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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.

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	Persistent	110	Saeed and Khan (unpublished)	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	Transient	53–0	Aysha and Gul (unpublished)	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	Persistent	700–20	Aysha and Gul (unpublished)	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

Table 2

Viability loss, germination and dormancy of halophyte seeds in natural and artificial seed banks (Mehrunnisa, unpublished).

Species	Viability loss (months)			Seed germination/dormancy (%)		
	Natural field	Dry green-house storage	Dry lab storage	Natural field	Dry green-house storage	Dry lab storage
<i>Arthrocnemum indicum</i>	12	10	12	20/80	5/95	10/90
<i>Arthrocnemum macrostachyum</i>	>25	>25	>25	60/40	30/70	20/80
<i>Cressa cretica</i>	14	15	14	20/80	25/75	35/65
<i>Cyperus arenarius</i>	>25	>25	>25	20/80	50/50	5/95
<i>Limonium stocksii</i>	>25	>25	>25	100/0	100/0	100/0

laboratory conditions. Packets were removed monthly to study germination and viability. These data (Table 2) indicate that all these seeds showed similar responses in all burial experiments exhibiting about 90% germination at the end of 14 months and remained viable for at least 25 months. Seeds of *Arthrocnemum indicum* had innate dormancy but gradually died after 12 months. Seeds of *Cyperus arenarius* had no dormancy but storage in soil induced dormancy and all seeds progressively lost their viability. There seems to be a clear cut difference when seeds are present directly in the soil or placed in a nylon packet. Seeds hardly ever germinated when soil cores were watered in laboratory conditions but seeds from packets did for some months. In the absence of biochemical data, it can only be speculated that there seems to be some ecological constraint which resulted in induced dormancy of seeds.

Several studies conducted in an inland salt-desert community to determine if seed exist in soil and whether they have a transient or persistent seed bank showed that a number of species (*Cressa cretica*, *Haloxylon stocksii*, *Salsola imbricata*, and *Sporobolus ioclados*) had a transient seed bank and depleted gradually in few months after dispersal (Khan, 1990; Zaman and Khan, 1992). *Suaeda fruticosa*, however, retained a persistent (necessarily for more than one season but could be for numerous seasons) seed bank of from 250 to 1000 seeds m⁻² (Khan, 1990, 1993). Seed densities of *Cressa*, *Salsola*, and *Sporobolus* species decreased from February until May and by June no seeds were left in the seed bank (Zaman and Khan, 1992). For a salt marsh, as opposed to the salt desert, Khan (1993) reported that *Cressa cretica* had a seed bank of 2800 seeds m⁻² in May in an Arabian Seacoast marsh site near Karachi, Pakistan. From February to December the seed bank decreased from 1600 to 300 seeds m⁻² but with the dispersal of new seeds, which begins in December and lasts up to February, the number of seeds in the seed bank increased to 2800 seeds m⁻². The lower recruitment by seeds in the salt-desert habitat rather than the salt marsh was because of the intense environmental stress caused by the high temperatures, low soil moisture and high soil salinity to which seeds were exposed in the salt desert (Khan, 1993), where some seeds of *Cressa cretica* germinated but most of the seedlings died indicating that recruitment was primarily through ramets.

For seed germination of the species that are distributed in the subtropical desert regions, availability of moisture rather than temperature is a more important signal without which there will be no germination. Scarcity of water leading to high salinity coupled with high temperature may cause heavy mortality in seeds of some species. For example *Arthrocnemum macrostachyum* produced a few hundred thousand seeds in every square metre of seed bank, but when viability test were performed every month for 12 months most of them died in a few months (Gul and Khan, 1998). Populations of *Aeluropus lagopoides* that grew both in salt marsh and on sand dunes had relatively more viable seeds in soil cores collected from sand dunes than those from the marsh (Gulzar and Khan unpublished data). Subtropical halophyte populations are dominated by ramet-producing rhizomatous perennials, but those populations that are recruited through seeds do so after a considerable monsoon rain, which washes salt away or dilutes it.

Why then are numerous seeds produced if recruitment through seeds is rare? It transpires that in order to succeed at the proximate level making copies of the same genotype may suffice to maintain the continuity of population. However, survival at the ultimate (evolutionary) scale would be at risk due to continuous change in the environmental conditions. In subtropical regions on average 5–10 episodes of high rainfall are recorded during a century. During these seasons rains start early and persist to the end of monsoon with about 3–4 times higher rainfall than the average. These seasons are conducive to introducing new genotypes and thereby increase the genetic diversity of the population that may ensure its survival at the ultimate scale.

In summary, seeds banks of subtropical halophytes showed a similar pattern across saline habitats. Most seeds after dispersal failed to germinate under natural conditions because of either innate or enforced dormancy. Again, most of the seeds both from coastal and near coastal populations begin to disappear quickly from the seed bank or loose ability to germinate. There are a few exceptions like *Arthrocnemum indicum* in coastal marshes and *Suaeda fruticosa* in near coastal marshes, which maintain a persistent seed bank. After a considerable rainfall, which occurs at intervals of a few years, a few seeds of *Arthrocnemum macrostachyum* germinate in coastal areas compared to a large number of *Suaeda fruticosa* in inland areas. It appears that the main strategies for recruitment in subtropical halophytes are through clonal growth and seeds are only produced to seek a chance of introducing a new genetic individual but also a rare long term dispersal to a safe site (Ungar, 1995).

2.2. Temperate moist marshes

Tolerance of seeds to high concentrations of salts with an ability to germinate at the first opportunity is the hallmark of temperate salt marsh halophytes (Ungar, 1995) because they can often remain in highly saline water for months. Seeds of species from this region usually maintain a large persistent seed bank and germinate readily during early spring (Table 1; Khan and Ungar, 1986a) when soil salinity is reduced and the temperature is warmer.

To meet any exigency, seeds in these temperate saline habitats may possess the following characteristics singly or in any combination: (1) the ability to germinate at seawater or higher salinity; (2) the induction and enforcement of dormancy under saline conditions; and (3) the capacity of seeds to remain viable after exposure to hyper-saline conditions (Ungar, 2001). Several investigators have reported that when seeds of halophytes have enforced dormancy under hyper-saline conditions, this is alleviated when they are subjected to non-saline conditions, while seeds of intolerant glycophytes survive for only a short time at seawater salinity levels (Ungar, 1978, 1995; Woodell, 1985; Keiffer and Ungar, 1997; Khan and Ungar, 1997a; Jutila, 1998). Saline conditions often inhibit the germination of halophyte seeds, but in contrast to intolerant species, halophyte seeds remain viable and are able to germinate when salinity is reduced (Darwin, 1857; Keiffer and Ungar, 1997; Khan and Ungar, 1997a,b; Jutila, 1998).

Tolerance at the germination stage can be determined by measuring two factors: the capacity of seeds to remain viable under hyper-saline conditions and the maximal salinity limit at which germination occurs (Ungar, 1991).

Seeds of halophytes in the temperate environment usually mature during the late fall and undergo a period of dormancy (innate, induced or enforced, Harper, 1977). These seeds commence germination during early spring which continues up to July (Khan and Ungar, 1996). Early germination in the presence of enough water confers an ecological advantage to these seedlings. Their size increases rapidly and they produce long and deep root system which protects them in the late spring and early summer when the frequency of rains decreases and drought may set in Khan and Ungar (1986b). This usually causes a substantial rise in soil salinity of the uppermost soil layer and the smaller and younger seedlings have little chance of survival.

2.3. Temperate dry cold deserts

There is little published data available on the survival and viability of playa species, particularly those of the Great Basin Desert, under natural conditions. During the spring, emergence of a large number of seedlings was recorded for both annual and perennial halophytes. Species like *Salicornia rubra*, *Halogeton glomeratus*, *Salicornia utahensis*, *Allenrolfea occidentalis*, *Atriplex prostrata*, *Atriplex rosea*, *Salsola iberica*, *Suaeda moquinii*, *Kochia scoparia*, *Kochia americana*, *Sarcobatus vermiculatus*, *Chrysothamnus nauseosus* and a number of others produced numerous seedlings that indicates that the seeds were able to survive high salinity, cold temperature and freezing stress and readily germinated as the temperature increased and water from melting snow lowered salt concentrations (Gul and Khan, personal observation). There is a need to collect this kind of information from these habitats to understand better their ecological responses.

In temperate cold deserts like the Great Basin, seeds are usually frozen in the playas that exist in the valleys but begin to germinate in early spring with warmer temperature and an increase in fresh water due to snow melt (Gul and Weber, 1998). Seedling emergence in these salt marshes is immense. Their germination begins in late March and April and continues up to June. Our data indicate that most of these seeds germinate with a temperature regime of 25–35 °C (Khan and Gul, 2006), but suffer heavy mortality as the daytime temperature rises and salinity increases, so that less than 10% of seedlings reach the flowering and fruiting stage.

2.4. Conclusions

It seems that different patterns of germination exist in all three climatic conditions. In the subtropical region, since a large number of species are perennials, there are few ecological compulsions for seeds to germinate so halophytes here do not usually possess elaborate dormancy systems. In the subtropical region availability of water is a primary factor and a critical quantity of moisture has to be available for seeds to germinate. Monsoon rains (July and August) decrease soil salinity as well as lower the ambient and soil temperatures along with providing appropriate photoperiod. Most species do not maintain a persistent seed bank. The seed bank size is generally much lower than reported for temperate saline habitats. Seeds are ready to germinate when dispersed but dormancy is induced on seeds quite rapidly under natural conditions. Recruitment primarily occurs through rhizomes. Seeds from the perennial species inhabiting subtropical saline sites survive poorly in their native soils. Seeds from temperate habitats (both moist and dry) survive winter, in saline and often wet conditions and germinate readily when the temperature becomes warmer during early spring.

3. Salinity, light and temperature

Salinity tolerance of seeds involves both the period in the soil (when seed may be exposed to high salinity as well as temperature extremes) and when they begin to germinate. Here we will discuss the level of their tolerance during the process of germination under laboratory conditions. Seeds of halophytes are quite salt tolerant although less than 10% may germinate in up to 1.7 M NaCl (Chapman, 1960). Species reported to have high salt tolerance at the germination stage include *Suaeda aralocapsica* (1.5 M NaCl, Wang et al., 2008) and *Limonium vulgare* (1.5 M NaCl, Woodell, 1985); *Sarcocornia perennis* (1.3 M NaCl, Redondo et al., 2004), *Haloxylon ammodendron* (1.3 M NaCl, Huang et al., 2003) and *Haloxylon persicum* (1.3 M NaCl, Tobe et al., 2000); *Tamarix* sp. (1 M NaCl Waisel, 1958; Ungar, 1967); *Kochia scoparia* (around 1 M NaCl, Khan et al., 2001b), *Arthrocnemum macrostachyum* (around 1 M NaCl, Khan and Gul, 1998), *Suaeda torreyana*, *Salicornia rubra* (around 1 M NaCl, Khan et al., 2000, 2001a), *Salsola iberica* (around 1 M NaCl, Khan et al., 2002a), and *Halogeton glomeratus* (around 1 M NaCl, Khan et al., 2001c). Additionally, seeds of around 50 halophytes can germinate in salinity above that of seawater which varies from 500 to 600 mM and sometimes more in the case of species found in sabkha. We will examine now the salinity tolerance of halophytes belonging to three different ecosystems.

3.1. Subtropical coastal habitats

Seeds of halophytes from this region vary in their salinity tolerance. Some species may germinate at 1.0 M NaCl while others hardly germinate in 0.2 M NaCl or less (Table 3). The most highly salt tolerant species reported so far is *Arthrocnemum macrostachyum* (1 M NaCl, Gul and Khan, 1998) followed by *Cressa cretica* (Khan, 1991), *Kochia prostrata* (Orolovsky et al., 2011), *Salsola imbricata* (Mehrunnisa et al., 2007) and *Halocnemum salicornicum* (El-Keblawy and Al-Shamsi, 2008) (0.8–0.9 M NaCl). A number of species showed about 10% germination at concentrations close to seawater (0.6 M NaCl; Table 3). However, many like *Zygophyllum simplex* (Khan and Ungar, 1997b), *Atriplex stocksii* (Khan and Rizvi, 1994), and *Eragrostis ciliaris* (Shaikh et al., unpublished) could not germinate at more than 0.2–0.35 M NaCl.

Most species of the region are sensitive to change in temperature and 30 °C day and 20 °C at night appears to be the optimal regime for germination (Table 4; Gul and Weber, 1999; Khan et al., 2001b, 2002a; Khan and Gul, 2002). Species like *Suaeda fruticosa*, *Arthrocnemum macrostachyum*, *Atriplex stocksii*, *Haloxylon stocksii*, *Limonium vulgare* and *Salsola imbricata* were less sensitive to temperature regime compared to *Aeluropus lagopoides*, *Desmostachya bippinata*, *Halopyrum mucronatum* and *Zygophyllum simplex* (Table 4).

Light (photoperiod) is an important factor in seed germination because in many seeds, phytochrome-mediated responses play a critical role in determining the time of germination and thus become a crucial part of the evolutionary strategy to impose conditional dormancy to protect seedlings from environmental extremes. The response of the seed of halophytes to light during seed germination varies from no germination (Khan and Gulzar, 2003; Ahmed and Khan, 2010; Saeed et al., 2011) through a substantial reduction (Khan and Gulzar, 2003; El-Keblawy et al., 2011a,b; Gulzar, unpublished) to some reduction (El-Keblawy and Al-Shamsi, 2008) and finally little control of light on germination (Zia and Khan, 2004; Li et al., 2005). Germination of seeds of various halophytes occurs during that time of the year when a combination of day length, temperature, and salinity are optimal (Table 5). Zaman et al. (2009) reported that *Tamarix aucheriana* seeds germinated better in light than in dark. In *Pancreatium maritimum* (Keren and Evenari, 1974) and *Calligonum comosum* (Koller, 1957) seeds germinate when the micropyle is aligned towards light and

Table 3

Sodium chloride concentration at which seed germination of subtropical halophytes was reduced from 75–100% to about >10% but not zero.

Species	Habit	NaCl (M)	References
<i>Arthrocnemum indicum</i>	SS	1.00	Khan and Gul (1998)
<i>Cressa cretica</i>	DF	0.85	Khan (1991)
<i>Kochia prostrata</i>	LS	0.85	Orlovsky et al. (2011)
<i>Salsola imbricata</i>	LS	0.8	Mehrunnisa et al. (2007)
<i>Haloxylon salicornicum</i>	SS	0.8	El-Keblawy and Al-Shamsi (2008)
<i>Salicornia brachiata</i>	SS	0.6	Joshi and Iyengar (1982)
<i>Prosopis juliflora</i>	DF	0.6	El-Keblawy and Al-Rawai (2005)
<i>Suaeda fruticosa</i>	LS	0.5	Khan and Ungar (1998b)
<i>Haloxylon stocksii</i>	SS	0.5	Khan and Ungar (1996)
<i>Phragmites karka</i>	G	0.5	Zehra and Khan (2007)
<i>Dicanthium annulatum</i>	G	0.5	Shaikh (unpublished)
<i>Aeluropus lagopoides</i>	G	0.5	Gulzar and Khan (2001)
<i>Sporobolus ioclados</i>	G	0.5	Khan and Gulzar (2003)
<i>Urochondra setulosa</i>	G	0.5	Gulzar et al. (2001)
<i>Desmostachya bipinnata</i>	G	0.5	Gulzar et al. (2007)
<i>Limonium stocksii</i>	DF	0.4	Zia and Khan (2004)
<i>Atriplex stocksii</i>	DF	0.35	Khan and Rizvi (1994)
<i>Cotula cornopifolia</i>	LS	0.34	Patridge and Wilson (1987)
<i>Eragrostis ciliaris</i>	G	0.25	Khan (unpublished data)

Note: SS, stem succulent; DF, Dicotyledonous Forb; LS, leaf succulent; G, grass.

Table 4

Germination response of halophytes from different habitats at various temperature regimes.

Habitat	Species	5/15	5/25	10//20	15/25	20/30	15/35	25/35	Reference
Sub tropical	<i>Aeluropus lagopoides</i>	–	–	+	+	+++	–	++	Gulzar and Khan (2001)
	<i>Arthrocnemum macrostachyum</i>	–	–	++	+++	+++	–	++	Khan and Gul (1998)
	<i>Atriplex stocksii</i>	–	–	+++	++	++	–	++	Khan and Rizvi (1994)
	<i>Cressa cretica</i>	–	–	+++	++	++	–	+	Khan (1991)
	<i>Desmostachya bipinnata</i>	–	–	+	+	++	–	+++	Gulzar et al. (2007)
	<i>Halopyrum mucronatum</i>	–	–	+	+	++	–	+++	Khan and Ungar (2001b)
	<i>Haloxylon stocksii</i>	–	–	+++	+++	+++	–	++	Khan and Ungar (1996)
	<i>Limonium stocksii</i>	–	–	+	++	+++	–	+	Zia and Khan (2004)
	<i>Limonium vulgare</i>	–	–	++	++	+++	–	++	Woodell (1985)
	<i>Salsola imbricata</i>	–	–	++	++	+++	–	++	Mehrunnisa et al. (2007)
	<i>Sporobolus ioclados</i>	–	–	++	++	+++	–	++	Khan and Gulzar (2003)
	<i>Suaeda fruticosa</i>	–	–	+	+++	+++	–	++	Khan and Ungar (1998b)
	<i>Urochondra setulosa</i>	–	–	+	++	+++	–	++	Gulzar et al. (2001)
	<i>Zygophyllum simplex</i>	–	–	+	+	+++	–	++	Khan and Ungar (1997a,b)
Temperate moist	<i>Atriplex centralasiatica</i> –Black seeds	–	–	++	+++	++	–	++	Li et al. (2008)
	<i>Atriplex centralasiatica</i> –Brown seeds	–	–	++	+++	++	–	+	Li et al. (2008)
	<i>Atriplex prostrata</i>	+	+++	+	–	++	–	–	Khan et al. (2003)
	<i>Cochlearia anglica</i>	+++	+	++	–	+	–	–	Ungar (1967)
	<i>Crithmum maritimum</i>	+++	++	++	–	–	–	–	Okusanya (1979)
	<i>Hordeum jubatum</i>	+++	+++	+++	–	+	–	–	Badger and Ungar (1989)
	<i>Polygonum aviculare</i>	+++	++	+++	–	+	–	–	Khan and Ungar (1998a,b)
	<i>Salicornia europaea</i>	++	+++	++	–	+	–	–	Ungar (1977)
	<i>Salicornia stricta</i>	+	+++	++	–	+	–	–	Langlois (1966)
	<i>Spergularia marina</i>	+++	+	++	–	–	–	–	Okusanya and Ungar (1983)
	<i>Suaeda depressa</i>	+	+++	++	–	–	–	–	Khan and Gul (2006)
	<i>Allenrolfea occidentalis</i>	–	–	+	++	+++	–	+++	Gul and Weber (1999)
	<i>Atriplex rosea</i>	+	–	++	++	+++	–	++	Khan et al. (2004)
	<i>Chloris virgata</i>	–	–	–	++	+++	–	–	Zhang et al. (2011)
Temperate dry	<i>Chrysothamnus nauseosus</i>	+	–	+	++	+++	–	+++	Khan et al. (1987)
	<i>Halogeton glomeratus</i>	++	–	+	++	+++	–	++	Ahmed and Khan (2010)
	<i>Kalidium capsicum</i>	–	–	++	–	–	+++	–	Li and Ximing (2007a)
	<i>Kalidium foliatum</i>	–	–	++	–	–	+++	–	Li and Ximing (2007a)
	<i>Kochia scoparia</i>	++	–	++	++	++	–	+++	Khan et al. (2001a,b,c)
	<i>Lepidium latifolium</i>	–	–	++	++	+++	–	+	Ahmed and Khan (2010)
	<i>Paganum hermala</i>	–	–	+	++	+++	–	++	Ahmed and Khan (2010)
	<i>Salicornia rubra</i>	+	–	++	++	+++	–	++	Khan et al. (2000)
	<i>Salicornia utahensis</i>	++	–	?	++	++	–	++	Gul and Khan (2006)
	<i>Salsola iberica</i>	+	–	++	++	+++	–	+++	Khan et al. (2002a)
	<i>Sarcobatus vermiculatus</i>	++	–	++	++	+++	–	++	Khan et al. (2002b)
	<i>Suaeda heterophylla</i>	–	–	+	++	+++	–	++	Hameed et al. (unpublished)
	<i>Suaeda moquinii</i>	++	–	++	++	+++	–	++	Khan et al. (2001a)
	<i>Suaeda physophora</i>	–	–	+++	–	–	++	–	Li and Ximing (2007b)
<i>Triglochin maritima</i>	–	–	++	++	+++	–	+++	Khan and Ungar (1999)	

Note: '–', not tested; '+', poor; '++', better; '+++', best germination.

Table 5
Germination percentages of halophytes from different habitats in photoperiod (which will vary from one habitat to other) with and without NaCl.

Habitat	Species	Non-saline		Saline		Reference
		Light	Dark	Light	Dark	
Sub tropical	<i>Aeluropus lagopoides</i>	100	84	31	6	Khan and Gulzar (2003)
	<i>Arthrocnemum indicum</i>	67	62	2	0	Saeed et al. (2011)
	<i>Cyperus arenarius</i>	99	13	5	2	Gulzar (unpublished data)
	<i>Cyperus conglomeratus</i>	80	40	–	–	El-Keblawy et al. (2011b)
	<i>Desmostachya bipinnata</i>	96	95	40	20	Gulzar et al. (2007)
	<i>Dicanthium annulatum</i>	100	94	10	0	Khan (unpublished data)
	<i>Halopyrum mucronatum</i>	95	96	0	3	Khan and Gulzar (2003)
	<i>Haloxylon salicornicum</i>	80	70	–	–	El-Keblawy and Al-Shamsi (2008)
	<i>Lasiurus scindicus</i>	75	85	–	–	El-Keblawy et al. (2011a,b)
	<i>Limonium stocksii</i>	100	100	3	1	Zia and Khan (2004)
	<i>Panicum turgidum</i>	75	85	–	–	El-Keblawy et al. (2011a)
	<i>Phragmites karka</i>	100	52	13	2	Zehra and Khan (2007)
	<i>Prosopis juliflora</i>	83	81	1	2	El-Keblawy and Al-Rawai (2005)
	<i>Salsola imbricata</i>	95	93	5	4	Mehrunnisa et al. (2007)
	<i>Sporobolus ioclados</i>	93	9	15	0	Khan and Gulzar (2003)
	<i>Urochondra setulosa</i>	100	50	9	0	Khan and Gulzar (2003)
	Temperate moist	<i>Atriplex centralasiatica</i>	94	96	20	20
<i>Cyperus capitatus</i>		86	89	76	82	Redondo-Gómez et al. (2011)
<i>Kalidium caspicum</i>		100	100	10	–	Tobe et al. (2000)
<i>Suaeda salsa</i>		98	97	38	45	Li et al. (2005)
<i>Suaeda salsa</i> (Black seed)		91	90	7	1	Song et al. (2008)
<i>Suaeda salsa</i> (Brown seed)		98	97	38	45	Song et al. (2008)
Temperate dry		<i>Allenrolfea occidentalis</i>	100	58	27	2
	<i>Halogeton glomeratus</i>	100	96	4	0	Ahmed and Khan (2010)
	<i>Halostachys caspica</i>	100	20	–	–	Tobe et al. (2000)
	<i>Haloxylon ammodendron</i>	81	82	1	–	Huang et al. (2003)
	<i>Lepidium latifolium</i>	100	0	10	0	Ahmed and Khan (2010)
	<i>Peganum harmala</i>	81	40	5	0	Ahmed and Khan (2010)
	<i>Salicornia pacifica</i>	90	50	55	5	Khan and Weber (1986)
	<i>Salsola affinis</i>	87	87	2	–	Wei et al. (2008)
	<i>Sarcocornia fruticosa</i>	85	55	4	14	Redondo et al. (2004)
	<i>Sarcocornia perennis</i>	90	0	5	0	Redondo et al. (2004)
	<i>Sarcocornia perennis</i> × <i>fruticosa</i>	90	0	2	0	Redondo et al. (2004)
	<i>Suaeda aralocaspica</i> Black seed	35	35	2	–	Wang et al. (2008)
	<i>Suaeda aralocaspica</i> Brown seed	90	90	10	–	Wang et al. (2008)
<i>Tanacetum cinerariifolium</i>	34	52	–	16	Li et al. (2011)	

light penetrates through this structure. In some species light alone controls germination while in others it operates in combination with salinity and temperature (Gutterman, 1993; Gutterman et al., 1995). Light has little effects in the absence of salinity except in the case of *Cyperus arenarius* and *Sporobolus ioclados* (Table 5). However, under saline conditions, the absence of light either partially or completely inhibited seed germination of *Aeluropus lagopoides*, *Dicanthium annulatum*, *Sporobolus ioclados* and *Urochondra setulosa* (Table 5).

3.2. Temperate moist habitats

Seeds of cool temperate halophytes are known to tolerate high salinity during their dormancy in the soil (Ungar, 1995). Halophytes from moist temperate regions also show a large variation in their ability to germinate in saline solutions (Table 6). For example, *Hordeum jubatum* tolerates 200 mM NaCl during germination compared to *Salicornia europaea* from the same salt marsh which is very highly salt tolerant, germinating in 600 mM NaCl (Keiffer and Ungar, 1997). Seeds of halophytes from moist temperate regions usually germinate optimally with a cool (5–15 °C) temperature regime (Table 4, Ungar and Capilupo, 1969; Ungar, 1977; Okusanya and Ungar, 1983; Khan and Ungar, 1984, 1998a; Badger and Ungar, 1989).

The effects of light and salinity on the germination of halophytes from cool moist region are poorly documented (but see Koller, 1957; Freeman, 1973; Binet, 1965; Datta, 1965; Barbour, 1968; De Villiers et al., 1994). Bakker et al. (1985) showed that light attenuation decreased the germination of halophytes (Table 5). Okusanya

and Ungar (1983) reported that seeds of *Spergularia marina* failed to germinate in the absence of light both under saline or non-saline conditions. Qu et al. (2008) reported higher germination of *Halocnemum strobilaceum* seeds in light than in darkness at all temperatures tested, indicating that a considerable portion of the seed population is light sensitive. The light requirement for germination of *H. strobilaceum* seeds ensures that they will germinate successfully on or near the soil surface when other conditions are suitable for seedling emergence.

3.3. Temperate dry habitats

Data presented in Table 7 indicate that six halophytes in this group have at least 10% germination at or above seawater salinity. A number of them could germinate in the salinity concentrations well above seawater (e.g. species of *Suaeda*, *Sarcocornia*, *Haloxylon*, *Salsola* and *Kochia*) while others (species of *Suaeda*, *Halogeton*, *Paganum* and *Lepidium*) are less tolerant. In comparison with other saline habitats, it appears that seeds of halophytes of temperate dry habitats, particularly those found in playa ecosystem like the Great Basin Desert of Utah, are among one of the most salt tolerant during germination as a group (Table 8). Most of the highly salt tolerant species are either stem or leaf succulents (Khan and Gul, 2006).

Diurnal variation in temperature plays a very significant role in the seed germination of halophytes from temperate dry habitats (Gul and Khan, 2006; Ahmed and Khan, 2010; Table 4). Halophyte species from playa habitats show a significant response to a change in temperature and warmer temperatures result in the improvement in the seed germination (Table 4; Khan and Weber, 1986;

Table 6

Sodium chloride concentration at which seed germination of temperate moist habitats' halophytes was reduced from 75–100% to about >10% but not zero.

Species	Habit	NaCl (M)	References
<i>Salicornia herbacea</i>	SS	1.7	Chapman (1960)
<i>Limonium vulgare</i>	DF	1.4	Woodell (1985)
<i>Spartina alterniflora</i>	G	1.03	Mooring et al. (1971)
<i>Kochia scoparia</i>	LS	1	Khan et al. (2001b)
<i>Suaeda japonica</i>	LS	0.9	Yokoishi and Tanimoto (1994)
<i>Halosarchia pergranulata</i>	SS	0.8	Short and Colmer (1999)
<i>Atriplex tornabeni</i>	DF	0.77	Binet (1965)
<i>Ruppia maritima</i>	G	0.68	Koch and Seelinger (1988)
<i>Puccinellia lemmoni</i>	G	0.6	Harivandi et al. (1982)
<i>Plantago lanceolata</i>	LS	0.6	Bakker et al. (1985)
<i>Cakile maritima</i>	LS	0.6	Barbour (1970)
<i>Salsola kali</i>	LS	0.6	Woodell (1985)
<i>Suaeda maritima</i>	LS	0.6	Boucaud and Ungar (1976)
<i>Cakile maritima</i>	LS	0.5	Debez et al. (2004)
<i>Atriplex centralasiatica</i>	DF	0.48	Li et al. (2008)
<i>Coachelaria danica</i>	LS	0.43	Bakker et al. (1985)
<i>Rumex crispus</i>	LS	0.43	Bakker et al. (1985)
<i>Arthrocnemum halocnemoides</i>	SS	0.4	Malcolm (1964)
<i>Kosteletzkya virginica</i>	DF	0.4	Poljakoff-Mayber et al. (1994)
<i>Salicornia patula</i>	SS	0.34	Berger (1985)
<i>Spergularia rupicola</i>	LS	0.3	Okusanya (1979)
<i>Silene maritima</i>	LS	0.3	
<i>Chenopodium album</i>	DF	0.3	Yao et al. (2010)
<i>Limonium lilacinum</i>	DF	0.3	Yildiz et al. (2008)
<i>Limonium iconicum</i>	DF	0.3	Yildiz et al. (2008)
<i>Tanacetum cinerariifolium</i>	DF	0.26	Li et al. (2011)

Note: SS, stem succulent; DF, Dicot forb; LS, leaf succulent; G, grasses.

Table 7

Sodium chloride concentration at which seed germination of temperate dry habitats' halophytes was reduced from 75–100% to about >10% but not zero.

Species	Habit	NaCl (M)	References
<i>Suaeda aralocaspica</i> Brown seeds	LS	1.4	Wang et al. (2008)
<i>Sarcocornia perennis</i> × <i>fruticosa</i> (hybrid)	SS	1.3	Redondo et al. (2004)
<i>Haloxylon ammodendron</i>	SS	1.3	Huang et al. (2003)
<i>Haloxylon persicum</i>	SS	1.3	Tobe et al. (2000)
<i>Salsola affinis</i> ^a	LS	1.2	Wei et al. (2008)
<i>Kochia americana</i>	LS	1.2	Clarke and West (1969)
<i>Salsola nitraria</i>	LS	1	Chang et al. (2008)
<i>Salsola iberica</i>	LS	1	Khan et al. (2002b)
<i>Sarcobatus vermiculatus</i>	LS	1	Khan et al. (2001a)
<i>Suaeda moquinii</i>	LS	1	Khan et al. (2001a)
<i>Salicornia bigelovii</i>	SS	1	Rivers and Weber (1971)
<i>Salicornia rubra</i>	SS	1	Khan et al. (2000)
<i>Atriplex rosea</i>	DF	1	Khan et al. (2004)
<i>Sarcocornia perennis</i>	SS	0.87	Redondo et al. (2004)
<i>Sarcocornia fruticosa</i>	SS	0.87	Redondo et al. (2004)
<i>Suaeda depressa</i>	LS	0.85	Ungar (1962)
<i>Salicornia europaea</i>	SS	0.85	Ungar (1962, 1967)
<i>Tamarix pentandra</i>	DF	0.85	Ungar (1967)
<i>Allenrolfea occidentalis</i>	SS	0.8	Gul and Weber (1999)
<i>Puccinellia fastucaeformis</i>	G	0.8	Onnis and Micelli (1975)
<i>Suaeda physophora</i>	LS	0.7	Zhang et al. (2010)
<i>Sarcocornia quinquefolia</i>	SS	0.69	Patridge and Wilson (1987)
<i>Salicornia pacifica</i>	SS	0.68	Khan and Weber (1986)
<i>Salsola vermiculata</i>	LS	0.6	Guma et al. (2010)
<i>Salicornia virginica</i>	SS	0.6	Zedler and Beare (1986)
<i>Atriplex laciniata</i>	DF	0.6	Ignaciuk and Lee (1980)
<i>Atriplex nummularia</i>	DF	0.52	Uchiyama (1987)
<i>Atriplex triangularis</i>	DF	0.51	Khan and Ungar (1984)
<i>Puccinellia nuttalliana</i>	G	0.51	Macke and Ungar (1971)
<i>Halocnemum strobilaceum</i>	SS	0.5	Song et al. (2006)
<i>Atriplex prostrata</i>	DF	0.5	Katembe et al. (1998)
<i>Suaeda heterophylla</i>	LS	0.4	Hameed et al. (unpublished)
<i>Halogenton glomeratus</i>	LS	0.4	Ahmed and Khan (2010)
<i>Paganum hermala</i>	DF	0.4	Ahmed and Khan (2010)
<i>Lepidium latifolium</i>	DF	0.3	Ahmed and Khan (2010)

^a 2% seed germination at 2.0M NaCl.

Note: SS, stem succulent; DF, Dicot forb; LS, leaf succulent; G, grasses.

Table 8
Number of species from different habitats and percentage of species at which seed germination was reduced from 75–100% to about 10% in different NaCl concentrations.

Habitat	Number of species	NaCl (M)			
		<0.2	0.21–0.40	0.41–0.60	>0.61
Subtropical	25	12	32	40	16
Temperate dry	33	0	0	24	76
Temperate moist	39	15	41	23	21
Mean %		9	24	29	38

Khan et al., 1987, 2001a,b,c; Gul and Weber, 1999; Khan and Gul, 2006) and optimal germination was obtained at a temperature regime of 25/35 °C (Khan and Weber, 1986; Gul and Weber, 1999; Khan, 1999; Khan et al., 2000, 2001a,b,c).

Unlike other groups, darkness has been shown to inhibit seed germination both in saline and non-saline conditions in comparison to germination in the light (Table 5). Darkness has synergistic effect in the presence of salinity in inhibiting seed germination (Table 11). Gul et al. (2000) reported that germination of seeds of *Allenrolfea occidentalis* was reduced to only 58% compared to seeds germinated in light and introduction of salinity substantially inhibited seed germination in dark.

3.4. Conclusion

Halophytes distributed in the temperate desert as a group show a higher degree of salt tolerance at germination than from the other habitats we have examined. Halophytes from temperate moist habitats germinate under cooler conditions; for subtropical halophytes, the optimum is 20–30 °C (12 h night/12 h day); however, optimal germination of temperate desert species occurred with a warmer temperature regime (25–35 °C). Light has variable effects on seed germination.

4. Recovery of seed germination from exposure to high salinity

The data reported in the literature on the seed germination of most halophytes indicate that their optimal germination occurs in fresh water and is inhibited by increases in salinity (Ungar, 2001) although the storage conditions can influence the response of germination to salt (Wetson et al., 2008). The term 'recovery' of germination is used to assess the ability of seeds that are subjected to high salinity to germinate when transferred to fresh water (Ungar, 1991). Khan and Ungar (1996) added a new dimension of temperature to check if this additional factor could modulate recovery from saline conditions. A number of publications have since appeared using the term recovery.

4.1. Subtropical habitats

Subtropical halophytes produce numerous seeds and are ready to germinate after dispersal; however, when they are prevented from germination due to unavailability of water, high temperature and high salinity, most of them lose their viability within a few months (Khan and Gul, 2006). Recovery of seed germination tested under laboratory conditions showed variable response. *Arthrocnemum macrostachyum* showed a substantial recovery from 1 M NaCl (Khan and Gul, 1998) while other species could recover from up to 0.6 M NaCl (Table 9). *Aeluropus lagopoides* (Gulzar and Khan, 2001), *Atriplex stocksii* (Khan, 1999), *Limonium stocksii* (Zia and Khan, 2004) and *Urochondra setulosa* (Gulzar et al., 2001) showed about 75% recovery at 0.6 M NaCl (Table 9) while *Cressa cretica* (Khan, 1999), *Haloxylon stocksii* (Khan and Ungar, 1996), *Salsola imbricata* (Mehrunnisa et al., 2007), *Suaeda fruticosa* (Khan and

Ungar, 1998b) and *Sporobolus ioclados* (Khan and Gulzar, 2003) showed poor recovery responses. *Cyperus arenarius* seeds died in high salt concentrations while seeds of *Limonium stocksii* showed higher germination after one month of exposure but remained dormant during rest of the germination period (Table 6).

4.2. Temperate moist marshes

Seeds of halophytes from temperate moist regions usually maintain viability at least for one season. They disperse in late October, pass winter in soil soaked with saline water under 0 to –15 °C temperatures and then begin to germinate during early spring. Several investigators have demonstrated that seeds of halophyte exposed to hyper-saline conditions maintained an enforced dormancy that is alleviated with the availability of fresh water (Ungar, 1978; Woodell, 1985; Keiffer and Ungar, 1997; Khan and Ungar, 1986a). Species like *Atriplex centralasiatica* and *Suaeda salsa* recovered fully in water after being subjected to 0.4 M NaCl (Liu et al., 2006, Table 9) while *Chenopodium glaucum* could recover from salinity levels equal to or higher than seawater salinity (Khan et al., 2001b; Duan et al., 2004).

4.3. Temperate dry deserts

Halophytes from the Great Basin desert similarly germinate during early spring when the temperature becomes warmer and salinity is substantially reduced. Halophytes like *Allenrolfea occidentalis* (Gul and Weber, 1999), *Kochia scoparia* (Khan et al., 2001a), *Salicornia rubra* (Khan et al., 2000) and *Salsola iberica* (Khan et al., 2002a) had 80% or higher recovery of germination when transferred from 1 M NaCl to distilled water (Table 9). A substantial recovery from germination occurred at the NaCl concentrations up to 0.6 M NaCl in *Halogeton glomeratus* (Khan et al., 2001b), *Sarcobatus vermiculatus* (Khan et al., 2002b), *Suaeda moquinii* (Khan et al., 2001a) and *Triglochin maritima* (Khan and Ungar, 1999).

4.4. Conclusion

Seed of halophytes from all the climatic zones were able to recover from highly saline conditions and most of them showed higher than 50% recovery.

5. Osmopriming

Seed priming is a treatment during imbibition leading to activation of the initial metabolic processes related to seed germination and prior to radicle emergence. Osmo/halo-priming involves imbibing seed in solutions of low osmotic potential that allows sufficient hydration and progression of metabolic processes but prevents germination (Ashraf and Foolad, 2005). The important factor here is to allow sufficient water to activate metabolic processes but not enough to allow cell expansion and growth. Usually osmotica like mannitol, polyethylene glycol (PEG) and salts may be used. This priming may cause complete or partial death of seeds,

Table 9

Percent recovery of germination in halophytes from different habitats at various NaCl concentrations.

Habitat	Species	NaCl (M)					Reference
		0.2	0.4	0.6	0.8	1	
Sub tropical	<i>Aeluropus lagopoides</i>	60	82	89	–	–	Gulzar and Khan (2001)
	<i>Arthrocnemum macrostachyum</i>	19	83	96	–	–	Khan and Gul (1998)
	<i>Atriplex stocksii</i>	38	71	75	–	–	Khan and Rizvi (1994)
	<i>Cressa cretica</i>	76	72	28	–	–	Khan (1991)
	<i>Desmostachya bipinnata</i>	30	70	–	–	–	Gulzar et al. (2007)
	<i>Haloxylon stocksii</i>	6	58	50	–	–	Khan and Ungar (1997)
	<i>Limonium stocksii</i>	82	98	98	–	–	Zia and Khan (2004)
	<i>Salsola imbricata</i>	1	17	19	–	–	Mehrunnisa et al. (2007)
	<i>Sporobolus ioclados</i>	19	21	39	–	–	Khan and Gulzar (2003)
	<i>Suaeda fruticosa</i>	40	80	80	–	–	Khan and Ungar (1997)
	<i>Urochondra setulosa</i>	88	75	60	–	–	Gulzar et al. (2001)
Temperate moist	<i>Kochia scoparia</i>	85	88	100	100	100	Khan et al. (2001b)
	<i>Atriplex centralasiatica</i>	100	98	–	–	–	Liu et al. (2006)
	<i>Chenopodium glaucum</i>	63	83	71	–	–	Duan et al. (2004)
	<i>Suaeda salsa</i>	100	100	–	–	–	Liu et al. (2006)
		<i>Allenrolfea occidentalis</i>	82	83	98	98	98
Temperate dry	<i>Halogeton glomeratus</i>	85	72	52	22	8	Khan et al. (2001c)
	<i>Haloxylon ammodendron</i>	–	–	–	73	–	Song et al. (2005)
	<i>Haloxylon persicum</i>	–	–	–	25	–	Song et al. (2005)
	<i>Lepidium latifolium</i>	100	100	–	–	–	Ahmed and Khan (2010)
	<i>Peganum harmala</i>	80	80	–	–	–	Ahmed and Khan (2010)
	<i>Salicornia rubra</i>	1	23	38	60	78	Khan et al. (2000)
	<i>Salsola iberica</i>	2	22	37	60	82	Khan et al. (2002b)
	<i>Sarcobatus vermiculatus</i>	0	61	47	22	0	Khan et al. (2002b)
	<i>Suaeda heterophylla</i>	20	15	–	–	–	Hameed et al. (unpublished)
	<i>Suaeda moquinii</i>	0	62	50	25	8	Khan et al. (2001a)
	<i>Triglochin maritima</i>	36	80	65	–	–	Khan and Ungar (1997)

Table 10

Salt stimulation/inhibition in seed germination of halophytes from different habitats through salt priming.

Species	Germination (%)		Recovery (%)	Cumulative germination (%)	Salt stimulation/inhibition (%)	NaCl conc. (mM)	Reference
	Non-saline (a)	Saline (b)					
Subtropical							
<i>Arthrocnemum macrostachyum</i>	26	0	62	62	138	1712	Rubio-Casal et al. (2003)
<i>Cyperus arenarius</i>	92	40	55	97	5	200	Unpublished
<i>Cyperus conglomeratus</i>	80	0	30	30	–63	100	El-Keblawy et al. (2011a,b)
<i>Desmostachya bipinnata</i>	90	20	80	84	–7	500	Gulzar et al. (2007)
<i>Haloxylon stocksii</i>	82	8	37	42	–49	500	Khan and Ungar (1996)
<i>Limonium stocksii</i>	100	3	100	100	0	500	Zia and Khan (2004)
<i>Phragmites karka</i>	100	10	65	75	–25	515	Zehra and Khan (2007)
<i>Salsola imbricata</i>	85	3	15	18	–79	800	Mehrunnisa et al. (2007)
<i>Sporobolus ioclados</i>	90	10	20	28	–69	500	Khan and Gulzar (2003)
<i>Suaeda fruticosa</i>	80	2	78	80	0	500	Khan and Ungar (1997)
<i>Urochondra setulosa</i>	100	10	50	55	–45	500	Gulzar et al. (2001)
<i>Zygophyllum simplex</i>	10	10	10	20	100	125	Khan and Ungar (1998b)
Temperate moist							
<i>Chenopodium glaucum</i>	25	70	5	75	200	50	Xue-hua et al. (2011)
<i>Salicornia ramosissima</i>	94	0	90	90	–4	1712	Rubio-Casal et al. (2003)
<i>Suaeda corniculata</i>	80	44	29	60	–25	500	Guan et al. (2010)
<i>Suaeda salsa</i>	91	50	24	62	–32	500	Guan et al. (2010)
<i>Triglochin maritima</i>	70	0	70	70	0	500	Khan and Ungar (1999)
Temperate dry							
<i>Artemisia scoparia</i>	78	0	98	98	26	200	Xue-hua et al. (2011)
<i>Artemisia sieversiana</i>	90	50	50	100	11	50	Xue-hua et al. (2011)
<i>Atriplex rosea</i> – Black seeds	100	15	80	83	–17	1000	Khan et al. (2004)
<i>Atriplex rosea</i> – Brown seeds	90	15	20	32	–64	1000	Khan et al. (2004)
<i>Halogeton glomeratus</i>	100	5	8	13	–87	1000	Khan et al. (2001a,b,c)
<i>Haloxylon ammodendron</i>	98	9	73	75	–23	684	Song et al. (2005)
<i>Haloxylon persicum</i>	93	7	25	30	–67	684	Song et al. (2005)
<i>Kochia prostrata</i>	80	50	95	98	22	513	Orlovsky et al. (2011)
<i>Lepidium latifolium</i>	100	0	100	100	0	500	Ahmed and Khan (2010)
<i>Peganum harmala</i>	80	0	100	80	0	500	Ahmed and Khan (2010)
<i>Salsola iberica</i>	100	20	18	34	–66	1000	Khan et al. (2002a,b)
<i>Suaeda moquinii</i> – Black seeds	90	0	80	80	–11	1000	Khan et al. (2001a,b,c)
<i>Suaeda moquinii</i> – Brown seeds	100	40	90	94	–6	1000	Khan et al. (2001a,b,c)
<i>Suaeda physophora</i>	95	10	51	56	–41	684	Song et al. (2005)

Table 11
Germination response of heteromorphic seed of halophytes.

Species	Morphs	Max. germination	NaCl tolerance (mM)	Opt. temp (°C)	Reference
Subtropical					
<i>Arthrocnemum indicum</i>	Brown	100	1000	10/30	Khan and Gul (1998)
	Black	90	800	10/20	
<i>Halopyrum mucronatum</i>	Brown (lighter)	100	300	20/30	Khan and Ungar (2001)
	Black (Heavier)	100	300	25/35	
Temperate moist					
<i>Atriplex centralasiatica</i>	Brown	100	480	20/30	Li et al. (2011)
	Black	90	240	20/30	
<i>Atriplex inflata</i>	Brown	98	–	–	Abdallah et al. (2011)
	Black	19	–	–	
<i>Atriplex prostrata</i>	Large	95	–	20/35	Carter and Ungar (2003)
	Small	95	–	5/25	
<i>Atriplex sagittata</i>	Large	80	–	22/15	Mandák and Pyšek (2005)
	Medium	35	–	22/15	
	Small	10	–	22/15	
<i>Atriplex triangularis</i>	Large	100	856	5/25	Khan and Ungar (1984)
	Medium	100	685	5/25	
	Small	98	342	5/25	
<i>Cakile edentula</i>	Large	Higher	–	–	Zhang (1993)
	Small	Lower	–	–	
<i>Chenopodium album</i>	Brown (larger)	100	300	–	Yao et al. (2010)
	Black (smaller)	10	200	–	
<i>Salicornia europaea</i>	Large	99	856	–	Ungar (1979)
	Small	61	514	–	
<i>Salsola komarovii</i>	Long winged	63	514	–	Yamaguchi et al. (1990)
	Short winged	28	171	–	
<i>Suaeda salsa</i>	Brown	98	1200	–	Li et al. (2005)
	Black	90	600	–	
Temperate dry					
<i>Atriplex rosea</i>	Brown (larger)	100	1000	20/30	Khan et al. (2004)
	Black (smaller)	100	1000	20/30	
<i>Salsola komarovii</i>	Large	Higher	–	–	Takeno and Yamaguchi (1991)
	Small	Lower	–	–	
<i>Suaeda acuminata</i>	Brown	95	–	20/35	Wang et al. (2012)
	Black	7	–	20/35	
<i>Suaeda aralocaspica</i>	Brown (larger)	90	1400	10/25	Wang et al. (2008)
	Black (smaller)	40	400	10/25	
<i>Suaeda moquini</i>	Brown (soft)	100	1000	5/15	Khan et al. (2001a,b,c)
	Black (hard)	90	600	5/15	
<i>Suaeda splendens</i>	Brown	37	900	5/15	Redondo-Gómez et al. (2008)
	Black	94	600	5/15	
<i>Tamarix ramosissima</i>	Spring	90	600	–	Yan et al. (2011)
	Summer	90	800	–	

induce dormancy, have no effect or may increase germination in comparison to the non-treated control (Khan and Gul, 2006).

5.1. Subtropical habitats

Halophytes from this region are generally not tolerant to salinity when stored under saline field conditions (see Section 3.1); however, some of them show higher germination when transferred from highly saline condition to low or no salt conditions (Table 10). *Arthrocnemum macrostachyum*, *Zygophyllum simplex* and *Chenopodium glaucum* seeds when exposed to high salinity for 20 days and then transferred to distilled water showed higher germination than untreated seed which were germinated in distilled water only (Khan and Ungar, 1998b; Rubio-Casal et al., 2003; Xue-hua et al., 2011), showing 138, 100 and 200% salt induced stimulation in germination. This effect is analogous to osmo/halo-priming. In species such as *Suaeda fruticosa* and *Limonium stocksii*, salt priming had no effect (Khan and Ungar, 1997a; Zia and Khan, 2004). While seed germination of *Salsola imbricata*, and *Sporobolus ioclados* after osmo-priming were lower than the germination in water (Khan et al., 2002a; Khan and Gulzar, 2003; Mehruunisa et al., 2007), showing ionic influence of salt on germination.

5.2. Temperate moist habitat

Most of these species after dispersal are exposed to highly saline and cold soil solutions and remain in a fully imbibed condition

through winter; they germinate during early spring when the temperature begins to rise (Ungar, 1995). Although a large number of seeds germinate after storage under laboratory conditions, their germination is lower than those which were not exposed to harsh saline conditions (Ungar, 1995; Keiffer and Ungar, 1995; Khan and Ungar, 1997a).

Germination of some species may even be stimulated when soaked under highly saline conditions suggesting priming of these seeds by salts (Wetson et al., 2008; Eley-Quirk et al., 2009; Li et al., 2011). The conditions to which halophyte seeds are exposed after dispersal (the storage conditions) also play a role in the subsequent seed germination (Wetson et al., 2008) and recovery from high temperature and salinity stress (Khan and Ungar, 1997a), although this response may be highly variable between species (Khan and Ungar, 1999). Salt stimulation due to osmo-priming may be as high as 200% in comparison to control in *Chenopodium glaucum* (Table 6) while in some species there was no effect and in still some others, inhibition up to 32% compared to non-treated control was observed (Table 6).

5.3. Temperate dry habitat

Germination increase due to salt priming can reach from 11 to 26% in comparison to control (un-primed seeds), but in most species there is an inhibition compared to control ranging from –6 to –87% (Table 6). In a number of species such as *Triglochin maritima* (Khan and Ungar, 1999), *Lepidium latifolium* and *Peganum harmala*

(Ahmed and Khan, 2010), seed germination after halopriming was similar to total germination in water, indicating osmotic constraint under saline condition. While germination in several other species like *Suaeda salsa* (Guan et al., 2010), *Salsola iberica* (Khan et al., 2002a) and *Haloxylon persicum* (Song et al., 2005) is lower than the germination in water.

5.4. Conclusion

It appears that osmopriming is a phenomenon that is not very common in species of any region. However some species in all habitats show positive effect of halopriming which ranges from almost none to 200% stimulation while others show significant reduction in germination when halo-primed.

6. Seed heteromorphism

Seed heteromorphism is a phenomenon in which an individual plant produces different morpho-physiological types of seeds, and it is common in Asteraceae, Chenopodiaceae (now Amaranthaceae) and Poaceae (Harper, 1977; Imbert, 2002). More than 200 species are reported worldwide to exhibit seed heteromorphism ranging from difference in colour, size and shape, as well as in dispersal capacity, germination characteristics, dormancy responses, ability to persist in a seed bank and seedling growth (Sorensen, 1978; Baker and O'Dowd, 1982; Khan and Ungar, 1984; Cheplick, 1994; Baskin and Baskin, 1998; Mandák and Pyšek, 2005; Imbert, 2002; Brändel, 2004; Lu et al., 2010).

The phenomenon of dimorphism or polymorphism most probably provides multiple opportunities for a population to maintain its continuity when faced with extreme variation in environmental conditions of saline habitats (Philipupillai and Ungar, 1984; Khan and Ungar, 1986a). Seed heteromorphism is not frequent but has been reported among annuals as well as perennials, irrespective of region or climatic conditions (Ungar, 1995; Khan and Gul, 2006). For instance, a number of halophytic taxa including *Arthrocnemum*, *Atriplex*, *Chenopodium*, *Cakile*, *Salicornia*, *Salsola*, *Spergularia*, *Suaeda* and *Trianthema* (Ungar, 1977; Galinato and van der Valk, 1986; Mohammad and Sen, 1991; Ungar, 1988; Morgan and Myers, 1989; Khan and Gul, 1998) show seed heteromorphism.

6.1. Subtropical habitats

Studies conducted in Jodhpur, India reported that seed of several halophytes (*Cressa cretica*, *Salsola imbricata*, *Sesuvium sesuvioides*, *Suaeda fruticosa*, *Trianthema triquetra* and *Zygophyllum simplex*) were heteromorphic (Mohammad and Sen, 1991). These variations in seed size and weight may be an adaptive response to a large variation in soil salinity at different habitats. Seed dimorphism is reported in a stem succulent halophyte, *Arthrocnemum macrostachyum*, which is frequently distributed in coastal salt marshes of the Arabian Sea including Pakistan. It produces dimorphic brown and heavier black seeds (Khan and Gul, 1998). Brown seeds germinated at 1 M NaCl while few black seeds germinated at 0.8 M NaCl. *Halopyrum mucronatum* is a perennial grass which is the second most common species along the Arabian Sea coast after *Arthrocnemum macrostachyum*; it produces seeds twice a year. Summer seeds produced during May are black and heavier than brown seeds which are produced during November (Noor and Khan, 1995). Summer seeds were found more tolerant to salinity than winter seeds and showed better germination in a warmer (20–30 °C) rather than a cooler (10–20 °C) temperature regime (Khan and Ungar, 2001a). Germination under saline conditions was improved by gibberellic acid, thiourea and nitrate in winter seeds and gibberellic acid, kinetin and betaine in summer seeds. Detailed biochemical analysis of these seeds showed that seed weight, seed

moisture, total lipids, total tr acyl glycerol, total phenols and total tannins were higher in black seeds (summer) while total soluble proteins, sugars (reducing and non-reducing both) were higher in brown (winter) seeds of *Halopyrum mucronatum* (Siddiqui and Khan, 2011). One aspect common in most of these species is that brown seeds are larger and more readily germinate under high temperature and saline conditions (e.g. *Hedypnois cretica*, *Crepis aspera* and *Suaeda salsa*; El-Keblawy, 2003; Li et al., 2005). In contrast, small and/or black seeds of *Arthrocnemum indicum*, *Salsola komarovii*, *Suaeda moquinii* and *Halopyrum mucronatum* are non-dormant (Takeno and Yamaguchi, 1991; Khan et al., 1998, 2001a; Khan and Ungar, 2001a).

6.2. Temperate moist habitat

A large number of halophytes from this climatic zone, from Japan to Europe and North America, are reported to have heteromorphic seeds. In most cases a different size or shape of seeds also signifies a difference in their physiological responses to various environmental cues. The ecological significance of these variable physiological responses is that it will provide a population multiple opportunities to recruit if exposed to sudden changes in the environment when distributed in extreme habitats.

Variation in seed size, colour and weight is seen in the seeds of *Atriplex triangularis* (Ungar, 1971; Khan and Ungar, 1984), *Salicornia europaea* (Grouzis et al., 1976; Philipupillai and Ungar, 1984), *Spergularia marina* (Okusanya and Ungar, 1983; Ungar, 1988) *Salsola komarovii* (Takeno and Yamaguchi, 1991) and *Plantago coronopus* (Schat, 1981). If all seeds were to germinate at the beginning of spring this could deplete the reserves for annuals so subsequent lack of rainfall or unusually higher temperature would result in high mortality and could cause the elimination of a population (Ungar, 1995). Seed heteromorphism provides opportunities for the seeds to ensure the continuity of the lineage (Khan and Ungar, 1986a). For example, differences in the longevity, salt tolerance, and dispersal range of seeds could be important in determining the spatial and temporal distribution of *Salsola komarovii* in salt marshes of coastal Japan (Takeno and Yamaguchi, 1991).

Seeds of *Salicornia europaea* and *Spergularia marina* have at least two seed morphs that vary in their salt tolerance, degree of dormancy, and light and stratification requirement for germination (Ungar, 1977; Philipupillai and Ungar, 1984; Okusanya and Ungar, 1983). Smaller seeds that were produced in lateral flowers were less salt tolerant and had a longer dormancy than seeds from central flowers on a shoot. Khan and Ungar (1984) determined that there were different levels of dormancy and salt tolerance in the two seed morphs of *Atriplex triangularis*. A small black seed morph had a longer dormancy and apparently formed a persistent seed bank (Wertis and Ungar, 1986). Field burial experiments in high-salt and low-salt habitats indicated that small seeds had a light requirement for germination under field conditions and that their germination was more inhibited in high salt habitats than was that of the larger seeds; surface and subsurface transplants of large seeds had similar germination patterns in both the high-salt and the low-salt environments (Khan and Ungar, 1986a). The seed morphs of *Atriplex triangularis* also had different physiological requirements for germination (Khan and Ungar, 1984): large seeds, which were found to be less sensitive to salinity stress, germinated in the spring when soil salinity levels were less than 1.5% NaCl, whereas germination of small seeds was more inhibited by high salinities under spring thermoperiods than the larger seeds and formed a persistent seed bank.

6.3. Temperate dry habitat

Seed heteromorphism is not widely reported in species from this region. However, data available for a few species indicate that

heteromorphism will provide multiple opportunities for the annual population to survive a high mortality of seedling due to sudden change in temperature and/or salinity. Seeds of *Atriplex rosea* from the Great Basin Desert, Utah are dimorphic: light brown, and 2–2.5 mm wide or black and 1–2 mm wide. Both brown and black seeds germinated at 1 M NaCl, and the optimal temperature for germination of both types was 20–30 °C (Khan et al., 2004). Variation in temperature, however, affected germination of black seeds more than brown seeds. Black seeds showed only 40–50% germination in non-saline conditions with a cool thermoperiod (5–15 °C and 10–20 °C) and was completely inhibited in saline medium. Brown seeds had a higher germination rate than black seeds at all temperature and salinity treatments. Recovery of black seeds decreased with increase in salinity at lower temperature regimes, increased with salinity at the optimal thermoperiod and had no effect at 20–30 °C. Brown seeds recovered poorly from salinity at all thermoperiods except 5–15 °C, where recovery decreased with an increase in salinity (Khan et al., 2004). Brown seeds are adapted to germination in the early part of the growing season, whereas black seeds are capable of surviving harsher conditions and can germinate in later time periods.

Wang et al. (2008) reported that freshly-matured brown seeds of *Suaeda aralocaspica* are non-dormant and black seeds have dormancy. Brown seeds of *Suaeda cuminata* are non-dormant, whereas black seeds have dormancy (Wang et al., 2012). *Atriplex prostrata* is also found in the Great Basin Desert, where large seeds from an Ohio population were non-dormant, and thus germinated to about 90%. However, small seeds had primary dormancy, a light requirement for germination and appeared to exhibit dormancy cycling (Carter and Ungar, 2003).

6.4. Conclusion

Seed heteromorphism based on size, colour, weight, time of production is found in all the habitats. Whatever the genetic basis, the effect of dimorphism is to provide seeds with multiple opportunities for germination to ensure the continuity of a population.

7. Summing up

The answer to the above-mentioned question is not as simple as the question itself. Halophyte seeds have high degree of variability within habitat, population, habit and climatic zone, so that it is difficult to give a generalized answer. Halophytes are distributed from coastal marshes, sand dunes, inland plains and marshes that may or may not be waterlogged and where soils are saline, saline-sodic or sodic; temperatures also vary considerably. In addition there is also micro-environmental variation within habitats and among populations from one year to the other. Conditions vary between extremes; from drought to flooding, from hot to freezing temperatures and from low salinity to approaching saturated saline soils. All this may change suddenly giving halophytes little chance to adapt during germination or early seedling growth. The available data is too little to make many generalizations, but here we have tried to highlight differences among various habitats.

Subtropical areas are characterized by very low rainfall and high temperatures. Here, many halophytes are perennials with no ecological compulsions for annual seed germination and they usually do not possess elaborate dormancy systems. Numerous seeds produced every year suffer heavy mortality and/or predation so that the majority of the populations do not maintain a persistent seed bank (with few exceptions, e.g. *Suaeda fruticosa*). Seeds are either blown away with sand, consumed by insects, birds and mammals and/or lose viability soon after dispersal. Seed bank sizes are generally much lower than reported for other more moist habitats.

However, seeds collected soon after maturity and stored under lab conditions readily germinate and remain viable for a number of years, but seeds from natural habitats live in a dormant state for few months and then lose viability a few weeks later. Sometimes during a period of long and extraordinary rainfall, seedling recruitment occurs, which appears to contribute in increasing genetic variability of the population. In these habitats the availability of water is a primary factor and a critical quantity of moisture has to be available for seeds to germinate. Monsoon rains (July and August) decrease soil salinity as well as lower the ambient and soil temperatures along with providing appropriate photoperiod.

Halophytes of temperate moist habitats are dominated by annuals or herbaceous perennials and maintain a persistent seed bank; germination occurs when temperatures become warmer and soil salinity is low. Seed usually show enforced dormancy and are ready to germinate when conditions are conducive to seedling growth. Some species show seed polymorphism and a group of seed remain dormant during the early season as a safety net to ensure the continuity of the population if heavy mortality occurs due to sudden changes in environmental conditions. These halophytes germinate in spring when temperatures increase but a requirement for light is variable.

The seed of halophytes occupying temperate deserts also germinate well when conditions become warmer. This group consists of species that are very highly salt tolerant during seed germination and germination is fastest in warmer temperatures but again with variable light requirements. Most of seeds show high recovery but the information regarding seed heteromorphism is scanty.

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