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Aerial seed bank affects germination in two small-seeded halophytes in Arab Gulf desert

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ABSTRACT

Aerial seed banks protect seeds against granivores, help seed dispersal over time and maintain seeds in a favorable microhabitat. We hypothesized that the aerial seed bank in maternal tissues could protect halophyte seeds from lethal salinity effects of soils. Effects of aerial (in plant canopy) and room-temperature (lab) storage on subsequent germination behavior were assessed for two small-seeded halophytes: *Halocnemum strobilaceum* (known to be salt tolerant, with a short-term aerial seed bank —less than 9 months) and *Halopeplis perfoliata* (less salt tolerant, with a long-term aerial seed bank more than 17 months). Seeds were germinated in different salinities in both light/dark regime and darkness treatments. Ungerminated seeds from the different salinities were transferred to distilled water to assess their ability to recover germination capacity. Salinity tolerance during germination was much greater in *H. strobilaceum*, compared to *H. perfoliata*. Storage in the aerial seed bank resulted in significant germination-reduction in *H. strobilaceum*, but not in *H. perfoliata*. In *H. strobilaceum* aerial-stored seeds were less tolerant of the salinity than were the room-temperature-stored seeds. These results support the notion that an aerial seed bank protects salt-sensitive seeds from effects of high soil salinity, especially in species that have short-term aerial seed banks.

1. Introduction

The seed bank in desert habitats can play a major role in plant recruitment and population dynamics (Kemp, 1989). Seeds are typically stored in the soil (the soil seed bank) but in some species may be retained in plant canopy (the aerial seed bank) until seed release is triggered (Günster, 1992). Skourou and Arianoutsou (2004) recorded gradual seed release from the aerial seed bank of *Cistus creticus* and *Cistus salviifolius*. Bastida and Talavera (2002) also reported an extended period of seed release (8–16 months) in *Cistus ladanifer* and *Cistus libanotis*. Aerial seed banks are widespread in regions with strongly seasonal climates, poor soils and recurrent fires (Bastida and Talavera, 2002; Simon and Pennington, 2012). They have also been described in arid and semi-arid regions, where they've been shown to play an important role in protecting seeds against soil-living granivores (Günster, 1994). Aerial seed banks can also stop seeds being washed away in surface run-off and may improve germination rates by spreading seed dispersal over a longer period of time (Ellner and Shmida, 1981). Aerial seed storage may also help build up the seed population until conditions are better-suited to seedling establishment (Lamont et al., 1991). Finally, an aerial seed bank may also promote the gradual dispersal of seeds when dead maternal plants of some species act as a seed bank hygrochastically releasing a proportion of their seeds whenever it rains (Gutterman, 1993).

Light is an important regulatory trigger for seed germination in desert plants. Seeds are typically sensitive to light intensity, spectral composition and the duration of exposure (Baskin and Baskin, 1998). Seeds in the aerial seed bank are exposed to diurnal fluctuations in temperature and to full light during storage. It is generally felt that a light requirement effectively prevents the germination of seeds that get buried too deep for the seedling to emerge, since physiologically active light fluxes rarely penetrate more than a few millimeters into the soil (Pons, 1992). Once dispersed in soil, small seeds have a good chance of getting buried and becoming part of an underground seed bank, since little light

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penetrates the soil (Bliss and Smith, 1985). There have been several studies on soil seed-bank light requirements in halophytes living in arid environments (Baskin and Baskin, 1998), but as far as we know there have been no studies that investigate the role of *aerial* seed banks on light requirements in halophytes.

The seeds of halophytes that do not have dispersal structures are generally deposited near the surface of saline soils, where salt concentrations are usually much higher than below the surface (Esechie, 1995). Survival of halophyte seeds in the below-ground seed banks will depend on their capacity for salt tolerance at the germination stage; their ability to tolerate hyper-saline conditions during storage in the soil; and/or their ability to avoid salinity (Ungar, 2001; Kozlowski and Pallardy, 2002). Several studies have concluded that seeds of a few stem succulent halophytes −including *Salicornia herbacea* (Chapman, 1960), *Salicornia rubra* (Khan et al., 2000) and *Salicornia pacifica* (Khan and Weber, 1986) −could germinate at salinities above that of seawater (*c.* 500 mM NaCl). Conversely, seeds of other halophytes such as *Halopeplis perfoliata* (Mahmoud et al., 1983), *Salicornia brachystachya* and *Salicornia dolistachya* (Huiskes et al., 1985) cannot germinate at salinity levels greater than seawater.

Similarly, the ability of the ungerminated seeds in saline solutions to recover their germination capacity after being transferred to distilled water is known to be very low in certain halophytes such as *Zygophyllum simplex* (Khan and Ungar, 1997), *Halogeton glomeratus* (Khan et al., 2001) and *Sporobolus ioclades* (Khan and Gulzar, 2003), suggesting they have greater sensitivity to the higher salinities. Seeds of halophytes that are more sensitive to higher salinity are more likely to die when stored in saline soils. Seed death of halophytes in saline soils has been attributed to osmotic shock effects and/or specific ion toxicity (Ungar, 1991). Many halophytes have very small seeds that are often buried in the soil and so less likely to attract granivores (Ungar, 1991). Hence retention of such seeds in the aerial seed bank may endow certain survival benefits. One expected advantage is protection of seeds from the lethal effects of salinity, especially in salt-sensitive species.

We hypothesized that extended seed storage in the maternal tissues of halophytes may protect them from the caustic effects of salinity below-ground in saline habitats, especially during summer when salinity levels are higher. We expect the role of the aerial seed bank in protecting seeds from soil salinity should be more apparent in salt-sensitive, compared to salt-resistant plants. The aim of this study was to assess the effects of the aerial seed bank on two abundant halophytes: *Halocnemum strobilaceum* and *Halopeplis perfoliata* (Chenopodiaceae), and their germination strategies in the hyper-saline salt marshes of the Arabia. The two species are common halophytes in both coastal and inland salt marshes (Zahran, 1998; EAD, 2012). *Halocnemum strobilaceum* is fairly salt resistant during the germination stage (Qu et al., 2008), while *H. perfoliata* is more salt sensitive (Mahmoud et al., 1983). In addition, *H. strobilaceum* has a fairly short-term aerial seed bank (less than 9 months) and is the most salt tolerant plant in the salt marshes, but *H. perfoliata* has a longer term aerial seed bank (more than 17 months) and is relatively less salt tolerant (Zahran, 1998; EAD, 2012). We assessed the effects of different salinities on final germination and mean germination time under a light/dark regime and in darkness for different seed lots stored at room temperatures and in the field aerial seed bank for different periods of time. We also assessed whether seeds that were not able to germinate in saline solutions could recover germination capacity following transfer to distilled water. Seeds able to recover their germination capacity were expected to be more tolerant to salinity stress.

2. Materials and methods

2.1. Seed retention in the aerial seed bank

In order to assess the durability of aerial seed storage in each species we completely removed all old fruiting structures from 15 tagged individuals of *H. strobilaceum* and *H. perfoliata* just before the onset of the new fruiting season in December, 2011. Fruit color was monitored during December 2011, April 2012, September 2012, November 2012 and April 2013. Fruit samples were collected randomly from the crowns of tagged individuals on the above dates. Fruits were separated and seeds of 50-g fruits were sampled, separated and counted.

2.2. Seed collection and storage

Halocnemum strobilaceum and *H. perfoliata* seeds were collected from a saline desert habitat in Al-Hamryah, Sharjah Emirate, UAE, on the Arabian Gulf coast (25°28′27.95″N and 55°31′46.8″E) during December 2012 and April 2013. Seeds were collected randomly from the large populations to represent the diversity in these species. In the December collection, newly ripened fruits of both species, which were all light brown in color, were separated and stored at room temperature for five months (hereafter referred to as five-month room temperature storage). The April collection of *H. strobilaceum* seeds from the aerial seed bank contained only light brown fruits that had matured in December 2012. These are referred to as five-month aerial seed bank storage. The *H. perfoliata* fruits collected in April from the aerial seed bank were separated according to their colors into light-brown fruits (matured in December 2012) and very dark or almost-black fruits (matured in December 2011). Hereafter, these two seed lots are called the five-month and 17-month aerial seed bank storage, respectively. Seeds from the different lots were air-dried, cleaned and stored in brown paper bags at room temperatures (20 ± 2 °C) until late April, 2013.

2.3. Effect of salinity on seed germination

Seeds from the different groups were germinated in a series of NaCl concentrations (0, 100, 200, 400, 600 and 800 mM for *H. strobilaceum* and 0, 100, 200 and 400 mM NaCl for *H. perfoliata*). These levels were based on preliminary tests that assessed the salinity tolerance of the two species. Seeds were germinated in 9 cm Petri dishes on two layers of Whatman No.1 filter paper, moistened with 10 ml of the test solution. The dishes were wrapped with parafilm to minimize evaporation and incubated at the optimum germination temperatures for the two species, known to be a daily 15/25 °C temperature regime, in either continuous darkness or alternating 12 h light/12 h darkness. The light period coincided with the higher temperature. The temperature regime is equivalent to the night/day temperatures during the rainy season. During dark treatment, the dishes were wrapped in aluminum foil to prevent any exposure to light. For each treatment three replicates of 25 seeds each were used. Radicle emergence was the germination criterion and the number of germinated seeds were counted daily for 14 days following seed soaking. Seeds incubated in the dark were only counted after 14 days.

2.4. Effects of salinity on germination recovery

After 14 days, all the seeds that failed to germinate under the light/dark or dark treatments after being exposed to the different NaCl concentrations were transferred to distilled water. The seeds were incubated at 15/25 °C with the lower temperature coinciding with 12 h darkness and higher temperatures coinciding with 12 h