate ( $F_{4,20} = 20.46, p < 0.05$ ), seed death rate ( $F_{4,20} = 16.21, p < 0.05$ ) and seedling biomass ( $F_{4,20} = 24.68, p < 0.05$ ) of *Caragana*. With an increased burial depth, the seed germination rate and seedling biomass first increased and then decreased. They were both highest at the intermediate burial depth

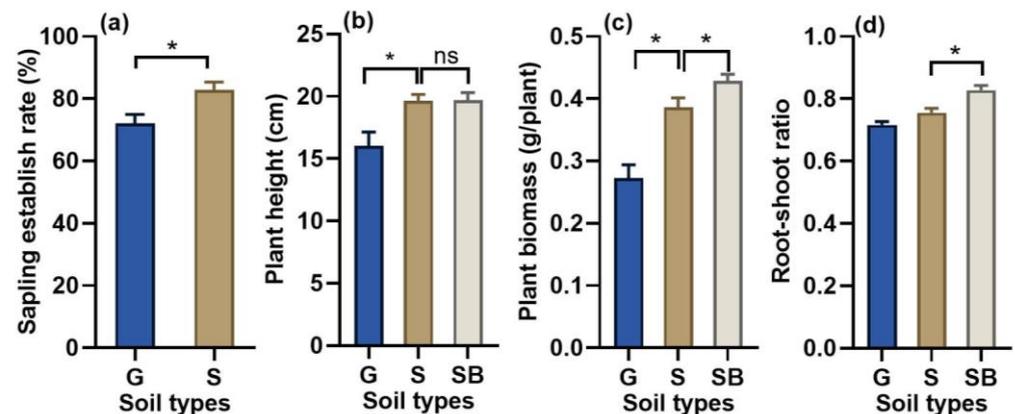
of 2 cm (Figure 1). In contrast to the seed germination rate and seedling biomass, the seed death rate first decreased and then increased with the increase of burial depth, and it was the lowest when burial depth was 2 cm (Figure 1).



**Figure 1.** Effect of burial depth on seed germination rate, seed death rate and seedling biomass of *Caragana stenophylla* (mean  $\pm$  SE). Different lowercase letters indicate significant differences among treatments,  $p < 0.05$ , Tukey HSD.

### 3.2. Effects of Sandy Soil on Sapling Establishment and Plant Growth

The sapling establish rate, plant height and biomass of *Caragana* was higher in sandy soil than in grassland soil (Figure 2a–c). Sand burial did not increase *Caragana* plant height, but significantly increased its biomass and root-shoot ratio (Figure 2b–d).

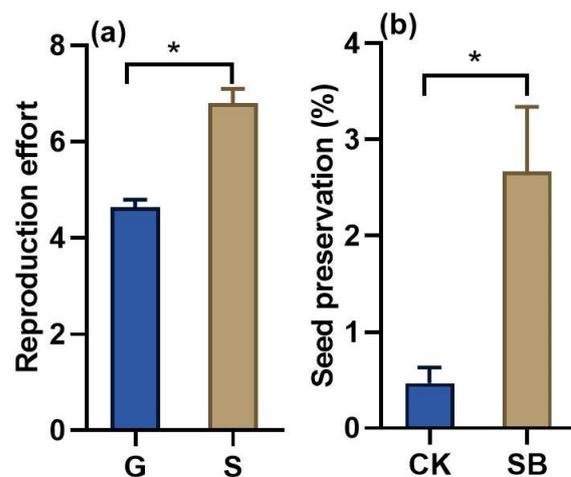


**Figure 2.** Effect of soil types on sapling establish rate (a), plant height (b), plant biomass (c) and root-shoot ratio (d) of *Caragana stenophylla* (mean  $\pm$  SE). G, grassland soil; S, sandy land soil; SB, sandy land + sand burial. \* indicate significant differences between G and S, and between S and SB,  $p < 0.05$ ,  $t$ -test. ns indicates not significant difference,  $p > 0.05$ ,  $t$ -test.

### 3.3. Effect of Sandy Habitats on Seed Production and Seed Preservation

The reproduction effort of *Caragana* increased in sandy land, as shown by the strongly increased biomass allocation to seeds. *Caragana* produced, on average, 4.63 seeds/g biomass in grassland, while 6.80 seeds/g biomass in sandy land (Figure 3a).

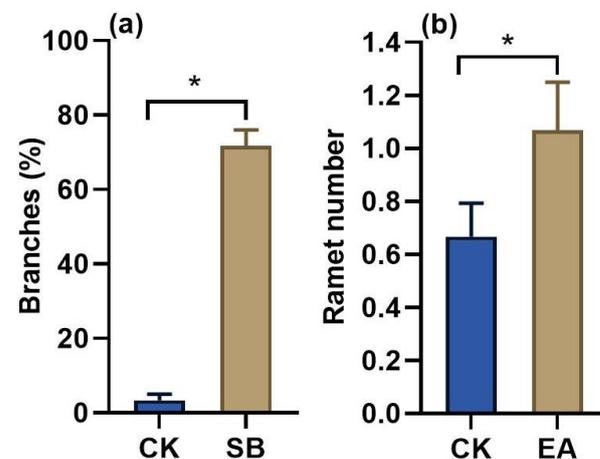
Sand burial significantly increased the seed preservation of *Caragana* (5.71 times higher than ground surface; Figure 3b). This indicated that sand habitat was beneficial to seed preservation in sandy land.



**Figure 3.** (a) Reproduction effort (seed/g biomass) of *Caragana stenophylla* in grassland and sandy land (mean ± SE). G, grassland; S, sandy land. \* indicate significant differences between grassland and sandy land,  $p < 0.05$ ,  $t$ -test. (b) Effect of sand burial on seed preservation of *Caragana stenophylla* (mean ± SE). CK, ground surface; SB, sand burial. \* indicate significant differences between sand burial and ground surface,  $p < 0.05$ ,  $t$ -test.

### 3.4. Effect of Sand Burial and Wind Erosion on Clonal Reproduction

Almost no adventitious roots were formed on the branches of *Caragana* under the control condition (no sand burial), and 70.0% of branches produced adventitious roots after soil burial, indicating that sand burial greatly facilitated branch-derived ramet formation (Figure 4a).



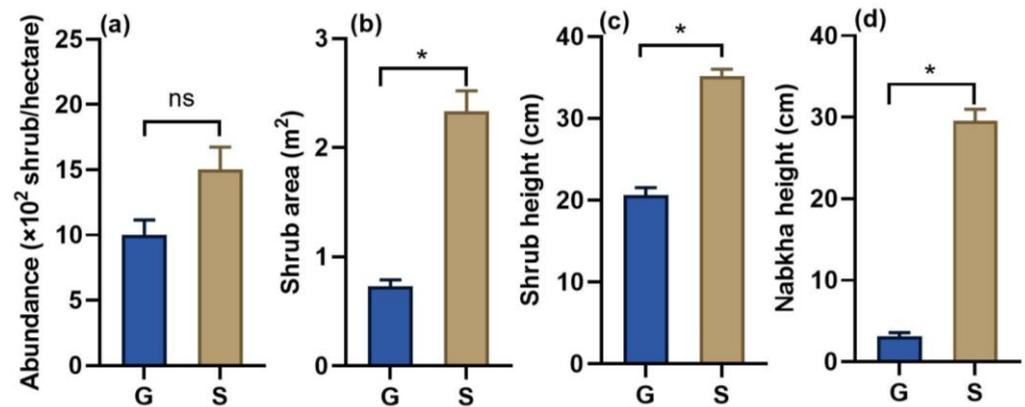
**Figure 4.** (a) Percentage of branches forming adventitious roots after *Caragana stenophylla* branches were sand buried (mean ± SE). CK, control; SB, sand burial. (b) Ramet establishment on the horizontal buried roots and the exposed roots for *Caragana stenophylla* (mean ± SE). CK, buried roots; EA, exposed roots. \* indicate significant differences between treatments,  $p < 0.05$ ,  $t$ -test.

*Caragana* produced more adventitious buds on horizontal exposed roots than buried roots. These results indicated that wind erosion could promote the ramet formation from root-derived clonal reproduction (Figure 4b).

### 3.5. Population Characteristics of *Caragana* in Grassland and Sandy Land

The *Caragana* population in grassland and sandy land had different quantity characteristics. The shrub abundance, area and height of *Caragana* in sandy land was higher than that in grassland (although marginally significant for shrub abundance;  $p = 0.07$ ; Figure 5a–c),

which indicates that sandy land enhances the population growth of *Caragana* in general. With an increasing shrub size and strong sand movement in sandy land, the nabkha height of *Caragana* in sandy land was 854% greater than that in grassland (Figure 5d).



**Figure 5.** Shrub abundance (a), shrub area (b), shrub height (c) and nabkha height (d) of *Caragana stenophylla* in grassland and sandy land (mean  $\pm$  SE). G, grassland; S, sandy land. \* indicate significant differences between grassland and sandy land,  $p < 0.05$ , ns indicates not significant difference,  $p > 0.05$ ,  $t$ -test or GLMMs.

#### 4. Discussion

##### 4.1. Sandy Habitats Facilitate Seed Germination and Seedling Growth of Shrubs

In the Alxa region, the wind is frequently strong and wind erosion occurs throughout the year. The bare land outside the shrub area is subjected to wind erosion, while the shrub area is frequently partially or completely buried by sand (Figure 5d). Some studies have shown that moderate burial improved seed germination, seedling survival and the growth of herbaceous plants, such as *Psammodochloa villosa* [35], *Leymus secalinus* [15], as well as of desert shrubs, such as *Nitraria sphaerocarpa* and *Haloxyylon ammodendron* [7], while others also found that seed germination of *Eremosparton songoricum* [14] and *Pinus thunbergii* [36] decreased after shallow partial burial treatment. We found that the seed germination and seedling biomass of *Caragana* reached the highest level at a sand burial depth of 1–2 cm. Similar results were observed for *Caragana korshinskii* [37]. Collectively, these results demonstrated that shallow sand burial stimulated germination and subsequent seedling recruitment. This is likely explained by the fact that sand burial could keep the seeds moist and stimulate seed germination. This led to higher shrub abundance in sandy habitats than in grassland habitats (Figure 5a).

##### 4.2. Sandy Habitats Facilitate Plant Growth of Shrubs

Soil texture changes the water, air, heat, and nutrition status of land, thereby affecting the growth and development of plants growing in the soil. Our results showed that sandy soil promoted the sapling establishment of *Caragana* (Figure 2a). Sladonja et al. (2014) [10] also found that the percentage of seedling of pyrethrum was positively related to sand content. This might be because the sandy soil substrate had good air permeability with loosely packed matrixes, which would be beneficial for seed respiration, seed germination, thus facilitating seedling emergence and root expansion.

Previous studies found that the relative proportions of sand had strong negative effects on plant performance in general [38]. For example, soils with a higher sand content reduced cover and biomass for both shrub and herbaceous species [11] and constrained the distribution of species [12]. In contrast, our study found that sandy substrates favored *Caragana* growth (Figure 2b,c), which could explain why the height and area of the *Caragana* shrub in the sandy land was larger than that in the grassland (Figure 5b,c). This indicates that *Caragana* possesses an inherent ability to respond to sandy soil, which is consistent with its role as a primary colonizer in dry areas with high sand content.

Following the successful establishment of saplings of *Caragana* in the sandy land, they will continue to be buried by wind-deposited sand (Figure 5d). The sand burial significantly facilitated sapling growth (Figure 2c), thus forming large shrubs (Figure 5b,c). Similar results were also reported that partial sand burial promoted biomass in *Hedysarum laeve* [39], *Ulmus pumila* [18], and *Agriophyllum squarrosum* [17], while others found that when whole or partial shoots were buried by sand, biomass production decreased [20,24,35]. Those results suggested that the responses of sapling growth to sand burial might be species-specific.

The allocation and utilization of resources is a fundamental and vital activity of plants. Our study found that sand burial increased the root growth and root-shoot ratio (Figure 2d), indicating that resource allocation to the root increased after burial. Such results were also shown in *Nitraria sphaerocarpa* [40]. In the hyper-arid region (such as Alax with annual precipitation of 110 mm), water is the major limiting factor affecting plant growth and development. *Caragana* that withstand sand burial could increase biomass allocation to roots, thus acquiring more water from dry sandy soil to support its growth. However, contrasting results have been reported for *Artemisia ordosica*, which showed more biomass investment in shoots under burial [26,41].

#### 4.3. Sandy Habitats Facilitate Seed Reproduction of Shrubs

The sexual reproductive efforts of *Caragana* in sandy land was higher than that in grassland (Figure 3a). Higher sexual reproductive efforts mean more seeds produced by *Caragana* in sandy land, thus forming more seedlings. This result was likely because sandy land enhanced the growth of *Caragana* (Figure 5b,c). The better the plant's growth, the stronger their fecundity capacity, and the more they invest in sexual reproductive organs, resulting in higher reproductive efforts in the sandy land.

In grassland, seed consumption by predators is very common, which immensely reduces seed quantity. Previous studies in the grassland of Loess Plateau showed that almost all *Caragana* seeds were eaten by seed predators within one week of the seeds falling on the ground [42]. However, in sandy land, shrubs can easily be buried by sand, thereby forming nabkhas of various sizes, from 20 to 40 cm in height, under shrub canopies due to wind-deposited sand (Figure 5d) [43]. In this case, *Caragana* seeds may fall under or next to shrub canopies where they were later buried at various depths in sand together with leaves of shrubs and other debris. Partial sand burial prevented seeds from predation and shielded dispersed seeds from wind, resulting in higher seed preservation (Figure 3b). Therefore, we hypothesized that sandy habitats facilitated the abundance of *Caragana* by improving seed preservation.

In summary, sandy soil substrate and sand burial are important environmental factors in sandy land, which increases seed number, seed preservation, seed germination, and subsequently improves sapling establishment and species fitness, and finally increases the individual numbers in population. This would explain why we found a higher abundance of *Caragana* in sandy land (Figure 5a). In addition, *Caragana*, cluster shrubs with a combined canopy, usually consists of many individuals of sexually reproduction [44]. An increase in sexual reproduction led to more individuals in each shrub cluster, resulting in an increase in shrub area (Figure 5b).

#### 4.4. Sandy Habitats Facilitate Clonal Reproduction of Shrubs

Most studies found that sand burial had negative effects on clonal reproduction (number of ramets) for *Spartina alterniflora* [24] and *Calligonum arborescens* [6,23]. However, our results showed that sand burial promoted clonal reproduction of *Caragana* by producing more adventitious roots on their branches (Figure 4a). Such adventitious roots would be capable of forming more branch-derived ramets, thereby leading to increase of shrub area (Figure 5b). The positive effect of sand burial on formation of adventitious roots was also found for *Artemisia* species [45].

Severe erosion had negative effects on the clonal reproduction of xylophyta, such as *Calligonum arborescens* [6,23] and *Calligonum mongolicum* [22]. In our study, the horizontal

roots, the reproductive organs of *Caragana*, could extend outward by more than 130 cm from the shrub [31]. Wind erosion exposed these horizontal roots to air, which promoted the formation of root-derived ramets (Figure 4b). Ramets close to the mother plant were interconnected with the mother plant to form larger shrubs (Figure 5b), while ramets away from the mother plant formed new shrubs that would increase the abundance of the *Caragana* population (Figure 5a). Our study suggested that spreading the horizontal roots may be an important adaptive strategy for shrub population persistence in sand habitats. Our results are contrary to Yu et al. (2008) [28], who showed that once rhizomes of *Psammochloa villosa* were exposed to the air, the associated ramets either died or became very weak, and ramet number decreased as erosion severity increased.

In summary, both concurrent branch-derived and root-derived clonal reproduction are important biological characteristics for *Caragana* to adapt to sandy environments. Sand burial favored the clonal reproduction of *Caragana* by promoting the formation of branch-derived ramets, while wind erosion benefited the clonal reproduction by facilitating the formation of root-derived ramets. Such mechanisms led to greater abundance and larger areas of *Caragana* shrubs in the sandy land.

## 5. Conclusions

Sandy habitats stimulated seed germination, promoted plant growth, increased sexual reproduction, and facilitated clonal reproduction of *Caragana* shrubs, which could explain why the abundance, area and height of the *Caragana* shrubs in sandy lands was higher than that in grasslands. Our results suggested that grassland degradation led to land desertification and such sandy habitats favored the population growth of *Caragana* shrubs, which was one of the important mechanisms for shrub encroachment in grasslands. In addition, the capability of fast growth and rapid population expansion in sandy land makes *Caragana* an ecological engineering species in ameliorate desertification.

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**Conflicts of Interest:** The authors declare no conflict of interest.

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