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Germination strategy of the temperate sandy desert annual chenopod *Agriophyllum squarrosum*

Zong-Ling Wang*†, Gang Wang*‡ & Xin-Min Liu†

* *State Key Laboratory of Arid Agroecology, Lanzhou University, Lanzhou 730000, Gansu, P.R. China*
†*Institute of Desert Research, Chinese Academy of Sciences, Lanzhou 730000, Gansu, P.R. China*

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Seed germination behaviour of the chenopod *Agriophyllum squarrosum* in the moving dunes of the Tenggeli Desert was studied. The response of seed germination with time, expressed as the proportion of seed germinated per day, presented a unimodal continuous process. Seeds began to germinate in less than 3 h and the germination rate peak was reached 7 days after watering. All seeds eventually germinated. Seeds were collected in 1993 and 1994, so the maternal plants had different growing periods, with different plant sizes and germination times. Germination in sand was tested in the second year and showed that there is no innate dormancy of *A. squarrosum* during the growing season. The mechanism for long-term survival of *A. squarrosum* in temperate sand dunes is discussed.

Keywords: *Agriophyllum squarrosum*; buried depth; fitness; germination curve; germination strategy; maternal plant; soil moisture; temperate sandy desert

Introduction

Seed germination behaviour plays a key role in the persistence and dynamics of annual desert plants. Most germination studies on desert annuals have been concerned with the proportion of seeds that could germinate in a growing season and the effects of specific environmental factors on seed germination (McWilliams *et al.*, 1968; Mott, 1974; Grime *et al.*, 1981; Mayer & Poljakoff-Mayber, 1982; Hacker, 1984; Bowers, 1987; Gutterman & Agami, 1987; Gutterman & Edine, 1988; Inouye, 1991; Baskin *et al.*, 1993). It is known that in growing seasons seeds of annual desert species germinate only after a threshold amount of rain has fallen (Juhren *et al.*, 1956; Tevis, 1958*a*; Beatley, 1974; Freas & Kemp, 1983; Gutterman, 1993, 1994). But deserts are unpredictable, and precipitation at the beginning of a growing season will not always be

‡ To whom correspondence should be addressed.

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followed by enough rainfall for there to be adequate soil moisture for plants to complete their life cycle and set seed (Tevis, 1958*a,b*; Beatley, 1967; Burk, 1982; Philippi, 1993*a,b*). Dormancy, the process of delaying germination in time, has the benefit of reducing the risk that all of a plant's progeny will germinate at the same time and die before reproducing because of a lack of subsequent rainfall. However, in a year favourable for growth and seed production, dormancy reduces the number of plants producing seeds and thus the total seed production for a lineage. Over the years, dormant seeds allow the persistence of that lineage beyond a single catastrophic year when all seeds that germinate die before flowering and setting new seeds (Philippi, 1993*a*). Probability models also predict that the evolutionary response to increasing environmental uncertainty would be an increased innate seed dormancy with only a part of a plant's seeds available to germinate each year (Cohen, 1966, 1968; Levins, 1969).

Deserts are unpredictable, but seedling survival of desert-inhabiting annual plants does not necessarily depend on the distribution of rainfall over a whole growing season. In some deserts, seedlings survival depends on the magnitude of the germination-inducing rain or irrigation. In the Negev Desert, Gutterman & Evenari (1994) found, even after only one irrigation in hot and dry summer conditions, plants survived for 4 months (from 45% to 66%) and produced seeds before the first rains of the following winter. Studies on the population dynamics of *Minuartia uniflora* and *Sedum smallii* found that both have high reproductive potentials, and that populations of both species have an extremely high mortality during the seed and seedling establishment phases of the life cycle. The individuals that survive beyond seedling establishment have relatively high expectations of completing their life cycle (Sharitz & McCormick, 1973). In the moving dunes of the Tenggeli Desert, a temperate sandy desert of northern China, *Agriophyllum squarrosum* also has high mortality during the seedling establishment phase of the life cycle (Wang *et al*., 1996). Time of seedling emergence also affects seedling survival and seed yield. Following a sufficiently heavy rain, the earlier that seedlings emerge the more likely they are to complete their life cycle and set seed. After a light rain or a brief precipitation the emerging seedlings barely survive after the rain.

Thus, annual plants in deserts, in addition to having mechanisms that allow only a portion of the seeds to germinate in a growing season, must have some other traits that allow them to persist in the face of environmental unpredictability and may have traits that specifically exploit it. The progress of seed germination is one form of adaptation to environmental uncertainty in desert annuals. However, there has been little experimental research dealing with the germination responses of desert annual plants in relation to the progress of germination and environmental uncertainty. The purpose of this study was to determine the progress of germination responses of the annual *A. squarrosum* which grows in the moving dunes in the Tenggeli Desert during the summer season with less reliable rainfall.

Site description

Agriophyllum squarrosum is an annual plant of sandy habitats and is widely distributed in moving dunes and low fixed dunes of temperate sandy deserts of central Asia. There are three annual species in the Tenggeli Desert. The other two species are *Corispermum mongolicum* and *Stilpnolepis centriflora*, but both are rarely seen in moving dunes. Thus, *A. squarrosum* is the dominant annual plant of moving dunes in the Tenggeli Desert, and it always appears as a single-species community. In nature, seeds of *A. squarrosum* can germinate from May to August after the soil has been moistened by an adequate precipitation. It flowers in September and may set from one to tens of thousands of seeds.

Seeds used in these experiments were collected from the Tenggeli Desert near Shapotou (37°27′ N, 104°57′ E), Ningxia Province, China. Shapotou Station is the Desert Experimental Research Station of the Chinese Academy of Sciences. The source of these seeds is classified as arid. Average annual rainfall in the Tenggeli Desert is 186·2 mm, and fluctuations between one year and another is high. In Shapotou, 88·3 mm of rain fell in 1957, and in the following year only 304·2 mm was measured. The distribution of rain during the season is also unpredictable. There is no reliable rainfall during the growing season (Li, 1991).

Materials and methods

In order to obtain seeds of known age, ripe seeds were collected directly from plants in early November each year. Seeds were collected on 5 November 1993 and 8 November 1994 from all plants within the same sand dune section, so that all the plants from which seeds were collected were in a similar microhabitat. Seeds were randomly collected from both large and small plants, and were thus represented in the sample in approximately their proportional contribution to that year's seed production. All the seeds for each year were mixed together and placed in a nylon mesh bag and then stored in a laboratory of the Shapotou Station with no heating or air-conditioning, and the windows were kept open throughout the year. The seeds were thus exposed to a close-to-nature daily and seasonal sequence of temperature changes.

Two aspects of seed germination were tested in this study: the progress of germination under adequate conditions, and the final germination fraction under different germination conditions. In order to examine the germination fraction per day, we used a light- and temperature-controlled chamber at Lanzhou University to match, as near as possible, the environmental conditions at Shapotou during the growing season. Immediately before the experiments, the seeds were divided into ten replicates of 200 seeds; germination tests began the day the seeds arrived from Shapotou.

The experiments began on 15 May 1995. Ten replicates of 200 seeds collected in the same year were placed on moistened filter paper in 15 cm glass Petri dishes. The seeds were exposed to daylight intermittently during counting but the chamber was not illuminated. The chamber was set on daily thermoperiods of 28/15°C, approximating the mean daily maximum and minimum temperature in 3-cm deep soil during rainy days in Shapotou from May to August. Once germination began, seedlings were counted and removed every day; at the same time, enough deionized water was added to the Petri dishes so that germination was unlikely to be limited by water. Counting continued until no additional germination was observed over a period of 5 days. Seeds which had not germinated by this time were removed from the Petri dishes and checked for viability using the method of MacKay (1972). Ungerminated seeds were soaked in water at 30°C for 24 h. Seed coats were removed and the embryo was soaked in 1% tetrazolium chloride for 24 h at 30°C. Pink embryos were scored as alive. The germination rate was calculated as the number of seeds germinated per day divided by the number of viable seeds; standard errors were also calculated.

In order to examine seed germination in the field, germination experiments were carried out in Shapotou Station. Germination tests on seeds from both years were conducted in flowerpots (20 cm in diameter, 25 cm tall) containing soil from the collection site. Any seeds contained in the soil were sifted out before the experiment began. Since the actual vertical distribution of seeds in a natural habitat is unknown, the seeds were planted in 2-cm increments at depths ranging from the surface to 10 cm to test germination fraction. Six replicates of 200 seeds from each year were planted, i.e. 72 flowerpots. The flowerpots were then placed in a non-temperature-controlled greenhouse (no heating or air-conditioning and open windows all year) at the Shapotou

Station. Beginning on 5 July 1996, all the flowerpots were watered evenly. Excessive amounts of water were provided twice every day (at 0900h and 1800h) so that germination was unlikely to be limited by water. For the first day, more than 50 mm of water were applied. This was followed by 20 mm of water on each of the following days. Although this amount of watering could not prevent the soil surface from drying out, it was sufficient to maintain constant soil saturation at 1 cm depth. Runoff from the bottom of the flowerpots was used for all subsequent waterings. Once germination began, seedlings were counted and removed every day. Watering was continued until there was no germination for 5 days. Seeds that germinated but did not emerge were scored as germinated. Seeds which had not germinated by this time were removed from the flowerpots and checked for viability.

Results

The responses of seed germination with time are expressed as the number of seed germinated per day for each of the 2 years (Fig. 1). The progress of germination presented a unimodal continuous curve in each of the 2 years. In the experiments, seeds began to germinate in less than 3 h after being watered. Prolonged exposure to moisture caused a significant increase in germination and the peak was reached 7 days after watering. Seeds collected in both years eventually exhibited 100% germination. There were differences in germination time (calculated as days to total germination) between the 2 years. Germination of the 1993 seeds was lower in the first 7 days; the accumulated germination percentage in the first 7 days was 68·8%, so the germination curve had a larger tail (Fig. 1). All germination occurred by 16 days after watering. Seeds collected in 1994 germinated faster under the same germination conditions, with 54·4% of the viable seeds germinating before the peak was reached. The germination fraction on the seventh day was 32·8%. All the viable seeds germinated within 12 days.

The germination proportion for both years' seeds at different buried depths is shown

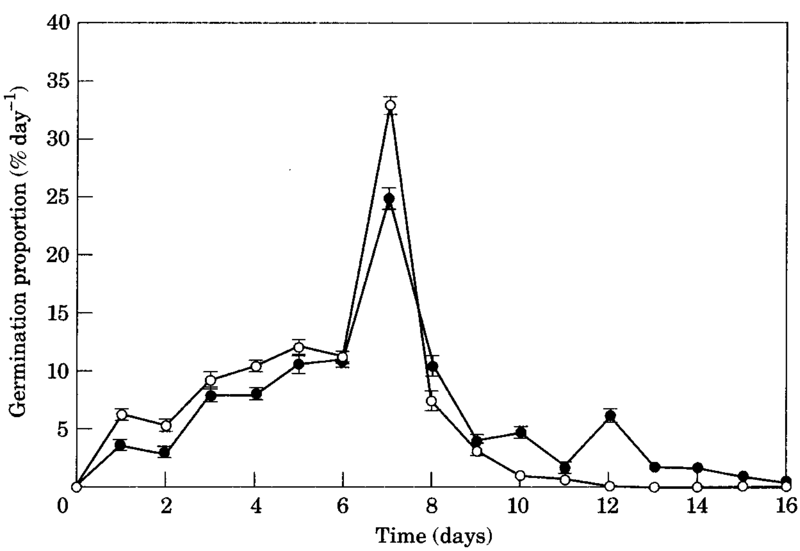

Figure 1. The response of seed germination with time, expressed as the proportion of seed germinated per day (mean ± SE, across Petri dishes) tested in May 1995: (●) = seeds collected in 1993 (all the viable seeds germinated in 16 days); (○) = seeds collected in 1994 (all the viable seeds could germinate in 12 days).

Table 1. *Germination of* Agriophyllum squarrosum *by depth of planting**

Depth (cm)	Germination (%)	
	1993 seeds	1994 seeds
Surface	5·6	6·8
2	96·3	92·6
4	69·8	58·5
6	43·9	50·9
8	23·3	16·8
10	0·6	1

* The results given are the total fraction of viable seeds germinating from six replicates of 200 seeds at each depth in 25 days. Seeds that germinated but did not emerge were scored as germinated.

in Table 1. All experiments lasted 25 days. There was no significant difference in germination between the seeds collected in the different years. Seeds buried at different depths had significantly different final germination. Seeds at the surface and 10 cm depth had the lowest germination. Seeds buried at 2 cm exhibited nearly complete germination. Seeds of both years buried below the surface all have similar viability (about 94%). Seeds at the surface have the highest viability (96·5% for 1993 seeds, 97·1% for 1994 seeds).

Discussion

Each desert-inhabiting plant species has its own complex set of strategies that enable it to continue to appear in a certain desert habitat (Gutterman, 1994). The germination response of *A. squarrosum* presents a unimodal progress within a growing season. These results suggest that the seeds of *A. squarrosum* can be triggered to germinate by a small amount of rainfall. The proportion of seeds germinated depends on both the magnitude and duration of the germination-inducing rain. As the amount of precipitation increases to a certain level and with proper distribution, the number of seedlings that emerge is higher. The 100% germination implies there is no dormancy of *A. squarrosum* during growing seasons. The apparent ‘non-dormancy’ in *A. squarrosum* is not equivalent to the ‘no innate dormancy’ of a summer desert annual plant in the Chihuahuan Desert, in which there is a fairly reliable environment in summer (Freas & Kemp, 1983). Nor is it consistent with Cohen’s (1966) model that increasing environmental uncertainty would result in increasing innate dormancy. The germination peak of *A. squarrosum* is not equivalent to the threshold amount of precipitation required to trigger germination in other desert annuals (Juhren *et al.*, 1956; Trevis, 1958*a*; Beatley, 1974; Inouye, 1991; Gutterman, 1994). The germination response of *A. squarrosum* is a unimodal continuous process. Even at the germination peak, the germination fraction is no more than 33% per day. It is another kind of germination strategy different from the partial dormancy strategy in desert annuals to environmental uncertainty. The benefit of such a germination behaviour of *A. squarrosum* in temperate sandy desert is obvious.

One characteristic of moving dunes is that, after a rainfall, the surface of the dunes will become dry quickly due to high evaporation in hot summer. Such conditions are very harmful to the establishment of annuals. On the other hand, as the soil of sand dunes is composed of tiny grains of sand, it could prevent deeper soil moisture being evaporated. So, even in a hot and dry summer, the thickness of the dry soil of the dunes is only about 18 cm, and beneath it the soil is damp. The moisture content of the damp soil varies from 2% to 3%. The wilting point for soil moisture in sand is 0·7%, and consequently there is between 1·3% and 2·3% moisture content in the damp soil that can be used by adult plants in dry seasons. It can be considered that under conditions of aridity the dunes are more favourable for plants (Tevis, 1958*b*). The most important question for a seedling after germination is how to break through the dry sand that overlies the damp soil. For annual plants, following a sufficiently heavy and well distributed precipitation, the seedlings germinated at the beginning of a rain would grow quickly during the period of the rain. Thus, after such a precipitation the plants could make use of the deeper moisture in the soil to complete their life cycle and set seed. Otherwise, if seedlings germinate just at the end of a rain sequence and, if after the rain, the soil moisture of the surface layer is inadequate for plant establishment during a hot summer, they will die. Thus, during a lengthy rainy season, the earlier seedlings emerge the more likely they are able to complete their life cycle. This might indicate that the better adapted desert plants have the ability to germinate faster after a rain (Went, 1949). However, under conditions of a light precipitation or short precipitation, which often occurs in the desert, seedlings germinating would quickly die. Thus, seedling survival depends on the duration of germination-inducing rain after its germination. In Shapotou, the amount of light rain ($\leq$ 10·0 mm) is about 50% of the annual rainfall. Moderate rains (10·0 mm−25·0 mm) form 39·4% of the annual rainfall. Seedlings germinated at different times during a rain would be expected to have different survival rates. However, no seedling's survival can be guaranteed irrespective of when it germinated. In evolutionary theory, any plants would best 'programme' seeds to germinate in order to maximize long-term production. The continuous germination progress, one form of delaying germination in time, has the benefit of reducing the risk that all of a plant's progeny will germinate at the same time and die before reproducing because of a too short rainy period. In a raining process, the germination rate at a certain time may relate to seedling's expected future survival rate after germination. The seeds that do not germinate due to insufficient rain will remain as viable seeds and have the ability to germinate in subsequent rains. For example, when a germination-inducing rain is sufficiently heavy and with proper distribution, there are a certain number of seedlings from germinated seeds that could survive and complete their life cycles after the rain until the germination peak is reached. Such germination behaviour would confer an individual a higher fitness. Under such circumstances, seed dormancy of an annual plant would be inefficient.

This has been observed in nature in the Tenggeli Desert near Shapotou (Wang *et al*., 1996). Regarding precipitation occurring at different times during the growing season, several groups of seedling of *A. squarrosum* emerged each year. The higher the amount and the longer the precipitation lasts, the more seedlings that will emerge. But germination was found only after a threshold amount of rain had fallen, whereas after light rain no seedlings were found. Seedlings germinating in light rain would undergo moisture stress immediately after germination or emergence from the ground, resulting in very few seedlings.

The difference between the germination rate of seeds collected in different years may be caused by the different climate that the maternal plant experienced or the different sizes among the maternal plants. There was very little difference between the annual precipitation for the 2 years (181·9 mm in 1993, 201·8 mm in 1994), and all the seeds were collected in the same sand dune section. On the other hand, the seedlings in different years experienced a very different growing period. In 1993, the first seedlings were found on 8 May, so they had more growing days, resulting in larger plant sizes. The largest plants of *A. squarrosum* were up to 1·6 m × 1·5 m × 1·5 m and set more than 90,000 seeds in 1993. Thus, they were the largest contributor to the year's seed production. In 1994, no seedlings were found until 5 July. The seedlings were all smaller and set only several hundred seeds. Thus, it may be inferred that seedling growth period, i.e. plant size, may have a very important influence on seed germination behaviour (Philippi, 1993*b*). Of course, verification of the influence on seed germination requires further experiments.

Burial depth is important for germination of seeds of *A. squarrosum*. In the desert, due to the high evaporation in summer, the soil on the surface may dry quickly even after heavy irrigation. So, in the experiments, seeds on or near the soil surface would be exposed to a high relative humidity only just after watering. Then, for most of the day, seeds would be exposed to low relative humidity and lose favourable germination conditions. When buried too deep, the seeds will be placed in enforced dormancy. Considering the germination in Petri dishes was tested in an unilluminated chamber, it seems that light is not the limiting factor to seed germination. However, seeds in deeper soil would be in bad air conditions because there is too much moisture in the soil. The nearly complete germination at 2 cm depth implies that seeds of *A. squarrosum* can all germinate under adequate conditions during a growing season.

Though the precipitation in Tenggeli Sandy Desert is unpredictable, a combination of a fairly reliable moisture at depth and a unimodal continuous germination progress could ensure long-term existence of the summer annual in such an environment. The continuous germination behaviour has the benefit of reducing the risk that all of a plant's progeny will germinate at the same time and die before reproducing because of a poor germination-inducing rain. The germination peak confers an optimal increase rate for that lineage.

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