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Some Ecophysiological Aspects of Seed Germination in Halophytes

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Abstract: Seed ecophysiology of halophytes in relation to their habitat, life form, salinity tolerance, and temperature regimes were 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 high 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.

Key words: Ecophysiology, Seed germination, Halophyte

The rapidly growing human population and changing global environment are driving us to explore new resources for satisfying to the increasing demands of everyday life (Lieth et at., 1997). Most important demand of all is the availability of good quality water for drinking and agriculture purposes. Second important demand is the availability of prime agricultural lands in the arid and semi-arid regions of the world which are becoming increasingly saline. About 15% of the arid and semi-arid lands are affected by salt (Glenn et at., 1998; Lieth et at., 1999ab) and one-third of all agricultural lands are also becoming saline (Glenn et at., 1999). Approximately 67% of the earth's surface is covered with saline water. At the same time there are growing indications that cultivation of crops with a high salt tolerance can be seen as interesting option for utilizing saline soils and conserving fresh water (Choukrallah, 1996) .Saline agriculture is a type 0£ agriculture on the saline soil in which crops (halophytes) that can with stand a higher salt content than normal agricultural crops are grown (Glenn et at., 1998, 1999; Lieth et at., 1999ab). Potential halophytic crops could broadly be grouped into three categories 1) Plants with a high salt tolerance: they grow in water with salt contents equal to or even higher than seawater, 2) Plants with average salt tolerance: they grow in brackish water and 3) Plants with moderate salt tolerance: they grow in slightly brackish water that is not suitable for conventional agriculture.

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: 1) Causing a complete inhibition of germination process at salinities beyond the tolerance limit of species, 2) Delaying the germination of seeds at salinities that cause some stress to seeds but do not prevent germination, 3) Causing the loss of viabilities of seeds due to high salinity and temperature and 4) Upsetting growth regulator balance in the embryo to prevent successful initiation of germination process. There is a great deal of variabilities in the response of halophytes to increasing salinity, moisture, light, and temperature stresses and their interactions (Khan and Ungar, 2000, 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.*, 1999b); 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, 1997). 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 from 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.

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 1.7M NaCl based on the reports published so far. Chapman (1960) reported that few seeds of a stem succulent halophyte *Salicornia herbacea* germinated at 1.7M 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 0.6M NaCl (moist temperate regions) to 0.7M NaCl (arid sub-tropical zones).

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	Clarke 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.*, 2000b
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

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 tolerance, 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 0.2M 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 6).

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
Salicornia brachystachya	0.24	Huiskes *et al.*, 1985
Salicornia dolistachya	0.24	Huiskes *et al.*, 1985
Arthrocnemum australacium	0.23	Clarke and Hannon, 1970

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 0.52M 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 0.6M salinity is significantly reduced to 20% (Table 5) while about 76% germinated below seawater and above 0.2M 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).

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).

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 0.2M NaCl (Table 6). Most halophytes belonging to other groups have germination tolerance ranges between 0.2to 0.6 M NaCl except for leaf succulents where one fourth could not germinate at or above 0.2M NaCl (Table 6).

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, 1966
Sperglaria rupicola	0.30	Okusanya, 1979
Samolus valerandi	0.25	Schat and Scholten, 185
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

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 prostrata	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

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, 2001a
Sporobolus ioclados	0.50	Gulzar and Khan, 2001b
Urochondra setulosa	0.50	Gulzar *et al.*, 2001
Hordeum marinum	0.45	Onnis and Bellatato, 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	45	20

Table 7 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	+	+	+++	++

* Stands for nighttime temperature/daytime temperature, hereinafter.

Table 8 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	—	++	++	+++	+++

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. Subtropical halophytes studied predominantly show optimal germination at 20—30℃ (Table 7) and any further increase and decrease in temperature affected the germination (Khan and Rizvi, 1994; Khan and Ungar, 1996—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℃ (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℃) 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).

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.

Table 9 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	+	++	+++	—

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