Seed Science Research (2017) **27**, 165–173
© *Cambridge University Press 2017*

doi:10.1017/S0960258517000162

REVIEW PAPER

The seed ecology of *Agriophyllum squarrosum*, a pioneer sand dune annual in Central Asia, with particular reference to seed germination

Shugao Fan[1], Carol C. Baskin[2,3], Jerry M. Baskin[2] and Yanrong Wang[1]*

[1]State Key Laboratory of Grassland Agro-ecosystems, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730000, China; [2]Department of Biology, University of Kentucky, Lexington, KY 40506, USA; [3]Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546, USA

(Received 19 August 2016; accepted after revision 29 March 2017; first published online 19 July 2017)

Abstract

In central Asia, *Agriophyllum squarrosum* is the first species to become established during natural succession on sand dunes. However, low germination percentages and thus poor stand establishment greatly inhibit the use of this key species in the stabilization of dunes. The aim of this review is to critically analyse published information on the seed biology of *A. squarrosum* with particular reference to identifying the factors limiting germination of seeds sown in the field. A conceptual model is used to illustrate the complexities of factors as well as the unknowns we found about the seed/seedling stage of the life cycle of this sand dune annual. A major result of this review is that we now know that high germination percentages can be obtained by storing freshly collected seeds dry at room temperatures for 2 to 3 months to allow dormancy break to occur via afterripening, and then storing them dry at low (e.g. 4–5°C) temperature to prevent them from entering secondary dormancy. Non-dormant seeds should be sown in the field in late spring when wind-blown sand will cover them, thus ensuring that they are in darkness, which promotes germination, at the time summer rains occur.

Keywords: afterripening, desertification, plant succession, restoration ecology, seed germination

Introduction

Wind erosion of poorly vegetated sand is an important factor contributing to desertification in arid, semi-arid and even some sub-humid regions in China, especially where human activities have resulted in disruption of the vegetation cover (Zhu, 1998; Zhao *et al*., 2005; Wang *et al*., 2006). Desertification in northern China mainly refers to 'sandy' desertification, and sand dune mobility is the dominant consequence of the loss of vegetation cover. Thus restoration of these desertified sandy lands requires the re-establishment of plants that will stabilize the sand surface.

Potential natural vegetation of much of the present-day sandy lands is grassland, and 65.4% of the total desertified land was once grassland (Jiang, 2005; Zuo *et al*., 2009a). Great effort has been made to control desertification and restore vegetation on sandy lands in China, and various revegetation strategies have been used with varying degrees of success. Many seeds have been sown in an attempt to help promote revegetation, and many methods of doing this have been tried, including dropping seeds from aircraft (Zheng *et al*., 2005b). One major problem with sowing seeds for restoration, e.g. air seeding, is that stand establishment may be poor due to low germination percentages (Zheng *et al*., 2003; He, 2013).

Sandy lands, especially moving dunes, are invaded by the summer annual chenopod *Agriophyllum squarrosum* (Linnaeus) Moq. (Amaranthaceae). This pioneer plant species is the first one to become established during natural succession on sand dunes in central Asia, including northern China (Nemoto and Lu, 1992; Cui *et al*., 2007). *Agriophyllum squarrosum* reproduces only by seeds, and due to its ability to initiate ecological succession on dunes it comes as no surprise that people have tried to restore vegetation in sandy desertified

---

* Correspondence
Email: yrwang@lzu.edu.cn

lands by sowing its seeds (Han, 2008). In fact, *A. squarrosum* is one of the species used for air seeding in Inner Mongolia. However, the efficiency of restoration from sowing seeds in the field is relatively low. Deng and Liu (2011) sowed *A. squarrosum* seeds in the Horqin Sand Land in Inner Mongolia, and seedling emergence was 12.2–34.1%. In a study by Liu *et al.* (2010), seedling emergence was less than 5% at five different burial depths (0.5, 1, 2, 3 and 5 cm) using seeds collected from the Tengger Desert in Gansu Province. Clearly, sowing seeds of *A. squarrosum* has great potential as a method of stabilizing dunes, but only if high germination percentages and thus good stand establishment can be obtained. However, although much research has been done on various aspects of the biology of *A. squarrosum*, we still do not know how to manage the species to ensure good population establishment by sowing seeds.

Thus we think it is time to review the literature on the ecological research done on *A. squarrosum*, with the aim of identifying the critical factors that may be contributing to poor stand establishment when seeds are sown in seemingly good habitats in the field. The purposes of this review are to (1) bring together information published in Chinese and English on various aspects of the seed ecology of *A. squarrosum*, and (2) use the combined information to construct a conceptual model of the seed/seedling dynamics of the species that will help identify research questions with regard to seeds that still need to be addressed. We have used the insight gained from this review to make recommendations on how to manage *A. squarrosum* seeds that are to be used in restoration of desertified sandy lands so that they are non-dormant at the time of sowing.

Geographical distribution

Agriophyllum squarrosum is a diploid (2n = 18) summer annual mainly distributed in eastern and central Asia, including Mongolia, China, Kazakhstan, Azerbaijan, Dagestan, Iran and southcentral Russia (Zhao *et al.*, 2014; Ghaffari *et al.*, 2015). In China, the species is found mostly in the cool temperate zone especially in the north, and it has a close association with sandy deserts (Fig. 1).

Habitat and succession

Agriophyllum squarrosum is a psammophyte (Fig. 2). Thus it occurs naturally only in sandy soil and is a dominant or co-dominant species on mobile sand dunes (Nemoto and Lu, 1992; Zuo *et al.*, 2009b; Zhao *et al.*, 2014). Its importance in the vegetation decreases significantly and quickly as sand dunes become semi-fixed or fixed (Liu *et al.*, 2009; Pan *et al.*, 2015; Zhou *et al.*, 2015). The sandy habitat of *A. squarrosum* is windy, unstable, nutrient-poor, drought-prone, cold in winter, hot in summer and subject to long daily periods of high solar irradiance during the growing season (Chen *et al.*, 2014; Zhao *et al.*, 2014). However, the species can grow in loess if seeds are sown on loess and covered with 0.5–2 cm of sand (Fan *et al.*, 2016).

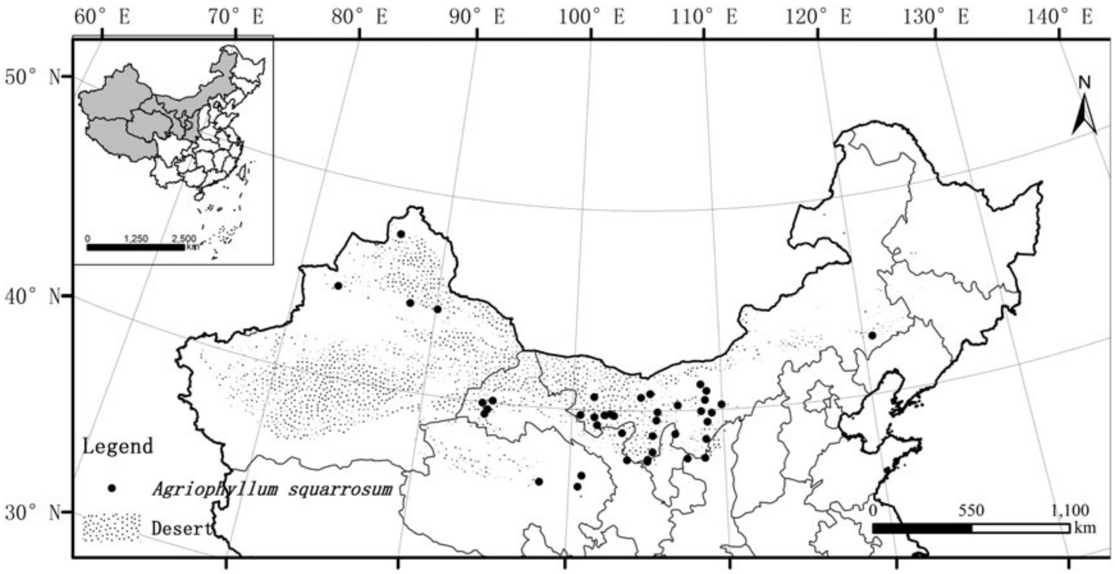

Figure 1. The distribution of *Agriophyllum squarrosum* and of the sandy deserts in northern China (data set provided by Environmental and Ecological Science Data Center for West China, National Natural Science Foundation of China). Each black dot represents a location of *A. squarrosum* reported by Zhao *et al.* (2014). The map was created using ArcGIS software.

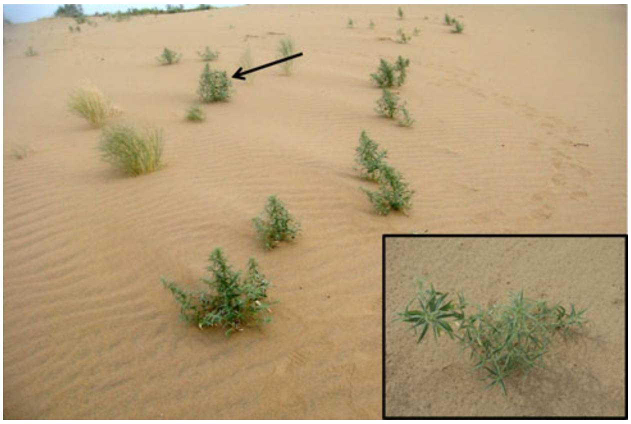

Figure 2. Photograph of *Agriophyllum squarrosum* in the sandy Gurbantunggut Desert, Xinjinag Province, China. An individual plant of *A. squarrosum* is shown in the inset. *Eremosparton songoricum* (arrow) is the other plant species in the photograph. Photographs by Jerry M. Baskin and Carol C. Baskin (inset), 28 June 2016.

Seeds of *A. squarrosum* can germinate on bare sand dunes in early May, which is the windy season and the beginning of the growing season. In Hunshandak Sandland, Inner Mongolia, it became the dominant species after 1 year of enclosure of a severely desertified vegetation recovery zone, but in the subsequent successional communities biomass of *A. squarrosum* decreased rapidly (Liu *et al*., 2009; Yan *et al*., 2015). At the Naiman Desertification Research Station, Inner Mongolia, *A. squarrosum* was the predominant species on mobile sand dunes and accounted for 68% of the total number of plants in the first 3 years. However, in the sixth year *Setaria viridis* and *A. squarrosum* became co-dominant species, accounting for 30 and 28%, respectively, of the total number of plants. In the tenth year, *Bassia dasyphylla* accounted for 32.9% of the plants and *A. squarrosum* only 0.7%. In the eighteenth year, *Artemisia halodendron* was dominant and accounted for 73% of the plants (Zhang *et al*., 2005). In Inner Mongolia, China, the relative importance of *A. squarrosum* on mobile, semi-fixed and fixed dunes was 0.42, 0.01 and 0.00, respectively (Qiao *et al*., 2012).

On unstable sand surfaces, limited soil moisture and nutrients prevent most plant species from becoming established. The quick germination response to precipitation and tolerance to burial that are characteristic of *A. squarrosum* allow this species to establish a pioneer community on sand. Its presence helps stabilize the sand and therefore provides favourable conditions for establishment of other species (Li *et al*., 2007). With development of the plant community, high transpiration rates of plants and low water infiltration rates caused by the soil crust lead to a decrease in number of *A. squarrosum* plants and an increase in drought-tolerant species such as *S. viridis* and *A. halodendron* (Li *et al*., 2007; Chen and Duan, 2015). Chang *et al*. (2005) found that variation in moisture content on different dune types was the main factor controlling the growth of *A. squarrosum*.

Plants of *A. squarrosum* take up and store nitrogen and thus play an important role at the ecosystem level in preventing nutrients from being leached out of the system by rainwater or being removed by wind erosion (Huang *et al*., 2009). Thus *A. squarrosum* acts as a nutrient reservoir, taking up nutrients during the rainy season, and it provides food for some animals and microbes (Chen *et al*., 2009).

Life cycle

On moving sand dunes, seeds of *A. squarrosum* typically germinate in May to June (Qiao *et al*., 2012), and plants produce branches in early June and flower from July to August; seeds ripen from August to October (Li and Chang, 1992; Qi *et al*., 2010). The length of the life cycle depends on habitat and year. The growth period is usually 100–140 days, but in drought years, emergence time can be delayed until July or August with the life cycle being completed in 90 days (Chen *et al*., 2014). Seedlings from seeds sown in the loessland in May in Lanzhou, China, and covered with 0.5–1.0 cm of sand started to emerge after 10 days, and plants had a 140-day life cycle (Chang *et al*., 2003). Seeds germinated about 5 days later on moving sand dunes than on semi-fixed sand dunes, and the plants on moving dunes had mature seeds 1–2 days later than those on fixed dunes (Qi *et al*., 2010).

Seed dispersal

Seeds or seeds in fruits attached to plant parts are dispersed via gravity, wind and animals (Liu *et al*., 2014). Delay of seed dispersal occurs in *A. squarrosum* with most seeds remaining attached to the mature, dead, upright plants during winter. The dry, dead plant with attached seeds can break off and be moved by the wind, thereby dispersing many seeds away from the home site (Liu and Wang, 2009). However, many dead plants remain in place, i.e. are not broken off (Liu and Wang, 2009). The number of canopy-stored seeds is significantly higher than the number released from September to the following March, after which large numbers of canopy-stored seeds are released (Liu and Wang, 2009). Gutterman (1994, 2002) and Liu *et al*. (2014) concluded that delayed seed dispersal is a protection strategy in extreme and unpredictable environment conditions, whereby a persistent soil seed bank is established and massive seed consumption by predators is prevented. The period of maximum seed release of *A. squarrosum* is in late April, when wind velocity is highest, and more than half of the seeds are released from March to May (Gao *et al*., 2014). Seed dispersal declines sharply at the end of July, and a small number of seeds is released subsequently (Gao *et al*., 2014).

Of the 69 species that Liu *et al*. (2004) studied in the Horqin Sandy Land, *A. squarrosum* had an intermediate seed mass. Zhang *et al*. (2005) reported that the small, flat seeds of *A. squarrosum* have good resistance against movement by wind and that they have good retention on the soil. Number and species composition of seeds dispersed to bare patches in the Horqin Sandy Land, Inner Mongolia, was investigated using seed traps during the growing season. There were 71–623 *A. squarrosum* seeds m^{-2} in the seed rain, which was a much higher number than that for any of the other species in the community (Deng and Liu, 2011). Seeds of *A. squarrosum* and 11 other species were collected and sown in bare patches in the Horqin Sandy Land, and seedling emergence was higher (12.2–34.1%) for *A. squarrosum* than for any of the other species (Deng and Liu, 2011). Seedling emergence of *A. squarrosum* in the non-vegetated habitat with moving sand was higher than that on vegetation-covered patches (Deng and Liu, 2011).

Seed dormancy and germination

Seeds of *A. squarrosum* are dormant at maturity in autumn. Germination of freshly matured seeds collected in the Gurbantunggut Desert (Xinjiang Province, China) was <10% at 15/5, 25/10 and 35/20°C (12/12 h) in light (30 $\mu mol\ m^{-2}\ s^{-1}$) and dark (Liu *et al*., 2013), and fresh seeds collected from Minqin, Gansu Province, China, in 2012, 2013 and 2014 germinated <10% at 30/20°C in the dark (Fan *et al*., 2016). Fan *et al*. (2016) concluded that *A. squarrosum* seeds have physiological dormancy, which is consistent with the class of dormancy known to occur in other members of the Amaranthaceae (Baskin and Baskin, 2014). Thus it is expected that gibberellic acid (GA_3) would promote germination and that abscisic acid (ABA) would inhibit it (Finch-Savage and Leubner-Metzger, 2006). At 30/20°C, seed germination percentage increased significantly with an increase in concentration of GA_3, reaching a maximum of 60% with 300 $\mu mol\ l^{-1}$ GA_3 (Liu *et al*., 2010). Fluridone, an inhibitor of ABA (Kucera *et al*., 2005), breaks dormancy in *A. squarrosum* and thus is useful in determining seedlot germination potential (Fan *et al*., 2016).

Since seeds of *A. squarrosum* mature in autumn and germinate in the field in spring, it is assumed that physiological dormancy is broken during winter. After 2 months of cold stratification at 5°C, 70% of the seeds germinated when tested in dark at 30/20°C; more than 95% of the non-germinated seeds were viable (Fan *et al*., 2016). All viable seeds collected in the Tengger Desert germinated after 1 and 2 years storage in an open non-heated room (Wang *et al*., 1998). As physiological dormancy can be broken via afterripening in dry storage at low as well as at high temperatures (Baskin and Baskin, 2014), it is possible that seeds of *A. squarrosum* could come out of dormancy in the field during winter although they may not be imbibed. However, as discussed below, the effects of dry storage at room temperature on seed dormancy/germination of this species are not well understood. In fact, seed germination decreased from 91.6% to 39.2% at 28/16°C (light/dark) after 6 months dry storage at room temperature (Li *et al*., 2006). These authors suggested that storage conditions may have induced the seeds into secondary dormancy.

Among the factors that could influence seed germination, temperature and light are considered to be the most important ones and thus have been studied intensively. Several studies have shown that light has a strong inhibiting effect on germination of *A. squarrosum* seeds. Zheng *et al*. (2004) collected mature seeds in the Mu Us Sandy Land in Inner Mongolia in August 2001 and stored them dry at 4°C for 2 months, after which they germinated to a significantly higher percentage in dark than in light at 15/5, 20/10, 25/15 and 30/20°C. At a photon irradiance of 25 $\mu mol\ m^{-2}\ s^{-1}$, germination at 10/20°C decreased from >70% to <20% when the photoperiod increased from 2 to 12 h (Zheng *et al*., 2004). Liu *et al*. (2013) found that germination was <10% at a 12 h photoperiod at 15/5, 25/10 and 35/20°C; however, they did not test seeds in total darkness. Taken together, the above results indicate that light inhibits seed germination of *A. squarrosum*, which helps explain why seeds can germinate in moving sand dunes where they are covered by wind-blown sand.

However, several studies have reported that the seeds germinate to >90% in alternating light and dark conditions (Tobe *et al*., 2005; Li *et al*., 2006; Liu *et al*., 2012). Furthermore, Tobe *et al*. (2005) found interaction effects of temperature and light at certain temperature regimes. Their seeds were collected in China (Ningxia Province) in October 1995 and stored at room temperature for 2–3 months before they were transported to Japan and then stored at about 0°C. Germination was >90% at alternating temperature regimes of 25/15 and 30/20°C and at constant temperatures of 20 and 25°C in both darkness and light/dark (Tobe *et al*., 2005). However, Zeng (2010) obtained <30% germination at 25/15 and 35/25°C in darkness; germination in light was not tested. Two other studies showed that germination percentage was significantly higher at alternating than at constant temperature in dark and that the optimal alternating temperature regime was 30/20°C (Zheng *et al*., 2004; Cui *et al*., 2007).

After 7 months of dry storage at room temperature, germination of *A. squarrosum* seeds was tested at different water potentials in darkness at 30°C. Germination percentages decreased significantly with an increase in water stress, and it was 50.3, 22.4 and 1.0% at water potentials of 0, –0.2 and –0.8 MPa, respectively (Cui *et al*., 2007). These data imply that germination can occur only when there is no or little water stress, which helps explain the survival strategy for seedlings. That is, seeds can germinate rapidly at a high water potential from May to August during the rainy season (Tobe *et al*., 2005; Zeng, 2010).

In the moving-sand habitat of *A. squarrosum*, burial in sand is one of the factors that could influence seedling survival and establishment. Seedling emergence of *A. halodendron* decreased from 89.8% at 0.5 cm burial depth to 32.0% at 1 cm depth, while that of *A. squarrosum* was 91.2 and 77.8%, respectively (Cui *et al*., 2007). These results may help explain the successional sequence of different species on mobile dunes. At the beginning of sand dune succession, *A. squarrosum* is more tolerant to sand burial and it is replaced by *A. halodendron* when the moving sand dune habitat is converted into a fixed sand dune.

Seedling emergence of *A. squarrosum* decreased from 91.2 to 41.2% when seed burial depth increased from 0.5 to 2 cm, but a few seedlings emerged from a depth >8 cm (Cui *et al*., 2007). Seeds were sown at depths of 0, 1.0, 1.5, 2, 3, 4 and 6 cm in sand in a growth chamber, and seedling emergence was highest at 0.5 cm (Zheng *et al*., 2005b). There was no significant effect on seedling growth in the field when they were buried in sand to 25% of their height (Zhao *et al*., 2013a). Seedling survival was up to 94.8% when sand burial equalled plant height, which indicates that the species has strong tolerance for being buried in sand (Zhao *et al*., 2013a). Zhao *et al*. (2013a, b) concluded that the main cause for seedling death was damage to cell membranes in the leaves due to increased malonaldehyde content. Liu *et al*. (2010) found that GA_3 significantly increased seedling emergence from burial depths of 0.5 and 1 cm.

Seed bank

A good understanding of seed bank ecology is critical to elucidating how species, especially pioneers, survive in unstable habitats (Liu *et al*., 2006; Wang *et al*., 2015). *Agriophyllum squarrosum* has both aerial (canopy-stored) and soil seed banks. A small fraction of *A. squarrosum* seeds fall onto the soil surface and form a soil seed bank before the peak of seed release in spring (Narita and Wada, 1998; Gao *et al*., 2014). However, a large fraction of the seeds is retained on the mother plants (aerial seed bank) until the following March (Ma *et al*., 2008). The size of the aerial seed bank was about three times that of the soil seed bank in April. Only 13.2% of aerial-stored seeds and 9.3% of soil-stored seeds were left at the end of the germination season in August, and seed release was positively related to wind velocity (Gao *et al*., 2014). After the growing season ended, seed release was delayed for a high number of seeds on plants covered by sand, thus keeping a large number of seeds in the home-site habitat (Liu *et al*., 2014).

Agriophyllum squarrosum forms a persistent soil seed bank (Ramawat, 2009; Li *et al*., 2004), but position on dunes and burial depth affect the number of seeds present (Bai *et al*., 2004; Liu *et al*., 2007). Seed bank samples collected along transects across mobile sand dunes in Horqin Sandy Land in Inner Mongolia revealed that an average of 292 viable seeds of *A. squarrosum* m^{-2} were stored in the sand for more than 1 year. Across the dunes, there were more seeds on the lower leeward slope and on the middle and upper windward slopes than at other positions along the transects (Liu *et al*., 2007). On the windward slope, mean seed density decreased gradually from the upper to the lower slope, while an opposite trend was found on the leeward slope (Liu *et al*., 2007). Seeds tended to be concentrated at depths of 20–70 cm, and burial depth gradually increased as follows: lower windward < middle windward < upper windward < upper leeward < middle leeward < lower leeward slope (Liu *et al*., 2007). In a sandy grassland enclosure in Hunshandak Sandland, the number of seeds in the soil seed bank, including those of *A. squarrosum*, increased with time (1, 4 and 9 years) since enclosure, and there was a high correlation with the standing vegetation density (Zheng *et al*., 2005a).

Aerial and soil seed banks play different roles in regulating timing of seed germination in the unpredictable dune ecosystem (Gao *et al*., 2014). In darkness, germination percentage of *A. squarrosum* seeds from the aerial seed bank was significantly higher at 20/10 and 25/15°C than that of seeds from the soil seed bank (Gao *et al*., 2014). At 25/10 and 35/20°C, it was significantly lower in light/dark than in continuous darkness. Germination was about 13 and 40% for seeds from soil and aerial seed banks, respectively, at 30/20°C in the dark.

Seedlings from soil and aerial seed banks emerge at different times, and this has a great impact on seedling survival. Gao *et al*. (2014) showed that seeds in the soil seed bank emerged only in the early part of the growing season (16 April to 15 May), and lack of shallowly buried seeds helped explain the absence of seedling emergence from the soil seed bank later in the growing season. The aerial seed bank is the main contributor to late-emerged seedlings. However, 33.4% of the early-emerged seedlings died within the first month, and almost all of them had done so by the end of the growing season due to frost and drought stress before the onset of the rainy season. On the other hand, survival to reproductive maturity of intermediate- and

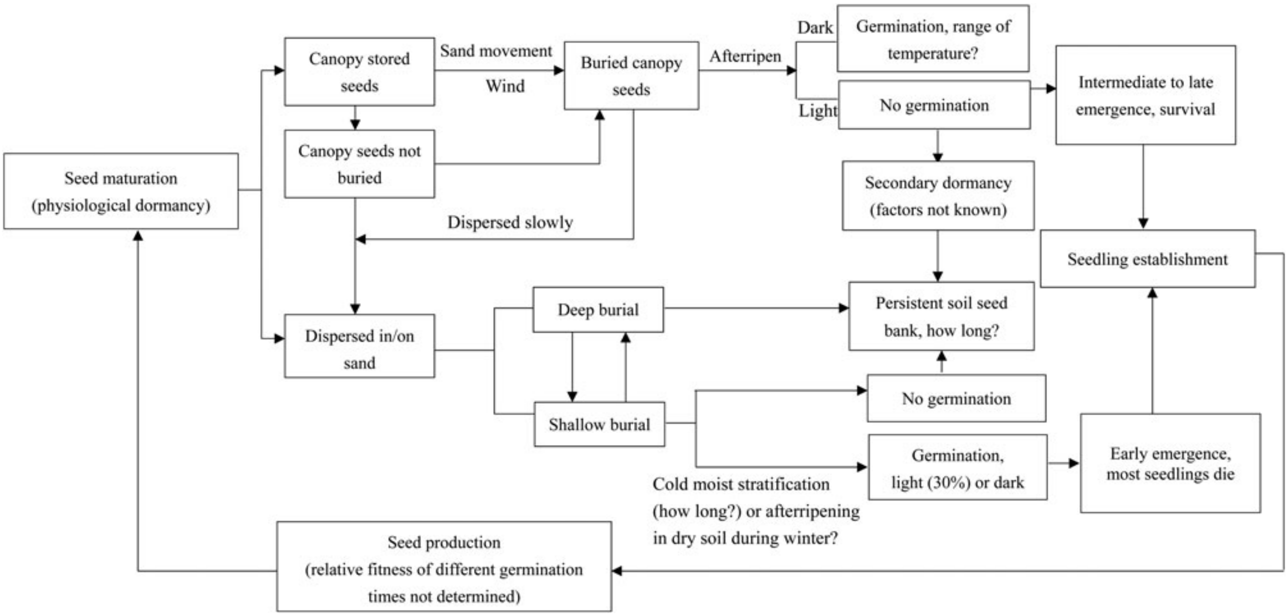

Figure 3. Conceptual model of the seed/seedling dynamics of *Agriophyllum squarrosum*.

late-emerged seedlings was 62.4 and 52%, respectively (Gao *et al*., 2014). These authors speculated that the two kinds of seed banks are a bet-hedging strategy.

Remaining questions about seed germination ecology

Although many studies have been conducted on *A. squarrosum*, a conceptual model of the seed/seedling stage of its life cycle reveals several questions that still need to be answered (Fig. 3). For example, we do not have a good understanding of the seed dormancy-breaking and germination requirements of *A. squarrosum* seeds in the field. As discussed above, 2 months of cold stratification (i.e. seeds imbibed at 4°C) significantly increased seed germination percentages, but more information is needed on the effects of different periods of cold stratification on dormancy break. Also, what are the temperature and light:dark requirements for germination after different periods of cold stratification? Furthermore, how much cold stratification do seeds receive in the field when buried in sand and when attached to dead mother plants during winter? Germination of dry stored *A. squarrosum* seeds was inhibited when tested in light; however, Fan *et al.* (2016) have shown that cold stratification can overcome this inhibition to a certain extent (*ca* 30% germination). To answer these questions, seeds need to be cold stratified for different periods of time and then tested for germination in light and in darkness over a range of temperatures.

Seeds need to be imbibed before they can be cold stratified. We need to know if seeds of *A. squarrosum* buried in the field actually are cold-stratified during winter. The moisture content of seeds in their microhabitats has not been measured during winter; nor has dormancy break of seeds buried in the field during winter been monitored. To better understand changes in germination responses of *A. squarrosum* seeds, they need to be buried in the natural habitat and samples periodically exhumed and tested for germination in light and dark at several temperatures from maturity in autumn until the end of the next germination season. Also, canopy-stored seeds need to be collected at intervals and tested over a range of temperatures in both light and dark. In both cases, seed moisture content needs to be determined each time the seeds are collected from the field. Experiments are also needed to determine the optimum temperature and relative humidity conditions for afterripening *A. squarrosum* seeds, as well as the rate (speed) at which it occurs. In addition, the conditions that induce seeds into secondary dormancy and the speed at which it occurs need to be determined.

New insights and recommendations

Mobile sand dunes are not a suitable habitat for most species, but *A. squarrosum* can become established in bare sand at the initial stage of desert restoration and help create conditions that promote natural plant succession (Nemoto and Lu, 1992). In the deserts of northern China, precipitation is limited and mainly occurs during 2 to 3 months in summer (Yatagai and Yasunari, 1995). If seeded at the right time, seeds of *A. squarrosum* will be buried by wind-blown sand, which provides suitable dark conditions for germination. The best seeding time is May or June, before the onset of the rainy season and high temperatures of summer. *Agriophyllum squarrosum* has a quick response to water and germinates in a short period of time if seeds are non-dormant.

The challenge, then, is to learn how to manage the seeds of *A. squarrosum* so that they are non-dormant at the time they are sown in the field. Our literature review has revealed a major deficiency in the germination studies of *A. squarrosum*. That is, there has been a general lack of testing of fresh seeds, and often seeds have not been tested until they were ≥1 month old. Thus for most studies we do not know if fresh seeds were non-dormant or if they were dormant and afterripened during dry storage at (usually) room temperature. For example, fresh seeds of *A. squarrosum* collected in 2011 at Minqin, Gansu Province, germinated to <10% at 30/20°C in darkness, but they germinated to 95% at three conditions after 3 months of dry storage (afterripening) at room temperature (Fan *et al*., 2016). Thus even if seeds are dormant when they are collected, dry afterripening at room temperatures results in dormancy break.

However, prolonged storage of seeds at room temperature may not necessarily mean that they will be non-dormant in early summer at planting time. In a study by Li *et al*. (2006), after 6 months of dry storage at room temperature germination decreased from 92 to 39%, suggesting that secondary dormancy had been induced since the seeds were still viable. Induction of secondary dormancy during dry storage at room temperatures has been reported in only a few species. For example, freshly collected seeds of *Arthropodium cirratum* (Liliaceae) were dormant, but during 6 months of dry storage at room temperature germination increased to 95%. However, after another 3 months of dry storage germination had decreased to about 55%, and 95% of the non-germinated seeds were viable (Conner and Conner, 1988). A similar pattern of dormancy break followed by dormancy induction during dry storage at room temperatures has been documented for achenes of *Ericameria nauseosa* (Asteraceae) (Love *et al*., 2014) and seeds of *Amaranthus tuberculatus* (Amaranthaceae) (Wu and Owen, 2015).

The answer to the problem of how to store *A. squarrosum* seeds so that they will be non-dormant when sown in the field is to allow the newly collected seeds to afterripen during dry storage at room temperature and then store them dry at a low temperature. Zheng *et al*. (2004) and Tobe *et al*. (2005) reported that when 1- and 3-month-old dry-stored seeds of *A. squarrosum* were subsequently stored at 0 and 4°C, respectively, for 3 months, they germinated to near 100%. Thus we recommend that the way to ensure that seeds of *A. squarrosum* will be non-dormant in early summer is to store them dry at room temperatures for 2–3 months and then dry at 0–5°C until used.

Acknowledgements

The authors would like to thank Liping Xu and Chao Guan for help with the figures. This work was supported by the National Basic Research Program of China (2014CB138700) and the Fundamental Research Funds provided by the State Key Laboratory of Grassland Agro-ecosystems (Lanzhou University).

References

Bai, W.M., Bao, X.M. and Li, L.H. (2004) Effects of *Agriophyllum squarrosum* seed banks on its colonization in a moving sand dune in Hunshandake Sand Land of China. *Journal of Arid Environments* **59**, 151–157.

Baskin, C.C. and Baskin, J.M. (2014) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd edn. San Diego: Elsevier/Academic Press.

Chang, G.Z., Wang, C.Y. and Wang, J.G. (2003) The research report of introduction and cultivation of *Calligonum mongolicum*, *Artemisia sphaerocephala* and *Agriophyllum squarrosum* in Lanzhou, China. *Journal of Traditional Chinese Veterinary Medicine* **1**, 47–49 (in Chinese).

Chang, Z.F., Zhao, M., Han, F.G. and Zhong, S.N. (2005) Study on the habitats of the vegetation on the dunes with the different stabilities in the Minqin sandy area. *Arid Zone Research* **21**, 384–388 (in Chinese).

Chen, B.M., Wang, G.X. and Peng, S.L. (2009) Role of desert annuals in nutrient flow in arid area of Northwestern China: a nutrient reservoir and provider. *Plant Ecology* **201**, 401–409.

Chen, G.X., Zhao, J.C., Zhao, X., Zhao, P.S., Duan, R.J., Nevo, E. and Ma, X.F. (2014) A psammophyte *Agriophyllum squarrosum* (L.) Moq.: a potential food crop. *Genetic Resources and Crop Evolution* **61**, 669–676.

Chen, X. and Duan, Z. (2015) Impacts of soil crusts on soil physicochemical characteristics in different rainfall zones of the arid and semi-arid desert regions of northern China. *Environmental Earth Sciences* **73**, 3335–3347.

Conner, A. and Conner, L. (1988) Germination and dormancy of *Arthropodium cirratum* seeds. *New Zealand Natural Sciences* **15**, 3–10.

Cui, J.Y., Li, Y.L., Zhao, H.L., Su, Y.Z. and Drake, S. (2007) Comparison of seed germination of *Agriophyllum squarrosum* (L.) Moq. and *Artemisia halodendron* Turcz. ex Bess, two dominant species of Horqin desert, China. *Arid Land Research and Management* **21**, 165–179.

Deng, X. and Liu, Z.M. (2011) Relative limitation between seed availability and seedling emergence on vegetation restoration of bare patches in degraded grassland. *Chinese Journal of Ecology* **30**, 2679–2684 (in Chinese).

Fan, S.G., Wang, Y.R., Baskin, C.C., Baskin, J.M. and Hu, X.W. (2016) A rapid method to determine germinability and viability of *Agriophyllum squarrosum* (Amaranthaceae) seeds. *Seed Science and Technology* **44**, 1–6.

Finch-Savage, W.E. and Leubner-Metzger, G. (2006) Seed dormancy and the control of germination. *New Phytologist* **171**, 501–523.

Gao, R.R., Yang, X.J., Yang, F., Wei, L.L., Huang, Z.Y. and Walck, J.L. (2014) Aerial and soil seed banks enable populations of an annual species to cope with an unpredictable dune ecosystem. *Annals of Botany* **114**, 279–287.

Ghaffari, S.M., Balaei, Z., Chatrenoor, T. and Akhani, H. (2015) Cytology of SW Asian Chenopodiaceae: new data from Iran and a review of previous records and correlations with life forms and C_4 photosynthesis. *Plant Systematics and Evolution* **301**, 501–521.

Gutterman, Y. (1994) Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review* **60**, 373–425.

Gutterman, Y. (2002) *Survival Strategies of Annual Desert Plants*. Berlin: Springer.

Han, X.D. (2008) Study on biological characters of *Agriophyllum squarrosum*, a pioneer plant for sand control. *Journal of Gansu Forestry Science and Technology* **32**, 3–8 (in Chinese).

He, Y. (2013) *Study on germination characteristics of psammophytic seeds and effectiveness of aerial seeding on sandland*. MSc dissertation, Beijing Forestry University, Beijing, China (in Chinese).

Huang, Y.X., Zhao, X.Y., Zhang, H.X., Japhet, W., Zuo, X.A., Luo, Y.Y. and Huang, G. (2009) Allometric effects of *Agriophyllum squarrosum* in response to soil nutrients, water, and population density in the Horqin Sandy Land of China. *Journal of Plant Biology* **52**, 210–219.

Jiang, L. (2005) *Seeding biology of the plant species used in air seeding in Ordos Plateau and the optimized scheme for vegetation restoration*. PhD thesis, Beijing Forestry University, Beijing, China (in Chinese).

Kucera, B., Cohn, M.A. and Leubner-Metzger, G. (2005) Plant hormone interactions during seed dormancy release and germination. *Seed Science Research* **15**, 281–307.

Li, S.G. and Chang, X.L. (1992) *Agriophyllum squarrosum* – study of a pioneer species on mobile sand dunes. *Journal of Arid Land Resources and Environment* **6**, 63–70 (in Chinese).

Li, Y.L., Meng, Q.T., Zhao, X.Y. and Zhang, T.H. (2007) Characteristics of species composition and plant diversity in the process of vegetation restoration on moving dunes in the Horqin Sandy Land. *Acta Prataculturae Sinica* **16**, 54–61 (in Chinese).

Li, X.H., Jiang, D.M., Liu, Z.M. and Li, X.L. (2006) Seed germination characteristics of annual species in temperate semi-arid region. *Acta Ecologica Sinica* **26**, 1194–1199 (in Chinese).

Liu, H.L., Song, M.F., Duan, S.M., Wang, X.Y., Zhang, D.Y. and Yin, L.K. (2012) Seed germination strategies of 32 Chenopodiaceae species on the southern Gurbantunggut Desert. *Journal of Desert Research* **32**, 413–420 (in Chinese).

Liu, H.L., Zhang, L.W., Yin, L.K. and Zhang, D.Y. (2013) Effects of temperature, dry storage, and burial on dormancy and germination of seeds of 13 desert plant species from sand dunes in the Gurbantunggut Desert, northwest China. *Arid Land Research and Management* **27**, 65–78.

Liu, M.Z., Jiang, G.M., Yu, S.L., Li, Y.G. and Li, G. (2009) The role of soil seed banks in natural restoration of the degraded Hunshandak Sandlands, northern China. *Restoration Ecology* **17**, 127–136.

Liu, Y.J., Ma, Q.L., Zhang, D.K., Ji, Y.F., Zhang, J.C. and Liu, H.J. (2010) Response of germination rate of three annual plant species to sand burial depths and GA_3 in southern marginal zone of the Tengger Desert. *Arid Zone Research* **27**, 699–704 (in Chinese).

Liu, Z.M., Li, R.P., Li, X.H., Luo, Y.M., Wang, H.M., Jiang, D.M. and Nan, S.H. (2004) A comparative study of seed weight of 69 plant species in Horqin Sandy Land, China. *Acta Phytoecologica Sinica* **28**, 225–230 (in Chinese).

Liu, Z.M., Liu, B. and Qian, J. (2014) Some mechanisms in reproduction of psammophyte to adapt to wind erosion on the active sand dune. *Advances in Geosciences* **1**, 1–8.

Liu, Z.M. and Wang, X.M. (2009) Functions of canopy-stored seeds in the dune ecosystem: conclusions from *Agriophyllum squarrosum* and *Artemisia wudanica*. *Frontiers of Biology in China* **4**, 486–490.

Liu, Z.M., Yan, Q., Baskin, C.C. and Ma, J. (2006) Burial of canopy-stored seeds in the annual psammophyte *Agriophyllum squarrosum* Moq. (Chenopodiaceae) and its ecological significance. *Plant and Soil* **288**, 71–80.

Liu, Z.M., Yan, Q., Liu, B., Ma, J. and Luo, Y. (2007) Persistent soil seed bank in *Agriophyllum squarrosum* (Chenopodiaceae) in a deep sand profile: variation along a transect of an active sand dune. *Journal of Arid Environments* **71**, 236–242.

Love, S.L., Tripepi, R.R. and Salaiz, T. (2014) Influence of harvest timing and storage interval on rabbitbrush seed germination, emergence, and viability. *Native Plants Journal* **15**, 98–108.

Ma, Q.L., Zhang, D.K., Chen, F., Li, Y. and Liu, Y.J. (2008) Study on seed characters of *Agriophyllum squarrosum*, a pioneer plant on mobile sand dune. *Seeds* **27**, 72–76 (in Chinese).

Narita, K. and Wada, N. (1998) Ecological significance of the aerial seed pool of a desert lignified annual, *Blepharis sindica* (Acanthaceae). *Plant Ecology* **135**, 177–184.

Nemoto, M. and Lu, X. (1992) Ecological characteristics of *Agriophyllum squarrosum*, a pioneer annual on sand dunes in eastern Inner Mongolia, China. *Ecological Research* **7**, 183–186.

Pan, Y.X., Wang, X.P., Zhang, Y.F. and Hu, R. (2015) Spatio-temporal variability of root zone soil moisture in artificially revegetated and natural ecosystems at an arid desert area, NW China. *Ecological Engineering* **79**, 100–112.

Qi, K., An, X.L. and Ye, S.H. (2010) Growth characteristics of *Agriophyllum squarrosum*. *Journal of Inner Mongolia Forestry Science and Technology* **36**, 19–21 (in Chinese).

Qiao, J., Zhao, W., Xie, X., Liu, G., Ye, X., Chu, Y., He, H. and Dong, M. (2012) Variation in plant diversity and dominance across dune fixation stages in the Chinese steppe zone. *Journal of Plant Ecology* **5**, 313–319.

Ramawat, K.G. (2009) *Desert Plants: Biology and Biotechnology*. Berlin: Springer.

Tobe, K., Zhang, L. and Omasa, K. (2005) Seed germination and seedling emergence of three annuals growing on desert sand dunes in China. *Annals of Botany* **95**, 649–659.

Wang, X.M., Chen, F. and Dong, Z. (2006) The relative role of climatic and human factors in desertification in semiarid China. *Global Environmental Change* **16**, 48–57.

Wang, Y.C., Ooi, M.K., Ren, G.H., Jiang, D.M., Musa, A., Miao, R.H., Li, X.H., Zhou, Q.L., Tang, J. and Lin, J.X. (2015) Species shifts in above-ground vegetation and the soil seed bank in the inter-dune lowlands of an active dune field in Inner Mongolia, China. *Basic and Applied Ecology* **16**, 490–499.

Wang, Z.L., Wang, G. and Liu, X.M. (1998) Germination stragegy of the temperate sandy desert annual chenopod *Agriophylllum squarrosum*. *Journal of Arid Environments* **40**, 69–76.

Wu, C. and Owen, M.D. (2015) When is the best time to emerge. II: Seed mass, maturation, and afterripening of common waterhemp (*Amaranthus tuberculatus*) natural cohorts. *Weed Science* **63**, 846–854.

Yan, S.G., Shen, Z.B., Li, X.D. and Xu, Q.T. (2015) Effects of spatial and temporal pattern of transition zones between active dunes and interdune lowlands on vegetation restorations. *Scientia Silvae Sinicae* **51**, 103–109 (in Chinese).

Yatagai, A. and Yasunari, T. (1995) Interannual variations of summer precipitation in the arid/semi-arid regions in China and Mongolia: their regionality and relation to the Asian summer monsoon. *Journal of the Meteorological Society of Japan* **73**, 909–923.

Zeng, Y.J. (2010) *Study on seed germination ecology of several dominant plant species growing in arid desert region, China*. PhD dissertation, Lanzhou University, Lanzhou, China (in Chinese).

Zhang, J.Y., Zhao, H.L., Zhang, T.H., Zhao, X.Y. and Drake, S. (2005) Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land. *Journal of Arid Environments* **62**, 555–566.

Zhao, H.L., Qu, H., Zhou, R.L., Li, J., Pan, C.C. and Wang, J. (2013a) Effects of sand burial on growth in two psammophyte seedlings and differences in their physiological responses. *Chinese Journal of Plant Ecology* **37**, 830–838 (in Chinese).

Zhao, H.L., Qu, H., Zhou, R.L., Wang, J., Li, J. and Yun, J.Y. (2013b). Effects of sand burial on growth and physiological process of *Agriophyllum squarrosum* seedlings in Horqin Sand Land of Inner Mongolia, North China. *Chinese Journal of Applied Ecology* **24**, 3367–3372 (in Chinese).

Zhao, L.Y., Li, Z.H., Li, F.R. and Zhao, H.L. (2005) Soil seed bank of plant communities along restoring succession gradients in Horqin Sandy Land. *Acta Ecologica Sinica* **25**, 3204–3211 (in Chinese).

Zhao, P., Capella-Gutíerrez, S., Shi, Y., Zhao, X., Chen, G., Gabaldón, T. and Ma, X.F. (2014) Transcriptomic analysis of a psammophyte food crop, sand rice (*Agriophyllum squarrosum*) and identification of candidate genes essential for sand dune adaptation. *BMC Genomics* **15**, 872. doi: 10.1186/1471-2164-15-872

Zheng, C.L., Cao, Z.L., Zhao, T.N. and Sun, B.P. (2005a) The study on the dynamic of soil seed banks in enclosing sandy grassland. *Research of Soil and Water Conservation* **12**, 169–171 (in Chinese).

Zheng, Y., Gao, Y., An, P., Shimizu, H. and Rimmington, G. M. (2004) Germination characteristics of *Agriophyllum squarrosum*. *Canadian Journal of Botany* **82**, 1662–1670.

Zheng, Y., Xie, Z.X., Gao, Y., Shimizu, H., Jiang, L. and Yu, Y. (2003) Ecological restoration in northern China: germination characteristics of nine key species in relation to air seeding. *Belgian Journal of Botany* **136**, 129–138.

Zheng, Y., Xie, Z.X., Yu, Y., Jiang, L.H., Shimizu, H. and Rimmington, G.M. (2005b) Effects of burial in sand and water supply regime on seedling emergence of six species. *Annals of Botany* **95**, 1237–1245.

Zhou, H., Zhao, W.Z., Luo, W.C. and Liu, B. (2015) Species diversity and vegetation distribution in nebkhas of *Nitraria tangutorum* in the desert steppes of China. *Ecological Research* **30**, 1–10.

Zhu, Z.D. (1998) Concept, cause and control of desertification in China. *Quaternary Sciences* **18**, 145–155.

Zuo, X.A., Zhao, H.L., Zhao, X.Y., Guo, Y.R., Zhang, T.H., Mao, W., Su, N. and Feng, J. (2009a) Species diversity of degraded vegetation in different age restorations in Horqin Sandy Land, northern China. *Acta Prataculturae Sinica* **18**, 9–16.

Zuo, X.A., Zhao, H.L., Zhao, X.Y., Guo, Y.R., Yun, J., Wang, S. and Miyasaka, T. (2009b) Vegetation pattern variation, soil degradation and their relationship along a grassland desertification gradient in Horqin Sandy Land, northern China. *Environmental Geology* **58**, 1227–1237.