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Germination strategies of halophyte seeds under salinity

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ABSTRACT

Halophytes are plants of saline habitats that grow under conditions that may vary in extremes of temperatures (freezing to very hot), water availability (drought to water logging) and salinity (mild to almost saturation). Halophytes may also face sudden micro-environmental variations within their habitats. In this review we examine some of the factors that determine the ability of seeds of halophytes to germinate when conditions are optimal for seedling growth and survival.

Seed dormancy (innate, induced or acquired) is an important means of initiating growth under appropriate conditions. Saline environments are often wet and so the seeds of halophytes may remain un-germinated over extended periods even after imbibition if the external environment does not favour germination and seedling survival. Many perennial halophytes, however, do not possess elaborate dormancy systems because they propagate largely through ramets and have no ecological compulsions for seed germination.

The seeds of halophytes also have the capacity to recover from a salinity shock and start germination once salinity is reduced, which may happen following rain. In some cases, imbibition in a low-salt solution may help in osmo-priming and improve germination. Seed heteromorphism is yet another strategy adopted by some halophytes, whereby seeds of different size and colour are produced that germinate consecutively at suitable intervals. Light-dependent germination may also help if the seed is under a dense canopy or buried in debris; germination only occurs once these restraints are removed thus increasing the chances of seedling survival.

1. Introduction

Halophytes are a group of plants that are distributed in a variety of saline habitat, which include inland (playa) or coastal (sabkha) salt-marshes, dunes, deserts, sabkha and playa among others. Not only are the habitats occupied by halophytes varied, but also are their habits, from ephemerals to shrubs and trees. Annual halophytes and perennial herbs generally dominate temperate regions while perennial shrubs are abundant in subtropical areas. There are different ecological and evolutionary compulsions on both annual and perennial halophytes. Annuals, being semelparous (a single reproductive event in a lifetime), produce seeds once in their life and develop elaborate dormancy mechanisms that usually maintain seed viability when exposed to conditions unfavourable for germination. Perennials, on the other hand, being iteroparous (many reproductive events in a lifetime) do not necessarily have to recruit (introduction of new genetic individuals) to their populations every year and use ramets to propagate clonally. Their ecological or proximate strategy (based on one life cycle) to be successful is to produce copies of the best available genotype; however, their ultimate or evolutionary strategy (based on numerous life cycles in evolutionary time) is recruitment from seeds during years when conditions for growth are good. This occasional recruitment of genets (new genetic individuals) contributes to increased genetic variation of the population for their ultimate success. In this review, we will discuss various strategies adopted by halophyte seeds from subtropical and temperate regions to negotiate extreme temperature and water stress under highly saline conditions.

2. Seed bank dynamics

The role of a seed bank of halophytes in a subtropical desert community appears to be different from that in a temperate salt marsh or salt desert community (Ungar, 2001). Halophytes that are distributed in temperate habitats are either annual or perennial herbs

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Table 1
Seed bank characteristics of halophytes from different habitats.

Habitat	Species	Seed bank type	Seed (m^2)	Reference
Sub tropical	*Arthrocnemum macrostachyum*	Persistent	141,509–2987	Gul and Khan (1998)
	Aeluropus lagopoides	Persistent	1550–50	Aziz and Khan (1996)
	Arthrocnemum indicum	Persistent	110	Saeed and Khan (unpublished)
	Atriplex stocksii	Persistent	810–180	Aziz and Khan (1996)
	Cressa cretica	Persistent	2800–250	Aziz and Khan (1996)
	Cyperus arenarius	Persistent	28,309–1769	Khan et al. (2008)
	Cyperus conglomeratus	Transient	380–0	Aziz and Khan (1996)
	Dactyloctenium scindicum	Transient	53–0	Aysha and Gul (unpublished)
	Halopyrum mucronatum	Transient	350–0	Aziz and Khan (1996)
	Haloxylon stocksii	Persistent	35–5	Khan (1993)
	Heliotropium currassavicum	Transient	440–0	Aziz and Khan (1996)
	Limonium stocksii	Persistent	5800–100	Zia et al. (2007)
	Polycarpaea spicata	Transient	30–0	Aziz and Khan (1996)
	Salsola drumondii	Persistent	700–20	Aysha and Gul (unpublished)
	Salsola imbricata	Transient	2654–0	Khan et al. (2008)
	Suaeda fruticosa	Persistent	900–250	Khan (1993)
	Zygophyllum simplex	Persistent	330–100	Aziz and Khan (1996)
Temperate moist	*Atriplex patula*	Persistent	2100	Welling et al. (1988)
	Atriplex prostrata	Persistent	6687–923	Ungar (2001)
	Atriplex prostrata	Persistent	108,280	Ungar (1984)
	Hordeum jubatum	Persistent	4715–1569	Ungar (2001) and Badger and Ungar (1994)
	Juncus gerardii	Persistent	13,669	Jutila (1998)
	Phragmites australis	Persistent	1400	Welling et al. (1988)
	Puccinellia maritima	Persistent	1130	Bernhardt and Handke (1992)
	Salicornia europaea	Persistent	85,000–35,000	Philipupillai and Ungar (1984)
	Salicornia-Hordeum	Persistent	479,200	Badger and Ungar (1994)
	Solidago sempervirens	Persistent	58	Lee (1993)
	Spartina alterniflora	Transient	42–0	Hartman (1988)
	Spartina patens	Transient	470–0	Shumway and Bertness (1992)
	Spergularia marina	Persistent	488,708–67,198	Ungar (2001)
	Suaeda maritima	Persistent	27	Hutchings and Russell (1989)
	Suaeda vera	Persistent	20,494	Ungar and Woodell (1993)
Temperate dry	*Allenrolfea occidentalis*	Persistent	86,602–5000	Gul and Weber (2001)
	Distichlis spicata	Persistent	850	Smith and Kadlec (1983)
	Holosteum umbelatum	Persistent	105,960–3311	Gul and Weber (2001)
	Kochia americana	Transient	509–0	Gul and Weber (2001)
	Kochia scoparia	Transient	509–0	Gul and Weber (2001)
	Salicornia rubra	Persistent	10,000–1000	Gul and Weber (2001)
	Salicornia utahensis	Persistent	2457–509	Gul and Weber (2001)
	Scirpus maritimus	Persistent	2194	Smith and Kadlec (1983)
	Suaeda depressa	Persistent	3057–509	Gul and Weber (2001)

(which die down over winter) with few woody species while those of subtropical salt marshes are primarily perennial shrubs. The role of dormancy differs in the two regions and it will be discussed in detail later in this section.

There are two levels of survival strategy: (1) to be successful in a given life-cycle time, referred to as ecological or proximate strategy and (2) to be successful in maintaining the lineage over evolutionary time, referred to as either evolutionary or ultimate strategy. Seed dormancy as a strategy for the success at the proximate scale makes sense for annuals as they have only one chance to produce seeds and, in order to perpetuate, it is necessary that they leave at least one descendent (Harper, 1977). To achieve this objective, seeds of annual halophytes have developed a plethora of tactics to survive drought, flooding, high salinity and extremes of temperatures (Ungar, 1995). For instance they have innate, enforced or induced dormancy to prevent them from germinating when conditions are not conducive for seedling survival (Khan and Ungar, 1996). Perennial halophytes, however, being iteroparous have a number of opportunities to produce seed. Therefore they are under no adaptive pressure to develop seed dormancy mechanisms to deal with extremes of various environmental factors and rely primarily on clonal growth to be successful at the proximate level. Remaining connected to the mother plant is advantageous to a young and vulnerable ramet through provision of nutrient and water in an environment which may be unusually harsh.

2.1. *Subtropical habitats*

Halophytes particularly in the subtropical desert area of the Arabian Seacoast around Karachi, Pakistan produce seeds every year and sometimes twice a year (Gul and Khan, 2006). Salt-marsh species from this area maintain a seed bank, although the maximum density of seeds in the subtropical marsh is only 1% of a coastal marsh from the temperate zone (Table 1). Gul and Khan (1998) showed that *Arthrocnemum macrostachyum*, the species with the maximum seed density in the above mentioned subtropical marsh (Table 1), maintained a persistent and a large seed bank (more than 140,000 seed m^{-2}) but there was little germination under field conditions. Even if soil cores were collected from such sites and watered regularly for months under laboratory conditions, no seed germinated. However when seeds were collected from underneath these populations immediately after dispersal, they remained viable for a few years and germinated well in Petri plates under high temperature and salinity in laboratory conditions (Khan and Gul, 2006).

We have conducted experiments for several years on four salt-marsh species (*Arthrocnemum macrostachyum*, *Arthrocnemum indicum*, *Cyperus arenarius* and *Limonium stocksii*) to investigate whether seeds in tropical habitats remained viable when buried in soil under natural or artificial conditions. Packets of seed were buried amongst their respective populations or in pots filled with beach sand placed in an open green house or, thirdly, stored under