

Limitations on the recruitment of the rare sand shrubby legume *Eremosparton songoricum* (Fabaceae) in Gurbantunggut Desert, China

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Abstract: *Eremosparton songoricum*, a rare and endemic sand dune plant, appears to be experiencing recruitment failure. The structure of five populations from the Gurbantunggut Desert, China, was investigated for recruitment patterns, and two of them were examined for flowering, pollination and seed germination limits on regeneration. The results showed that total 150 seedlings only occurred on line transects in riverside Dure population, but they all died half a month later; no seedlings occurred in other four hinterland desert populations indicating recruitment was a failure at all populations although flowers were plentiful. Reproductive success depends on pollinators. Nectar is 'reward' for pollinators, with 0.06 μL –0.12 μL and 0.15 μL –0.35 μL per flower in Dure and Kabu populations, respectively, in continuously two secreting days. Spontaneous self pollination is rare with nearly zero fruit production. Geitonogamous self pollination is predominant with 14.47% fruit set. Seed mass in the riverside Dure population was significantly greater than that in other hinterland desert populations. Consequently, the Dure population exhibited a significantly higher germination rate (about 90%) than those in other populations (about 30%). Results suggested that recruitment failure of *E. songoricum* is not due to flower shortage, pollination limitation, or poor seed germination but environmental pressure and/or human disturbance.

Keywords: seedling recruitment; sand dunes; regeneration; population structure; pollination ecology

1 Introduction

Since exploitation of oil and gas resources in Gurbantunggut Desert, China, started in the 1970s, there has been serious disturbance and damage to desert vegetation (Zhang, 1988; Qian *et al.*, 2002). This, combined with threats from overgrazing, illegal collection of medicinal plants, and land-use change toward farming and sheep ranching, has resulted in sharp declines or regional extinctions of certain native vegetation species (Tang *et al.*, 2008; Wang *et al.*, 2009). One plant species, *Eremosparton songoricum* Vass. (Fabaceae), a rare sandy legume, is now limited to scattered distribution in the southeast part and northern locations of the Gurbantunggut Desert, China (Chen *et al.*, 1983), and dunes around Balkash Lake in Kazakhstan (Va-

sipchenko, 1941). *E. songoricum* is only found on mobile and semi-mobile sand dunes, and is considered a pioneer plant on active sand dunes (Zhang *et al.*, 2008). *E. songoricum* is listed as Rare Species and Gradually Declining (Yin *et al.*, 2006). Anecdotal evidence suggests that the reason for its local extinction and limited distribution is sexual recruitment failure (Yin *et al.*, 2006). Seedlings are rarely observed in the wild (Shi and Wang, 2010a, b), despite the potential for a large fruit crop with *E. songoricum* flowering profusely. The regeneration of the *E. songoricum* population mainly relies on underground rhizome clonal growth.

Eremosparton ecology has received little attention

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in the literature. In 1978 the geographical distribution and habitat environment of *Eremosparton* in China was first reported by a comprehensive investigation group (Zhang and Hai, 2002), and then, its water physiological characters (Jiang, 1989), introduction trials (Liu *et al.*, 1997), community characters (Zhang and Hai, 2002) and chemicals (Ding *et al.*, 2005) were reported. In recent years, there have been studies of its bio-ecological characteristics (Zhang *et al.*, 2008), flowering biology (Ma *et al.*, 2008; Shi *et al.*, 2010a, b), seed biology (Ma *et al.*, 2006), genetic diversity (Lu *et al.*, 2007; Liu *et al.*, 2010a, b) and clonal population dynamics (Wang *et al.*, 2009a, b; Zhang *et al.*, 2009). Seedlings are rarely observed in the wild, which means the species has been recruitment failure in nature. However, there has been no concerted effort to study the reasons for this limitation.

Knowledge of recruitment limitation is essential to understanding a range of phenomena in plant population dynamics (Crawley, 1990). Recently, there has been an increase of studies concerned with the effect of various types of limitation on the population size of local species and their distribution pattern at the landscape scale (Zuzana and Tomas, 2005). The basic alternatives of recruitment limitation are “availability of seeds” or “availability of microsites” (Eriksson and Ehrlén, 1992). Klinkhamer and de Jong (1989) pointed out that recruitment rate is dependent on both seed availability and microsite availability. Crawley (1990) suggested that, in general, microsite limitation is predominant in plant populations. While Eriksson and Ehrlén (1992) argued that a concept of combined limitation by seed and microsite availability may prove to be more meaningful for analyses of recruitment regulation in plant populations. It was their opinion that the importance of seed limitation in plant populations had been underestimated. The relative importance of seed availability and microsite availability varies in response to diverse environmental conditions, and their contribution to recruitment failure is expected to differ. In many clonal plants, the recruitment of new seedlings of sexual origin is relatively rare or sporadic (Ricardo *et al.*, 2005), especially in arid environments where the population dynamics of many plant species is highly variable due to extreme temperatures and unpredictable rainfall events

(Ricardo *et al.*, 2005). However, our knowledge of the influence of seed availability vs. microsite availability on the low seedling recruitment rate in dune species is still quite limited.

In the paper, the mechanism of recruitment limitation of *E. songoricum* was studied, with special focus on the consequence of “seed availability” on recruitment. We used five separate *E. songoricum* populations in the Gurbantunggut Desert to examine recruitment failure, addressing three questions: (1) Is poor recruitment (an absence of seedlings) apparent from the population structure? (2) Is floral biology and pollination limiting seed production? (3) If any seed is produced, is it able to germinate?

2 Materials and methods

2.1 Study areas and materials

The study was conducted in five populations: Dure (in the northern riverside location, A), Kabu (6 km from Dure population, B), Cainan (in the southern part, C), Shamo (in the south-eastern part, D) and Fukang (in the southern location, E) (Fig. 1) located in the Gurbantunggut Desert. Only one population, at Dure, is quite close to Fuhai River, that makes water content of soil significantly higher than that in sand dunes of population Kabu, although only 6 km far away (Wang *et al.*, 2009). The Fukang population is quite small (60 m²) without seeds in three consecutive years. Field investigation and laboratory experiment were conducted in 2007 and 2008.

The Gurbantunggut Desert is situated in the center of the Junggar Basin, Xinjiang Uygur autonomous region of China, and is the second largest desert in China with an area of 48,800 km². Because of the “blocking effect” of the Himalayan Range, moist air currents from the Indian Ocean fail to reach the Gurbantunggut Desert, resulting in a vast expanse of arid terrain. Mean annual precipitation is approximately 79.5 mm, and the mean annual evaporation is 2,606.6 mm. The average temperature is 7.26°C (Zhang *et al.*, 2006).

E. songoricum is a dwarf shrubby legume, 50–85 cm tall, with many green and slender branches at its base. The leaf is extremely reduced to squamiform, only 1 mm long, which is why the plant is also called “leafless legume”. Flowers are papilionaceous, solitary,

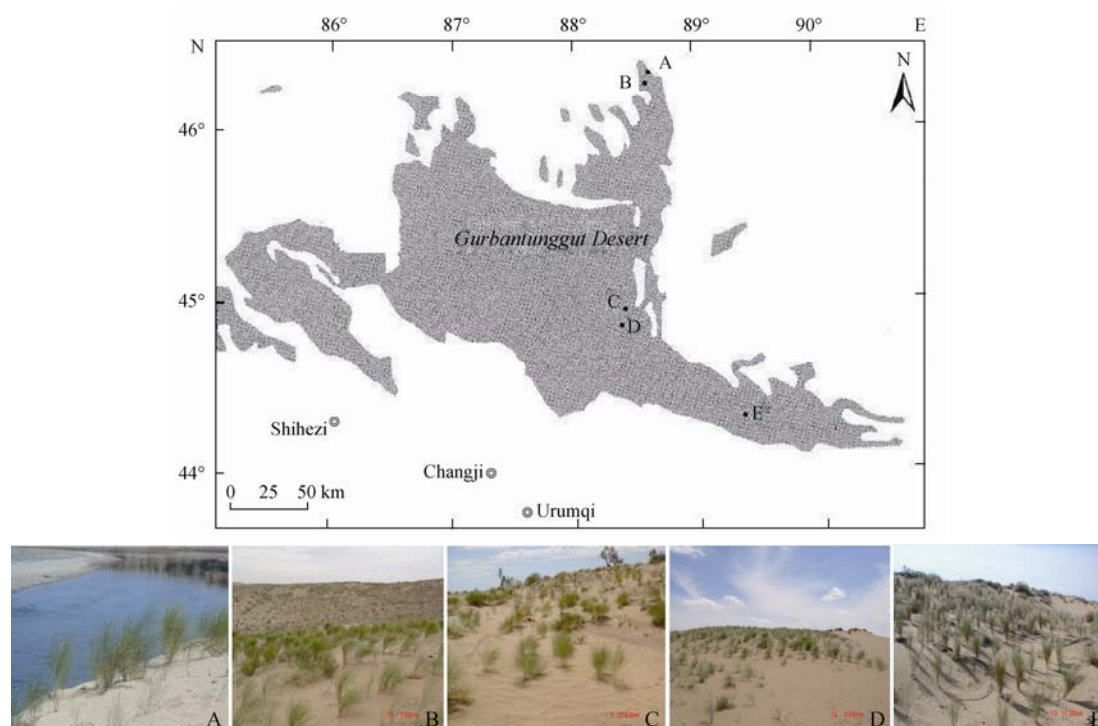


Fig.1 The location and habitat of five populations of *E. songoricum* in Gurbantunggut Desert

forming long racemes (10–15cm) on branches (Shi *et al.*, 2010a, b). It is a hermaphrodite flower species. Seed pods are slightly turgid, membranous, ovate or oval, 6–12 mm long, and contain 1 or 2 reniform seeds. Flowering time is from late May to late June, and fruiting time is from mid July to late August.

2.2 Population structure

The total area of each of the five populations was measured during May 2007. A separate search was made for seedlings using transects. Three 50 m transect were laid from the foot to the crest of the dune at each site (except Fukang), and, a careful search was made for seedlings in 10 continuous 5 m×5 m quadrats. The distance (m) to the nearest neighbor (edge to edge) of 20 randomly selected plants at each site was measured to investigate the density of the populations. In order to estimate the total surface area of substrate covered by each plant, plant area [$= \pi \times 0.25 (\text{length} \times \text{width})$] was calculated, which assumes an elliptical plant shape. Maximum height above the substrate was measured at the centre of the plant. Twenty plants were selected randomly from each population, and, in a 2 m×2 m square centered on each plant, slope was measured along the line of greatest slope.

2.3 Floral and pollination biology

Flowering duration was determined in four populations (not the Fukang population) in 2007 and 2008. Field experiments were carried out in the Dure and Kabu populations in 2008 to examine insect foraging behavior and to quantify nectar secretion. Insects were captured for examination of pollen types using fuchsin gel (Liu and Koptur, 2003). The gel is applied to the insect's body and melted onto a slide for examination under an optical microscope at 100× magnification. The pollinators that carried *E. songoricum* pollen and contacted anthers and/or stigmas in the wild were considered to be the effective pollinators. At least five individuals of each pollinator species were collected for later identification. To examine the major pollination mode in *E. songoricum*, the most frequent effective pollinator was followed and recorded the visits within and between plant individuals, for a total of 30 replicates. Nectar secretion was quantified by bagging 140 flowers at anthesis in the morning at both populations. Nectar was evaluated by measuring the amount of accumulated nectar with a 0.5 mm internal diameter capillary micropipette. Nectars were collected every two hours from 09:00 to 20:00 on the first and the

second day and each collection has ten replicates.

The Dure population was used to assess fruit set under different pollination treatments in late May of 2007. Three flowers growing in the same position were chosen from each of ten individual plants, for a total of three replications, to apply the following treatments: (1) Natural pollination, in which flowers had the opportunity to be pollinated via naturally occurring vectors; (2) Spontaneous self-pollination, in which buds were bagged throughout their flowering period without emasculation; (3) Hand self-pollination, in which bagged flowers were hand pollinated with their own pollen; (4) Hand geitonogamous pollination, in which bagged and emasculated buds were hand pollinated with pollen from other flowers of the same individuals; (5) Hand out-crossed pollination, in which emasculated flowers were pollinated with pollen from another plant at least 20 m away (to avoid the genetic material coming from the same clone). Fruit set was calculated as the percentage of fruits in relation to total number of flowers produced, which was calculated at phase I when the fruit was beginning expansion with embryo (fertilization) and also at phase II when the fruit was completely mature, because more than half of the fruits were aborted between fertilization and maturity, based on field observation. Seed set was defined as the proportion of ovules that developed into seeds in all the mature fruits within an inflorescence.

2.4 Seed trait and seed germination

Twenty randomly selected fruits, and extracted seeds (after fruit measurement) from each population were measured for each variable (Table 3) to evaluate size and weight differences between populations.

In order to determine whether the seeds possessed a physical dormancy, a seed sample was either (1) mechanically scarified, (2) treated with sulphuric acid, and compared with a sample of (3) unscarified seeds. Mechanical scarification involved making a 2 mm long incision through the testa at the cotyledon end with a razor blade. In the sulphuric acid treatment seeds were dipped in sulphuric acid for about 30 min and then washed with tap water for 5 min, and blotted with filter paper to dry them. Four replicates of each treatment (1. Scarified; 2. Treated with sulphuric acid; and 3. Unscarified) were used each of 100 seeds of *E.*

songoricum. Scarified, sulphuric acid treated and unscarified seeds were placed in Petri dishes on filter paper moistened with distilled water and allowed to imbibe at room temperature (22°C). Immediately after the initial wetting and at 30 min intervals for 6 h, all seeds were blotted dry, weighed to the nearest 0.01 mg and returned to wet filter paper at 22°C. The amount of water taken up was determined as actual increase in seed weight: $W = (W_i - W_d)/W_d$, where W_i and W_d are weights of imbibed and dry seeds, respectively.

In order to detect the characteristics of seed germination and its relationship with seed mass, seed germination trials were conducted in two populations, being the riverside Dure population and the hinterland Cainan population. One group of seeds ($n=100$) was mechanically scarified using a scalpel, another group was not scarified and used as a control. The seeds were then placed on water-soaked filter paper in a 20°C constant temperature room with a 12 hour light/dark cycle, a treatment in which germination most often occurs for all species (Dawson *et al.*, 2005). Three replicates of 25 seeds were used for each treatment. Percentage germination was evaluated daily, and germination was defined as radical emergence to 1 mm (Bewley and Black, 1994). Germinated seeds were separated after counting. The trials continued for 30 days.

2.5 Data analysis

Tukey methods of One Way ANOVA were performed to compare plant area and height among different populations, and fruit set among different pollination treatments. Seed germination data were analyzed by Chi-square. Data normality was comprehensively considered using the Kolmogorov-Smirnov and Shapiro-Wilk Indices. The Levene test was used to assess homogeneity of variance.

3 Results

3.1 Population structure

Over the 5 populations, most of the *E. songoricum* plants are growing on severely wind eroded mobile and semi-mobile sand dunes on the windward slope of the foredunes, and are usually distributed from the lower to upper part of a dune, seldom in the swale between dunes. The total areas of the five populations are quite different, extending over only 60 m² up to

7,200 m². Fukang is the smallest and most isolated population with only 116 plants. The line transects, intensively searching 250 m² at each of the five sites, found no seedlings except in the Dure population. In the Dure population, a total of 150 seedlings were counted in flat sandy areas, but all these seedlings died half a month after counting. No seedlings were observed at any site in the course of other work. The *E. songoricum* had individual plant areas averaging 0.003 m² to 0.758 m² (Table 1), and 95% of the plants at each site were less than 0.5 m². There were significant differences in plant area between sites (Table 1). There were no significant differences in mean plant height between the Dure, Kabu, Cainan and Shamo sites, but plants at these sites were all taller than at the Fukang site (Table 1). The tallest plants were found at the Dure site and the smallest were found at Fukang. There was no correlation between height and plant area.

3.2 Floral and pollination biology

Flowering of the population lasted 21–23 days in all five populations, extending from mid May to late June. Flower phenology is about 10 days earlier in southern compared with northern populations. Under natural condition, floral longevity was 3 days, no matter which located. Total flower numbers varied greatly between plant areas, ranging from 200 to 3,000 flowers per individual.

Nectar was secreted from the base of the ovary. Nectar production lasted for 2 days with an approximate volume of 0.12 µL and 0.06 µL on the first and second day in the Dure population (Fig. 2a) and 0.35

µL and 0.15 µL on the first and second day in the Kabu population (Fig. 2b). The peak nectar secretion at both these sites occurred at 13:00–15:00 (Fig. 2a, b). *E. songoricum* was pollinated exclusively by bees. The effective pollinators in both Dure and Kabu populations were *Colletes popovi* Nosk., *Megachile terminate* Morawitz, *Coelioxys* sp. and *Bembix planifrons* F. Mor. The most frequent effective pollinator in the Dure population in 2008 was *C. popovi* Nosk., accounting for 79.2% of all the visits. In addition, 30 *C. popovi* were observed to be pollinating many flowers of the same inflorescence or within individual plants ($65.8 \pm 1.1\%$), and only $34.1 \pm 2.1\%$ cross-pollination happened between different individuals. Therefore, geitonogamy is probably common in *E. songoricum*.

Fruit abortion in *E. songoricum* was frequent, with nearly 70% of its fruits aborted between the post zygotic stage and fruit maturation (Table 2). Fruit set by natural pollination and hand outcross pollination in phase I was almost equal, but significantly different in phase II, indicating outcross pollen is limited in natural populations. Spontaneous self-pollination set generally lower fruit (8.90%) in phase I and almost zero in phase II, thus, there was no spontaneous selfing in *E. songoricum*. Hand self-pollination could set significantly more fruit than spontaneous selfing in both phase I and II (Table 2), indicating that facilitated autogamy could occur.

3.3 Seed traits and seed germination

Size and weight of fruits and seeds from the Dure

Table 1 Location, habitat, population, and reproductive characters of the five studied populations of *E. songoricum*

Parameters	Sites				
	Dure	Kabu	Cainan	Shamo	Fukang
Latitude	46°31'N	46°28'N	44°58'N	44°56'N	44°37'N
Longitude	88°33'E	88°33'E	88°24'E	88°29'E	88°15'E
Average slope (°)	10.2±6.5	19.2±13.1	27.5±17.7	32.8±12.9	18.2±10.5
Total area of site (m ²)	120 m×60 m	85 m×56 m	125 m×40 m	85 m×48 m	6 m×10 m
Largest plant area (m ²)	0.758	0.585	0.283	0.320	0.109
Mean plant area (m ²)	0.328±0.036 ^a	0.205±0.024 ^b	0.101±0.017 ^c	0.135±0.021 ^{bc}	0.030±0.002 ^d
Smallest plant area (m ²)	0.043	0.049	0.016	0.048	0.003
Mean height (cm)	61.11±1.44 ^a	54.92±2.64 ^a	50.54±1.76 ^{ab}	50.87±2.78 ^a	39.23±1.26 ^b
Mean neighbor distance (cm)	62.06±4.33 ^a	39.82±1.01 ^{bc}	51.63±3.16 ^{ab}	46.48±1.76 ^{bc}	36.98±0.81 ^c

Note: Values are means ±S.E.; The different lowercase indicated significance at the 0.01 level.

population are significantly larger than those from the three populations at Kabu, Cainan and Shamo (Table 3). There was no significant difference in fruits and seeds between the Cainan and Shamo populations, although weight and size are variable.

The mass of scarified and sulphuric-acid treated freshly matured seeds increased by 121% and 101.9% in 3 h, respectively, and both reached 169.4% (fully imbibed) in 10 h, whereas the mass of non-scarified seeds only increase 3.6% in 10 h. This result shows freshly matured *E. songoricum* seeds have physical dormancy (Fig. 3).

Scarified seeds showed high levels of germination compared with unscarified seeds in both the Dure and Cainan populations. As a result, seed scarification is a requirement for successful germination of *E. songoricum*. Seeds from the Dure population had a significantly higher germination rate than seed from the Cainan population (Fig. 4).

4 Discussion

Five populations of *E. songoricum*, from different locations in the Gurbantunggut Desert, were selected and investigated to determine if recruitment failure is occurring and, if so, whether this was caused by the floral biology and the pollination regime or by seed germination patterns. Our data do demonstrate a recruitment failure in *E. songoricum*, since we failed to

locate any surviving seedlings.

4.1 Floral biology and pollination limitation on recruitment failure

Reproductive failure is one of the plausible explanations for a lack of recruitment. In *E. songoricum*, geitonogamy is predominant due to pollinator behavior or foraging within or between flowers of a single individual plant. Geitonogamy leads to self-fertilization

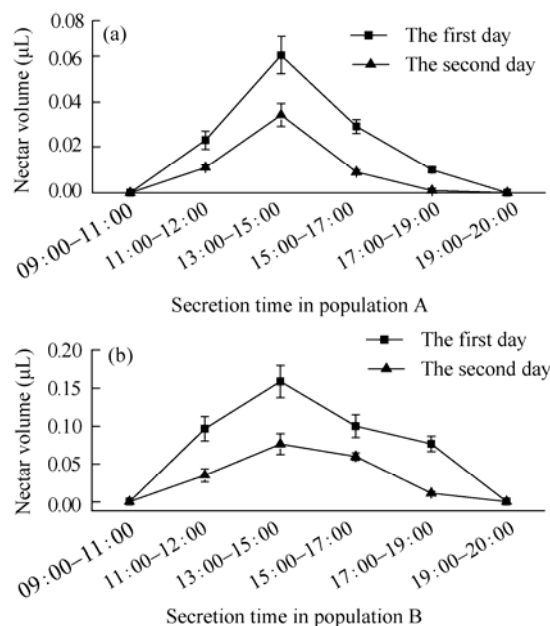


Fig. 2 Variation pattern in time series of nectar production (Mean \pm SE) at two hours intervals in population Dure (a) and Kabu (b) in 2008

Table 2 Fruit set of *E. songoricum* is compared within each treatment in different phases (lowercase letters) and between each pollination treatment (uppercase letters) in 2007

Treatments	Natural pollination	spontaneous self-pollination	Hand self-pollination	Hand geitonogamous pollination	Hand outcross pollination
	(%)				
Phase I	88.61 \pm 3.31 ^{a, A} (n=1453)	8.90 \pm 0.85 ^{a, B} (n=90)	88.56 \pm 2.17 ^{a, A} (n=89)	89.99 \pm 1.20 ^{a, A} (n=88)	88.55 \pm 2.52 ^{a, A} (n=90)
Phase II	14.47 \pm 1.20 ^{b, B} (n=1453)	0.02 \pm 0.01 ^{a, C} (n=90)	13.05 \pm 0.32 ^{b, B} (n=89)	12.93 \pm 1.28 ^{b, B} (n=88)	34.10 \pm 1.31 ^{b, A} (n=90)

Note: Phase I and phase II mean the times when the fruits are beginning expansion and completely mature, respectively; n means the number of total manipulated flowers in each treatment; Values are means \pm S.E.; The different lowercase and uppercase letters indicated significance at 0.01 level.

Table 3 Fruit and seed traits of *E. songoricum* from five populations.

Characters	Dure	Kabu	Cainan	Shamo
Fruit length (mm)	10.51 \pm 0.35 ^a	9.23 \pm 0.29 ^{ab}	8.18 \pm 0.26 ^b	8.37 \pm 0.27 ^b
Fruit width (mm)	5.64 \pm 0.09 ^a	5.32 \pm 0.06 ^{ab}	5.03 \pm 0.08 ^b	5.06 \pm 0.06 ^b
Fruit weight (g)	4.15 \pm 0.05 ^a	3.86 \pm 0.05 ^b	3.42 \pm 0.08 ^c	3.51 \pm 0.05 ^c
Seed length (mm)	5.15 \pm 0.10 ^a	4.79 \pm 0.03 ^b	4.57 \pm 0.06 ^b	4.61 \pm 0.04 ^b
Seed width (mm)	3.72 \pm 0.06 ^a	3.44 \pm 0.07 ^b	3.13 \pm 0.05 ^c	3.16 \pm 0.06 ^c
Seed weight (g)	1.97 \pm 0.05 ^a	1.76 \pm 0.04 ^b	1.51 \pm 0.05 ^c	1.53 \pm 0.04 ^c

Note: The values are means \pm S.E. of each populations (n=20); Means with different letters are significantly different at 0.05 level.

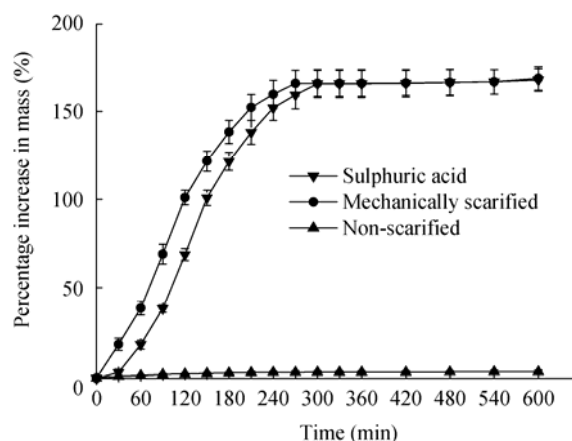


Fig. 3 The percentage increase in seed mass of *E. songoricum* with the treatments of non-scarified, scarified and sulphuric acid during a 10-hour period on moist filter paper at 22°C

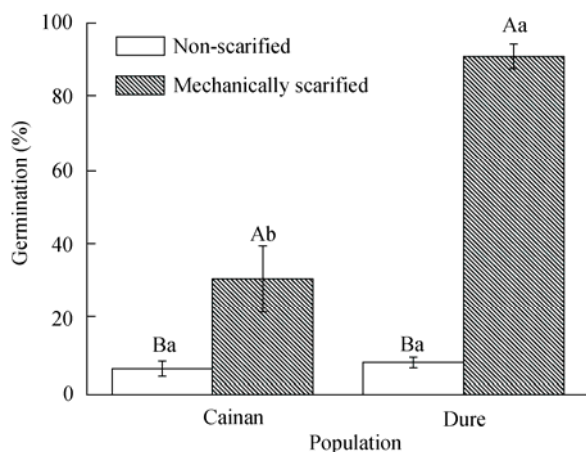


Fig. 4 Percentage germination of scarified and non-scarified seeds of *E. songoricum* after a 30-day incubation period at 20°C with a 12-hour photoperiod. Different uppercase letters indicate significant differences in germination percentages among different treatments of the same population. Different lowercase letters indicate significant differences in germination percentages of seeds with the same treatment across two populations

and may cause inbreeding depression in self-compatible species (Young *et al.*, 1996; Yang *et al.*, 2005). That may be the reason why open pollination significantly decreased the fruit set (phase II) compared with that of hand outcross pollination in *E. songoricum*. In addition, pollen limitation inevitably occurred since out-cross pollen is seldom deposited on the stigma. Although suffering from inbreeding depression and pollen limitation, *E. songoricum* still could maintain a rate of about 15% fruit set, which could at least provide moderate levels of seed production in natural populations.

Fruit set in *E. songoricum* may be inhibited by pol-

lination failures, since the reproductive success of *E. songoricum* strictly depends on pollinators. However, extrinsic environmental factors, including wind, rain and temperature, will seriously affect pollination in moving sand dune habitat. For example, pollinators were observed to visit less frequently or even not at all and flowers remained closed on cloudy or rainy days. Pollinators preferred visiting on sunny days with air temperatures 16–17°C, but were inactive in high temperature (> 39°C) or on windy days when wind speed exceeded 4.5 m/s (Shi, 2008). We thus assume that opportunities for out-crossing by flying insects might be much more limited than imagined, and that selfing may increase proportionately. Plant-pollinator relationships have been subjected to human interference, especially for the rare species (Moody-Weis and Heywood, 2001; Rocha and Aguilar, 2001). Chris and Ruth (2002) considered that when the threshold density and/or population size is reached, below which pollinators no longer make visits to flowers, plants in small or sparse populations cannot replace themselves and will be exposed to a high risk of extinction. This phenomenon was observed in the Fukang population, where the area is so small (6 m×10 m) that, almost no pollinators were observed for the entire observation period, consequently, no fruit was found. Therefore, pollination failure inhibits fruit production of *E. songoricum* in some quite small populations. When the population area exceeds the threshold and pollinators visit flowers successfully, pollination failure would be an unlikely explanation for the observed regeneration failure in *E. songoricum*.

4.2 Seed trait, seed mass and seed germination on recruitment failure

In order to establish a new individual, seed must be deposited at a suitable microsite and germinate, and the developing plant must survive the hazards facing it at that site (Eriksson and Ehrlén, 1992). Little is known about mechanisms of seed dispersal in this genus. In *E. songoricum*, seed was enclosed in turgid fruits and either rolled to the bottom of dunes by gravity, or were stopped and deposited against the roots of stumps (Zhang *et al.*, 2008). The bottom of dunes with high moisture is covered by diversified desert plants including *Artimisia*, *Ephedra* and ephemeral plants, and well-developed soil biological crust (Wang *et al.*,

2006). The pressure exerted by these competing species is greatest for seeds germinating at a dune foot or in swale between dunes. Continuous field observations of the three years of showed that no seedlings of *E. songoricum* occurred at the dune foot or in swales between dunes. Plants of *E. songoricum* are generally displaced by other species in these microsites, in accordance with the hypothesis that rare taxa are typically weaker competitors (McNaughton and Wolf, 1970). As a result, the pressure exerted by other plant species growing at a dune foot or in swale between dunes may be the most direct cause of the observed current distribution (i.e. lower to upper windward slopes of severely wind eroded mobile and semi-fixed sand dunes) (Zhang *et al.*, 2008), essentially enemy-free spaces. In the Dure population, the relatively 'flat' sand dune (Table 1) made it possible for seeds to be dispersed to suitable microsites by wind, to germinate after suitable rainfall events, as observed in the field.

Seed mass of *E. songoricum* showed an obvious relation to microsite differences (Table 3). For instance, seeds in the Dure population showed a significantly greater germination rate than lighter seeds in the Cainan population. The result is in accordance with the conclusion that larger seed may be associated with increased emergence, survival and growth as studied in numerous species (Navarro and Guitian, 2003). Such a seed germination pattern may be part of complex germination strategies. Almost all larger seed germinated quickly after rainfall, showing an opportunistic strategy (Guterman, 1994) (i.e. at least some seeds germinate after any favorable event), while only a small part of the lighter seed germinated (< 35%), showing a cautious (Guterman, 1994) or 'bet-hedging' (Philippi and Seger, 1989) germination strategy (i.e. only a portion of seeds germinate even under optimal conditions) to achieve higher seedling survival. This seed germination phenomenon had evolutionary advantage for plants located in different habitats and confronted with different water conditions. In the Dure population, rainfall is more abundant in early spring, the time when seed germinated, compared with other hinterland populations (data from Fuyun and Fukang weather stations). As a result, quick germination of all larger seeds in the Dure population after rare rainfall events could make full use of water and promote ger-

mination success. On the other hand, only partial germination of lighter seeds in hinterland desert locations leaves seed in the seed bank, which would be advantageous if and when the first seeds to germinate suffer an establishment failure due to the variable rainfall conditions.

After germination, seeds must have the ability to emerge from below the sand, since seed deposited in an environment as dynamics as mobile sand dunes, may be rapidly and deeply buried for prolonged periods (Zhang and Maun, 1994). This ability to withstand burial by sand is especially critical for seeds and seedlings of dune species (Maun and Lapierre, 1986; Maun, 1998). It is possible that the rate of sand deposition has increased in areas that *E. songoricum* currently occupies, and that this now exceeds the emergence depth for seeds and/or the growth rate of seedlings. Dunes currently accrete on the hinterland of Gurbantunggut Desert (affecting the Cainan, Shamo and Fukang sites) at a rate of 0.43–0.54 mm/d (top of sand dune) and 0.09–0.18 mm/d (upper windward slope), and deposition over a year will average 90–110 mm (top of sand dune) and 20–50 mm (upper windward slope) (Wang *et al.*, 2005), which is extremely fast. However, at the riverside Dure population, the dunes are much less dynamic, which favors the emergence of seedlings.

After emergence, the developing seedling must survive the hazards they face. Although some seeds germinated and emerged from sands after rainfall at the Dure site, they all died eventually. We thus speculate that water conditions could not meet the requirement of seedling growth, maybe due to high evaporation or quick water downward movement as reported in other desert species (Yang *et al.*, 2010).

As a result, there is only a narrow window in dune dynamics in which a seedling can successfully established. This pattern is similar to that observed in other clonal species where seedling recruitment is rare or restricted to 'narrow windows of opportunity' even when seeds are regularly available (Eriksson, 1993; Mandujano *et al.*, 2001). It will be very interesting in future work to measure the moisture requirement and downward movement of plant-available moisture during the germination and plant establishment period, and the depth limitation for seedling emergence on seed buried in sand.

5 Conclusion

All the populations in this study show a bias towards medium to larger plants with no surviving seedlings, indicating recruitment failure in *E. songoricum*. It is clear that the plants produce flowers which can be fertilized, and pollen that can fertilize ovules. Furthermore, pollination vectors exist which transfer the pollen, though viable seed can be produced even without out-crossing and can germinate (in controlled conditions). Thus, there is no pollination failure. Therefore, seed germination and seedling survival appear to be the vulnerable stage in the life cycle of *E. songoricum*, causing the recruitment failure. The relative roles of

dune dynamics (effect of seed burial in sand) and the quantitative analyses on microsite moisture requirements and availability from seed germination to seedling growth stage under natural conditions requires further investigation in order to fully understand the recruitment failure of *E. songoricum*, and to provide a guide for the study of recruitment failure in other species.

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