Halophyte seed germination: success and pitfalls

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Short title: Seed germination of halophytes.

Summary

Seed ecophysiology of halophytes in relation to their habitat, life form, salinity tolerance, and temperature regimes would be discussed. Halophyte seed germination, although display a higher degree of inter and intra-specific variability, show some pattern of germination responses to various environmental factors. High salinity tolerance is reported from all kinds of halophytes but stem succulent have the highest percentages of them. The salt tolerance decreased progressively from leaf succulent, secreting to grass halophytes. Seed germination of cold desert halophytes may progressively increase with an increase in temperature while germination of warm desert halophytes shows better germination at cooler temperature for that ecosystem. Halophyte from moist temperate regions germinated better at cooler temperatures. The percentage of un-germinated seeds that recovered when they were transferred to distilled water varied significantly with variation in salinity and temperature regimes in different species. Seeds of some species failed to germinate when exposed to high salinity and temperature stress. While seeds of other halophytic species showed various levels of recovery ranging from 20% to complete recovery of germination. There are some species where recovery of germination is higher then untreated control. Higher temperature inhibited germination recovery for most of the species reported.

Introduction

In recent years there has been increasing recognition that the scarcity of fresh water and the salinization of agricultural areas are becoming much more global problems. Both trends represent a threat to the world's food supply. Currently the domestic, industrial and agricultural consumption of fresh water and ground water has increased many folds and the fresh water shortage can be expected all over the world. This is already the case in several places. Surface and ground water of agricultural areas in many places of the world are rapidly becoming brackish and saline, particularly in arid tropical and subtropical areas. Furthermore, salt deserts (caused by a lack of fresh water) and saline inland basins (caused by the level of saline ground water rising as a result of leakage of drainage water) are being created. FAO data show that at least 40% of the world is affected by salinization in one way or another. The actual impact of this estimate is not yet entirely clear. However, it is known that large areas in Australia, India, Pakistan, Egypt, Central Asia, South America, Mexico and the United States are faced with salinization.

Halophytes are the plants capable of growing and surviving in the saline environment. Halophytes as a group have one or more of several physiological adaptations that allow for the survival in the saline environment. Of these strategies, most common among halophytes is the ability to adjust osmotically allowing for the uptake of water into the plant despite the salt content. In other words, the plants essentially become "saltier" than the soil water in a sense. In order for the plant to adjust osmotically and yet still function physiologically, the plant adjusts both by absorbing and sequestering salts and also by the manufacture of organic plant derived osmotica. The ability of many halophytes to sequester and compartmentalize ionic compounds (salt, including metals) even when these ionic compounds are in high concentration in the soil, make them ideal candidate for saline agriculture. Particularly when the site has primary or secondary contamination with ordinary brine or sea salts.

Halophytes are distributed in a variety of climatic conditions ranging from coastal areas to mountain valleys (Khan 2002). It appears that most of the tropical halophytes are perennial and most of the moist temperate halophytes are annual. However, in cold deserts like Great Basin, USA a large number of perennial halophytes are also reported. In addition halophytes utilized a broad range of variation in their physiological adaptation to salinity and these include stem succulents, leaf succulents, secretings forbs and grasses, annual and perennial grasses, pseudohalophytes and non-halophytes (Breckle 1983).

The success of saline agriculture is greatly dependent on the germination response of their seeds (Ungar 1995). The soils where halophytes normally grow becomes more saline due to rapid evaporation of water particularly during summer, therefore, surface of the soil tend to have higher soil salinity and more negative water potential (Khan and Gul 1998; Khan and Ungar 1998). Seed germination in arid and semi-arid regions usually occurs after the rains which help in reducing soil surface salinity (Khan 1999). The germination of halophytes inhibited by salinity for the various reasons: i) causing a complete inhibition of germination process at salinities beyond the tolerance limit of species, ii) delaying the germination of seeds at salinities that cause some stress to seeds but do not prevent germination, iii) causing the loss of viability of seeds due to high salinity and temperature and iv) upsetting growth regulator balance in the embryo to prevent successful initiation of germination process. There is a great deal of variability in the response of halophytes to increasing salinity, moisture, light, and temperature stresses and their interactions (Khan and Ungar 2000a; 2001).

The information available on the germination of halophytic seeds is far from complete (Khan 1999). From the total of about 2400 species reported (Lieth *et al.* 1999); the patchy data is available for about few hundred species (Baskin and Baskin 1998; Ungar 1995). There are several factors which determine the germination responses of halophytic seeds. These include salinity, temperature, light, habit, life form, habitat, water etc (Khan and Ungar 1997a). It would be interesting to determine if there is any pattern of germination based on any of these factors. Present study is an attempt to look for pattern if there is any based on the characteristics mentioned above.

Halophytes vary a great deal in their ability to tolerate salt. Tolerance also varies with stages of their life cycle which could be expressed as 1. The ability to tolerate high salinity with out loosing viability while stored in the soil (seed bank), 2. The ability to germinate at high salinities and 3. The ability to complete its life cycle at high salinities.

Table 1. Sodium chloride concentration at which seed germination of halophytes was reduced from 75 – 100% to about 10%.

Species	NaCl (M)	References
Salicornia herbacea	1.70	Chapman 1960
Kochia americana	1.20	Clark and West 1969
Spartina alterniflora	1.03	Mooring *et al*. 1971
Kochia scoparia	1.00	Khan *et al*. 2001b
Salsola iberica	1.00	Khan *et al.* unpublished data
Arthrocnemum macrostachyum	1.00	Khan and Gul 1998
Sarcobatus vermiculatus	1.00	Khan *et al.* 2002
Salicornia bigelovii	1.00	Rivers and Weber 1971
Suaeda moquinii	1.00	Khan *et al.* 2001a
Salicornia rubra	1.00	Khan *et al.* 2000
Suaeda japonica	0.90	Yokoishi and Tanimoto 1994
Cressa cretica	0.86	Khan 1991
Salicornia pacifica	0.86	Khan and Weber 1986
Suaeda depressa	0.85	Ungar 1962
Salicornia europaea	0.85	Ungar 1962; 1967
Tamarix pentandra	0.85	Ungar 1967
Allenrolfea occidentalis	0.80	Gul and Weber 1999
Halosarchia pergranulata	0.80	Short and Colmer 1999
Salsola imbricata	0.80	Khan, unpublished data
Pccinellia fastucaeformis	0.80	Onnis and Miceli 1975

Most halophytes studied are relatively more salt tolerant at first and third stages and their tolerance to salinity substantially decreased during the germination process (Khan *et al.* 2001abc). A cursory look on the responses of halophytes during growth under salinity stress indicates that usually stem succulents are highly salt tolerant, followed by leaf succulents, secreting and grass species (Khan and Ungar 1999; 2000ab; 2001). Although departures from this trend are also reported (Mooring *et al.* 1971; Gulzar and Khan 2001). This pattern does not hold true when we look at the germination responses to salinity (Table 1).

Highest salinity concentration at which a seed could germinate is 1.7 M NaCl based on the reports published so far. Chapman (1960) reported that few seeds of a stem succulent halophyte *Salicornia herbacea* germinated at 1.7 M NaCl. This followed by leaf succulent species, *Kochia americana* and a grass *Spartina alterniflora* (Clarke and West 1969, Mooring *et al.* 1971). The three highly salt tolerant halophytic species during germination have different life forms (Table 1). This would help to put things in perspective to mention that the seawater concentration varies from 0.6 M NaCl (moist temperate regions) to 0.7 M NaCl (arid sub-tropical zones).

Table 2. Sodium chloride concentration at which seed germination of stem succulent halophytes was reduced from 75 – 100% to about 10%.

Species	NaCl (M)	References
Salicornia herbacea	1.70	Chapman 1960
Arthrocnemum macrostachyum	1.00	Khan and Gul 1998
Salicornia bigelovii	1.00	Rivers and Weber 1971
Salicornia rubra	1.00	Khan *et al.* 2000
Salicornia europaea	0.85	Ungar 1962; 1967
Allenrolfea occidentalis	0.80	Gul and Weber 1999
Halosarchia pergranulata	0.80	Short and Colmer 1999
Sarcocornia quinquifolia	0.69	Patridge and Wilson 1987
Salicornia pacifica	0.68	Khan and Weber 1986
Salicornia brachiata	0.60	Joshi and Iyengar 1982
Salicornia virginica	0.60	Zedler and Beare 1986
Haloxylon stocksii	0.50	Khan and Ungar 1996
Arthrocnemum halocnemoides	0.40	Malcolm 1965
Halopeplis amplexicaulis	0.40	Tremblin and Binet 1982
Salicornia patula	0.34	Berger 1985
Halopeplis perfoliata	0.25	Mahmoud *et al.* 1983
Salicorni brachystachya	0.24	Huiskes *et al.* 1985
Salicornia dolistachya	0.24	Huiskes *et al.* 1985
Arthrocnemum australacicum	0.23	Clarke and Hannon 1970

Salt tolerance at germination stage for stem succulent species is reported in the Table 2. About 44% of the species reported could germinate above seawater salinities (Chapman 1960; Khan and Gul 1998; Rivers and Weber 1971; Khan *et al.* 2000; Ungar 1962; 1967; Gul and Weber 1999; Patridge and Wilson 1987; Khan and Weber 1986; Joshi and Iyengar 1982). However seeds of species like *Halopeplis perfoliata*, *Salicornia brachystachya*, *S. dolistachya*, and *Arthrocnemum australacium* failed to germinate at concentrations above 0.25M NaCl (Clarke and Hannon 1970; Mahmoud *et al.* 1983; Huiskes *et al.* 1985). The data presented in the Table 1 clearly indicates that a large percentage of the stem succulent halophytes are highly salt tolerant, however, some species could not germinate at salinities above 0.3M NaCl (Table 2).

Twenty seven percent of leaf succulent halophytes are reported to germinate at or above seawater salinity (Table 3), however, all of them are not as salt tolerant and about 26% halophytes failed to germinate at concentrations above 0.2 M NaCl (Kingsbury *et al.* 1976; Ungar 1991; 1962; 1967; Joshi and Iyengar 1977; Khan *et al.* 1987; Rozema 1975; Bakker *et al.* 1985). Leaf succulent halophytes share equal distribution of halophytes in all salinity tolerance levels (Table 3).

Table 3. Sodium chloride concentration at which seed germination of leaf succulent halophytes was reduced from 75 – 100% to about 10%.

Species	NaCl (M)	References
Kochia americana	1.20	Clark and West 1969
Kochia scoparia	1.00	Khan *et al.* 2001b
Salsola iberica	1.00	Khan *et al.* unpublished data
Sarcobatus vermiculatus	1.00	Khan *et al.* 2001c
Suaeda moquinii	1.00	Khan *et al.* 2001a
Suaeda japonica	0.90	Yokoishi and Tanimoto 1994
Suaeda depressa	0.85	Ungar 1962
Salsola imbricata	0.80	Mehrunnisa & Khan, unpub.data
Cakile maritima	0.60	Barbour 1970
Plantago lanceolata	0.60	Bakker *et al.* 1985
Salsola kali	0.60	Woodell 1985
Suaeda maritima	0.60	Boucaud and Ungar 1975
Suaeda fruticosa	0.50	Khan and Ungar 1998
Cochelaria danica	0.43	Bakker *et al.* 1985
Rumex crispus	0.43	Bakker *et al.* 1985
Ceratoides lanata	0.34	Workman and West 1967
Cotula cornopifolia	0.34	Patridge and Wilson 1987
Plantago maritima	0.34	Macke and Ungar 1971
Sperglaria media	0.34	Ungar and Binet 1975
Silene maritima	0.30	Binet 1968
Spergularia rupicola	0.30	Okusanya 1979
Samolus valerandi	0.25	Schat and Scholten 1985
Lasthenia glabrata	0.20	Kingsbury *et al.* 1976
Sperglaria marina	0.17	Ungar 1991
Suaeda limearis	0.17	Ungar 1962
Suaeda nudiflora	0.17	Joshi and Iyengar 1977
Iva annua	0.13	Ungar 1967
Chrysothamnus nauseosus	0.09	Khan *et al.* 1987
Glaux maritima	0.09	Rozema 1975
Sperglaria salina	0.09	Bakker *et al.* 1985

Secreting halophytes which could germinate above seawater salinity are only 19% (Table 4, Woodell 1985; Khan 1991; Ungar 1967; Binet 1965; Ignaciuk and Lee 1980). Most secreting halophytes show germination at NaCl concentrations ranging from 0.34 to 0.52 M NaCl. While few of them have low salt tolerance during germination (Mahmoud *et al.* 1983; Ladiges *et al.* 1981; Fernandes *et al.* 1985). Grass species which could tolerate above 0.6 M salinity is significantly reduced to 20% (Table 5) while about 76% germinated at levels below seawater and above 0.2 M NaCl (Macke and Ungar 1971; Gulzar and Khan 2001ab; Gulzar *et al.* 2001; Onnis and Bellatato 1972; Cluff and Roundy 1988; Hyder and Yasmin 1972; Breen *et al.* 1977; Ungar 1974; Harivandi *et al.* 1982; Khan and Ungar 2001).

Table 4. Sodium chloride concentration at which seed germination of secreting dicotyledonous halophytes was reduced from 75 – 100% to about 10%.

Species	NaCl (M)	References
Limonium. Vulgare	1.40	Woodell 1985
Atriplex rosea	1.00	Khan *et al.* (unpublished data)
Cressa cretica	0.85	Khan, 1991
Tamarix pentandra	0.85	Ungar 1967
Atriplex tornabeni	0.77	Binet 1965
Atriplex. Laciniata	0.60	Ignaciuk and Lee 1980
Atriplex nummularia	0.52	Uchiyama 1987
Atriplex triangularis	0.51	Khan and Ungar 1984
Atriplex prostrate	0.50	Katembe *et al.* 1998
Atriplex canescense	0.40	Mikheil *et al.* 1992
Atriplex. Lentiformis	0.40	Mikheil *et al.* 1992
Atriplex polycarpa	0.40	Mikheil *et al.* 1992
Limonium stocksii	0.40	Zia and Khan, unpublished data
Atriplex stocksii	0.35	Khan and Rizvi 1994
Atriplex halimus	0.34	Zid and Boukhris 1977
Atriplex patula	0.34	Ungar 1996
Mesembryanthemum australe	0.34	MacKay and Chapman 1954
Atriplex glabriuscula	0.24	Ignaciuk and Lee 1980
Limonium axillare	0.17	Mahmoud *et al.* 1983
Melulaca ericifolia	0.17	Ladiges *et al.* 1981
Atriplex. rependa	0.09	Fernandez *et al.* 1985

It seems that when we compare the salinity tolerance of halophytes from different groups that differ significantly at their salt tolerance above seawater levels (Table 6).

Table 5. Sodium chloride concentration at which seed germination of monocotyledenous halophytes was reduced from 75 – 100% to about 10%.

Species	NaCl (M)	References
Spartina alterniflora	1.03	Mooring *et al.* 1971
Puccinellia fastucaeformis	0.80	Onnis and Miceli 1975
Ruppia maritima	0.68	Koch and Seelinger 1988
Puccinellia lemmoni	0.60	Harivandi *et al.* 1982
Puccinellia nuttalliana	0.51	Macke and Ungar 1971
Aeluropus lagopoides	0.50	Gulzar and Khan 2001
Sporobolus ioclados	0.50	Gulzar and Khan 2001
Urochondra setulosa	0.50	Gulzar *et al.* 2001
Hordeum marinum	0.45	Onnis and Bellattato 1972
Distichlis spicata	0.43	Cluff and Roundy 1988
Sporobolus airoides	0.38	Hyder and Yasmin 1972
Sporobolus virginicus	0.38	Breen *et al.* 1977
Hordeum jubatum	0.32	Ungar 1974
Puccinellia distans	0.30	Harivandi *et al.* 1982
Halopyrum mucronatum	0.20	Khan and Ungar 2001

Table 6. Sodium chloride concentration at which seed germination of halophytes was reduced from 75 – 100% to about 10%.

Adaptations	Number of Species	NaCl (M)			
		<0.2	0.21-0.40	0.41-0.60	>0.61
Stem Succulents	18	0	39	17	44
Leaf Succulents	30	26	13	24	27
Secreting	21	6	26	46	19
Grasses	23	7	27	46	20

Forty four percent stem succulent species could germinate above seawater followed by 27% in leaf succulent and about 20% both in secreting and grass species (Table 6). It is also interesting to note that all stem succulent halophytes could germinate in salinities higher than 0.2 M NaCl (Table 6). Most halophytes belonging to other groups have germination tolerance ranges between 0.2 to 0.6 M NaCl except for leaf succulents where one fourth could not germinate at or above 0.2 M NaCl (Table 6).

The enforced dormancy response for halophyte seeds to saline conditions is of selective advantage to plants growing in highly saline habitats because seeds could withstand high salinity stress and provide a viable seed bank for recruitment of new individuals, but seed germination would be limited to periods when soil salinity levels were within the species tolerance limits (Ungar 1982). However, halophyte seeds differ in their ability to recover from salinity stress and germinate after being exposed to hyper-saline conditions (Table 7 and 8). Halophytes from the Great Basin desert (a cool temperate area) are highly salt tolerant to salinity (Table 7). 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.* unpublished data) had 80% or higher recovery of germination when exposed to 1000 mM NaCl (Table 1). A substantial recovery from germination occurred at the NaCl concentrations up to 600 mM NaCl in *Halogeton glomeratus* (Khan *et al.* 2001b), *Sarcobatus vermiculatus* (Khan *et al.* 2002), *Suaeda moquinii* (Khan *et al.* 2001a) and *Triglochin maritima* (Khan and Ungar 1999). This data showed that seeds of Great Basin halophytes have the ability to tolerate high salinity when present in the seed bank. All the species reported here recovered substantially up to 600 mM NaCl but some could almost completely recover from the NaCl concentration of 1000 mM NaCl (Table 7).

Table 7. Percentage recovery of germination of temperate halophytes at various NaCl concentrations (mM).

Name of species	NaCl (mM)					
	0	200	400	600	800	1000
Kochia scoparia	0	85	88	100	100	100
Salsola iberica	1	2	22	37	60	82
Halogeton glomeratus	100	85	72	52	22	8
Allenrolfea occidentalis	0	82	83	98	98	98
Salicornia rubra	0	1	23	38	60	78
Sarcobatus vermiculatus	0	0	61	47	22	0
Suaeda moquinii	0	0	62	50	25	8
Triglochin maritima	15	36	80	65	-	-

Recovery of germination of sub-tropical halophytes also showed some variability (Table 2) and they appeared to be less salt tolerant while in the seed bank when compared with temperate desert species (Table 1 and 2). *Arthrocnemum macrostachyum* showed a substantial recovery at 1000 mM NaCl (Khan and Gul 1998) while all others recovered in up to 600 mM NaCl (Table 2). *Aeluropus lagopoides* (Gulzar and Khan 2001), *Atriplex stocksii* (Khan 1999), *Limonium stocksii* (Zia and Khan, unpublished data) and *Urochondra setulosa* (Gulzar *et al.* 2001) showed about 75% recovery at 600 mM NaCl (Table 2). While *Cressa cretica* (Khan 1999), *Haloxylon stocksii* (Khan and Ungar 1996), *Salsola imbricata* (Khan, unpublished data), *Suaeda fruticosa* (Khan and Ungar 1998) and *Sporobolus ioclados* (Gulzar and Khan, unpublished data) showed poor recovery responses.

Several factors (water, temperature, light and salinity) interact in the soil interface, which regulate seed germination. They may even co-act with the seasonal variation in temperature to determine the temporal pattern of germination. Variation in temperature under saline conditions has differential effects on the germination of halophytes (Ungar 1995) and this variation could due to ecological regions of the world where they belong. Sub-tropical halophytes studied predominantly show optimal germination at 20-30 ^{o}C (Table 7) and any further increase and decrease in temperature affected the germination (Khan and Rizvi 1994; Khan and Ungar 1996; 1997; 1998;

Table 8. Percentage recovery of germination of sub-tropical halophytes at various NaCl concentrations (mM).

Name of species	NaCl (mM)			
	0	200	400	600
Aeluropus lagopoides	0	60	82	89
Arthrocnemum macrostachiyum	0	19	83	96
Atriplex stocksii	23	38	71	75
Cressa cretica	4	76	72	28
Haloxylon stocksii	20	6	58	50
Limonium stocksii	0	82	98	98
Salsola imbricata	0	1	17	19
Sporobolus ioclados	40	19	21	39
Suaeda fruticosa	70	40	0	0
Urochondra setulosa	38	88	75	60

1999; 2000; 2001; Gulzar and Khan 2001; Gulzar *et al.* 2001). All halophytic species studied from the cold Great Basin desert modify their seed germination with changes in temperature (Khan and Weber 1986; Khan *et al.* 1987; Gul and Weber 1999; Khan *et al.* 2001abc). Germination increased with an increase in temperature (Table 8) and optimal germination was obtained at temperature regime of 25 – 35 ^{o}C (Khan and Weber 1986; Gul and Weber 1999; Khan 1999; Khan *et al.* 2000; 2001abc). Germination of halophytes from moist temperate regions usually shows better germination at lower temperature (5-15 ^{o}C) regime (Table 9, Khan and Ungar 1984; Badger and Ungar 1989; Khan and Ungar 1998; Ungar 1977; Okusanya and Ungar 1983; Ungar and Capilupo 1969).

Seed germination of halophytes under natural conditions is regulated by variation in soil salinity and ambient thermoperiod (Khan and Ungar 1984; Badger and Ungar

1989; Ungar 1995). The salt tolerance of seeds appears to be affected by thermoperiod (Morgan and Myers 1989; Khan and Ungar 1996). Seeds of halophytes are known to tolerate high salinity during their presence in the soil and are known to germinate when soil salinities reduced (Khan and Ungar 1996; Ungar 1995).

Table 9. Percentage germination of subtropical halophytes at different temperatures.

Species	10/20	15/25	20/30	25/35
Aeluropus lagopoides	+	+	+++	++
Arthrocnemum macrostachyum	++	+++	+++	++
Atriplex stocksii	+++	++	++	++
Cressa cretica	+++	++	++	+
Halopyrum mucronatum	+	+	++	+++
Haloxylon stocksii	+++	+++	+++	++
Limonium vulgare	++	++	+++	++
Salsola imbricate	++	++	+++	++
Sporobolus ioclados	++	++	+++	++
Suaeda fruticosa	+	+++	+++	++
Urochondra setulosa	+	++	+++	++
Zygophyllum simplex	+	+	+++	++

Table 10. Percentage germination of Great Basin halophytes at different temperatures.

Species	5/15	10/20	15/25	20/30	25/35
Allenrolfea occidentalis	- - -	+	++	+++	+++
Atriplex rosea	+	++	+++	+++	+++
Chrysothamnus nauseosus	+	+	++	+++	+++
Halogeton glomeratus	++	++	+++	+++	+++
Kochia scoparia	++	++	+++	+++	+++
Salicornia rubra	+	++	++	+++	+++
Salicornia utahensis	++	?	++	++	++
Salsola iberica	+	++	+++	+++	+++
Sarcobatus vermiculatus	++	++	+++	+++	++
Suaeda moquinii	++	++	+++	+++	+++
Triglochin maritima	- - -	++	++	+++	+++

Table 11. Percentage germination of moist temperate halophytes at different temperatures.

Species	5/15	10/20	5/25	20/30

Atriplex prostrata	+	+	+++	++
Cochlearia anglica	+++	++	+	+
Crithimum maritimum	+++	++	++	-
Hordeum jubatum	+++	+++	+++	+
Polygonum aviculare	+++	+++	++	+
Salicornia europaea	++	++	+++	+
Salicornia stricta	+	++	+++	+
Spergularia marina	+++	++	+	-
Suaeda depressa	+	++	+++	-

Recovery of germination responses has been demonstrated in *Salicornia europaea* (Ungar 1962), *Spergularia marina* (Ungar 1967), *Suaeda depressa* (Ungar and Capilupo 1969), *Suaeda linearis* (Ungar 1962), *Arthrocnemum australsicum, Triglochin striata, Suaeda australis, Juncus maritimus,* and *Casuarina glauca* (Clarke and Hannon 1970). Boorman (1967, 1968) and Woodell (1985) also reported salt stimulation of seed germination following treatment with seawater for a number of salt marsh species. Woodell (1985) classified germination responses to salinity into three categories; Type 1 species, usually found in dunes or on the drift line, were all inhibited by half strength seawater. Recovery was relatively high, but no salt stimulation was observed in this group. Seeds of Type 2 species were strongly inhibited by half-strength seawater but had recovery germination (56% to 98%) from seawater in distilled water that was similar to the original germination percentages in the control. Type 3 species has less than 10% germination in seawater, were salt stimulated and had greater than 60% germination in distilled water recovery treatments. Keiffer and Ungar (1995) exposed seeds of 5 halophytes (*Atriplex prostrata*, *Hordeum jubatum, Salicornia europaea*, *Spergularia marina*, and *Suaeda calceoliformis*) to an extended period of salinity treatments and determined their recovery responses when transferred to distilled water. They used Woodell (1985) classification system and placed *Atriplex prostrata* seeds in the Type 1, *Hordeum jubatum* and *Spergularia marina* in the Type 2, and *Salicornia europaea* and *Suaeda calceoliformis* in the Type 3 category.

Role of temperature in the recovery of germination was poorly reported and most studies only focused on the recovery of seed germination based on the variation in salinity (Ungar 1962; 1967; Clarke and Hannon 1970; Ungar and Capilupo 1969; Boorman 1967; 1968; Woodell 1985; Keiffer and Ungar 1995). Khan and Ungar (1996) reported that variation in the recovery responses of *Haloxylon stocksii* seeds with the change in thermoperiod under various NaCl salinity treatments. They reported better recovery of germination at warmer thermoperiod. A number of studies on the effect of temperature regimes on the recovery of germination have since been conducted on the various kinds of halophytes from many parts of the world (Table 12). Best seed germination of temperate desert halophytes occurred at 25 – 35 ^{o}C (Khan and Gul 2002), however optimal recovery of germination of temperate desert halophytes occurred at various temperature regimes (Table 12). Optimal seed germination of *Allenrolfea occidentalis* (Gul and Weber 1999), *Halogeton glomeratus* (Khan *et al.* 2001b), *Sarcobatus vermiculatus* (Khan *et al.* 2002), *Salsola iberica* (Khan *et al.* 2002) were reported in 25 – 35 ^{o}C while at 10 – 20 ^{o}C and 15 – 25 ^{o}C temperature regimes

Table 12. Percent recovery of germination of temperate halophytes in 400 mM NaCl various thermoperiods (^{o}C) .

Name of the species	5-15	10-20	15-25	20-30	25-35
Allenrolfea occidentalis	39	5	51	100	98
Suaeda moquinii	66	100	93	26	15
Salicornia rubra	80	98	99	58	58
Kochia scoparia	79	93	94	57	57
Sarcobatus vermiculatus	69	52	46	40	61
Salsola iberica	46	36	38	30	81
Triglochin maritima	-	10	30	-	-

seeds of *Suaeda moquinii* (Khan *et al.* 2001a), *Salicornia rubra* (Khan *et al.* 2000), *Kochia scoparia* (Khan *et al.* 2001c) recovered better while *Triglochin maritima* showed a better recovery at 5-25^{o}C (Khan and Ungar 1999). The *Polygonum aviculare*, a native of moist temperate region showed best recovery at colder temperature regimes (5-15 ^{o}C) (Khan and Ungar 1998).

Recovery of seed germination of subtropical halophytes does not show any pattern (Table 13). Few halophytes (*Aeluropus lagopoides* and *Limonium stocksii*) showed almost complete recovery at all temperature regimes studied (Gulzar and Khan 2001, Zia and Khan, unpublished data). *Atriplex stocksii* and *Suaeda fruticosa* showed about 70% recovery at 20-30 ^{o}C and 15-25 ^{o}C respectively (Khan and Ungar 1998; Khan 1999), While most other halophytes showed a recovery response about 50% or less *Arthrocnemum macrostachyum* (Gul and Weber 1998), *Haloxylon stocksii* (Khan and Ungar 1996), *Salsola imbricata* (Khan, unpublished data), while still other made little recovery at any temperature regime, *Cressa cretica*, (Khan 1999), *Sporobolus ioclados* (Gulzar and Khan 2001), *Urochondra setulosa* (Gulzar *et al.* 2001). It appears from the published data the recovery of germination of most subtropical halophytes are poor in comparison to temperate halophytes and they do not show any consistent pattern of recovery of germination responses with the change in temperature.

Table 13. Percentage recovery of germination of sub-tropical halophytes in 400 mM NaCl at various thermoperiods (^{o}C).

Name of the species	10-20	10-30	15-25	20-30	25-35
Aeluropus lagopoides	42	-	65	89	88
Arthrocnemum macrostachyum	34	39	42	-	45
Atriplex stocksii	15	38	-	75	0
Cressa cretica	4	-	17	17	12
Haloxylon stocksii	55	30	40	-	6
Limonium stocksii	95	-	98	92	98
Salsola stocksii	03	-	4	15	3.2
Sporobolus ioclados	11	-	4	25	8
Suaeda fruticosa	30	38	71	-	51
Urochondra setulosa	11	-	27	57	29
Zygophyllum simplex	3	4	15	-	3.2

Physiology of halophyte seed germination is not properly understood. There is great deal of variations in the seed germination responses and there are so many different factors involved. The physiological response of seed germination is perhaps evolved to make the particular halophyte to suit better under specific environmental conditions. The clue for clear understanding of the causes of seed dormancy would come by identifying environmental cues that lead to the specific physiological signals. The data base on seed germination at large and halophytic seed germination in particular is too small to make ecological arguments for physiology and biochemistry of halophyte seed dormancy.

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