CHAPTER 2

HALOPHYTE SEED GERMINATION

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Abstract. Halophyte seed germination, although displays a high degree of inter- and intra-specific variability, shows some patterns in response to various environmental factors. Seeds of stem succulent species germinated better in highly saline conditions. The salt tolerance decreased progressively from leaf succulent, secreting to non-secreting grass halophytes. Seed germination of cold desert halophytes progressively increased with an increase in temperature while seeds of warm desert halophytes showed better germination at cooler temperatures. Halophytes 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. Germination regulating chemicals like GA_3, kinetin, ethylene, fusicoccin, proline, betaine, thiourea and nitrate released the innate dormancy in seeds of some sub-tropical species while GA_3 was most effective. Germination regulating chemicals had better effect in releasing innate dormancy of Great Basin halophytes and fusicoccin appeared to be more effective. Alleviation of salinity induced dormancy using different chemicals was more successful in Great Basin species in comparison to sub-tropical species. Fusicoccin and ethephon succeeded with subtropical species while all chemicals alleviated either partially or completely the salinity-induced dormancy in Great Basin halophytes except for proline, betaine and nitrate.

1. INTRODUCTION

Halophytes, plants capable of growing and reproducing in saline conditions, as a group have several physiological adaptations that facilitate their survival in saline environments. Of these, most common among halophytes is the ability of osmotic adjustment i.e., 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. 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 candidates for saline agriculture. Halophytes are distributed in a variety of climatic conditions

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from coast to mountain valleys (Khan, 2003b). Generally, most tropical halophytes are perennials while majority of the moist temperate halophytes are annuals. However, in cold deserts like Great Basin, USA a large number of perennial halophytes are also reported. Halophytes utilize a broad range of physiological adaptations to salinity and may be stem succulents, leaf succulents, secreting forbs and grasses, annual and perennial grasses, pseudohalophytes and non-halophytes (Breckle, 1983).

The success of halophyte populations is greatly dependent on the germination response of their seeds particularly in temperate conditions while seed germination in subtropical habitats confers an ultimate advantage (Khan, 2003a). The soils where halophytes normally grow become more saline due to rapid evaporation of water particularly during summer, therefore, the soil surface tends to have higher soil salinity and higher water potentials (Khan & Gul, 1998; Khan & Ungar, 1998b). Seed germination in arid and semi-arid regions usually occurs after the rains by reducing surface soil salinity (Khan, 1999). The germination of halophytes could be inhibited under saline conditions due to: i) 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, 2003a).

The information available on the germination of halophytic seeds is far from complete (Khan, 1999). From a total of about 2400 species reported (Lieth et al., 1999); patchy data is available for only about a few hundred species (Baskin & Baskin, 1995; Ungar, 1995). Several factors determine the germination responses of halophytic seeds including salinity, temperature, light, habit, life form, habitat, water etc (Khan, 2003a). It would be interesting to determine patterns of germination if any due to these factors. Present study is an attempt to look for patterns if there are any based on the characteristics mentioned above.

2. SALINITY EFFECTS

Seeds of many halophytic species are reported to germinate best under fresh water conditions or at salinities below 100 mM NaCl (Ungar, 1991) indicating that seeds do not require low water potential for germination (Ungar, 1995). Halophytes vary considerably in their ability to tolerate salt (Table 1). The seawater concentration varies from about 0.6 M NaCl (temperate) to 0.7 M NaCl (arid sub-tropical). The highest salinity concentration at which a seed is reported to germinate is 1.7 M NaCl. Chapman (1960) reported that few seeds of a stem succulent halophyte *Salicornia herbacea* germinated at 1.7 M NaCl and seeds of *Haloxylon ammodendron* and *H. persicum* germinated at 1.3 M NaCl (Tobe et al., 2000). This is followed by a leaf succulent species, *Kochia americana* (1.2 M NaCl;

Clarke & West, 1969) and a grass *Spartina alterniflora* (1.02 M NaCl; Mooring et al., 1971). The first three highly salt tolerant species are stem succulent followed closely by a grass and a leaf succulent (Table 1).

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
Haloxylon ammodendron	1.30	Huang et al., 2003
Haloxylon persicum	1.30	Tobe et al., 2000
Kochia Americana	1.20	Clark & West, 1969
Spartina alterniflora	1.03	Mooring et al., 1971
Sarcocornia perennis	1.03	Redano et al., 2004
Kochia scoparia	1.00	Khan et al., 2001b
Salsola iberica	1.00	Khan et al., 2002c
Halogeton glomeratus	1.00	Khan et al., 2001c
Arthrocnemum macrostachyum	1.00	Khan & Gul, 1998
Sarcobatus vermiculatus	1.00	Khan et al., 2002a
Salicornia bigelovii	1.00	Rivers & Weber, 1971
Suaeda moquinii	1.00	Khan et al., 2001a
Salicornia rubra	1.00	Khan et al., 2000
Suaeda japonica	0.90	Yokoishi &Tanimoto, 1994
Cressa cretica	0.86	Khan, 1991
Salicornia pacifica	0.86	Khan & Weber, 1986
Halocnemum strobilaceum	0.86	Pujol et al., 2001
Suaeda depressa	0.85	Ungar, 1962
Salicornia europaea	0.85	Ungar, 1962, 1967
Tamarix pentandra	0.85	Ungar, 1967
Allenrolfea occidentalis	0.80	Gul & Weber, 1999
Halosarchia pergranulata	0.80	Short & Colmer, 1999
Salsola imbricata	0.80	Khan, unpublished data

2.1. Salinity tolerance during seed germination of stem succulent halophytes

This indicates that high salinity tolerance during germination is quite independent of plant life form (Table 1). Salt tolerance at germination stage for stem succulent species is reported in the (Table 2). About 60% of the species reported could germinate above seawater salinities (Chapman, 1960; Ungar, 1962, 1967; Rivers & Weber, 1971; Joshi & Iyengar, 1982; Khan & Weber, 1986; Patridge & Wilson, 1987; Khan & Gul, 1998; Gul & Weber, 1999; Khan et al., 2000; Tobe et al., 2000). However, seeds of species like *Halopeplis perfoliata*, *Salicornia brachystachya*, *S. dolistachya* and *Arthrocnemum australacium* failed to germinate at concentrations above 0.25 M NaCl (Clarke & Hannon, 1971; Mahmoud et al., 1983; Huiskes et al., 1985). The data presented in (Table 2) 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).

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
Haloxylon ammodendron	1.30	Huang et al., 2003
Haloxylon persicum	1.30	Tobe et al., 2000
Sarcocornia perennis	1.03	Redano et al., 2004
Sarcocornia fruticosa	1.03	Redando et al., 2004
Salicornia bigelovii	1.00	Rivers & Weber, 1971
Salicornia rubra	1.00	Khan et al., 2000
Salicornia europaea	0.85	Ungar, 1962, 1967
Allenrolfea occidentalis	0.80	Gul & Weber, 1999
Halosarchia pergranulata	0.80	Short & Colmer, 1999
Sarcocornia quinquifolia	0.69	Patridge & Wilson, 1987
Salicornia pacifica	0.68	Khan & Weber, 1986
Salicornia brachiata	0.60	Joshi & Iyengar, 1982
Salicornia virginica	0.60	Zedler & Beare, 1986
Haloxylon stocksii	0.50	Khan & Ungar, 1996
Arthrocnemum halocnemoides	0.40	Malcolm, 1964
Halopeplis amplexicaulis	0.40	Tremblin & 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 & Hannon, 1970

2.2. Salinity tolerance during seed germination of leaf succulent halophytes

Twenty seven percent of leaf succulent halophytes are reported to germinate at or above seawater salinity (Table 3). However, and about 26% failed to germinate at concentrations above 0.2 M NaCl (Kingsbury et al., 1976; Ungar, 1962, 1967, 1991; Joshi & Iyengar, 1982; Khan et al., 1987; Rozema, 1975; Bakker et al., 1985). Leaf succulents share equal distribution among halophytes at all salinity tolerance levels (Table 3).

2.3. Salinity tolerance during seed germination of secreting halophytes

Few secreting halophytes (only 19%) which could germinate above seawater salinity (Table 4, Woodell, 1985; Khan, 1991; Ungar, 1967; Binet, 1965; Ignaciuk & Lee, 1980; Raccuia et al., 2004). Most secreting halophytes show germination at NaCl concentrations ranging from 0.34 to 0.52 M NaCl (Prado et al., 2000; Carter & Ungar, 2003). While few of them have low salt tolerance during germination (Mahmoud et al., 1983; Ladiges et al., 1981; Fernandes et al., 1985).

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 & West, 1969
Kochia scoparia	1.00	Khan et al., 2001b
Salsola iberica	1.00	Khan et al., 2002c
Sarcobatus vermiculatus	1.00	Khan et al., 2001a
Suaeda moquinii	1.00	Khan et al., 2001a
Suaeda japonica	0.90	Yokoishi & Tanimoto, 1994
Suaeda depressa	0.85	Ungar, 1962
Salsola imbricata	0.80	Mehrunnisa (unpublished 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 & Ungar, 1976
Suaeda fruticosa	0.50	Khan & Ungar, 1998b
Cakile maritima	0.50	Debez et al., 2004
Cochelaria danica	0.43	Bakker et al., 1985
Rumex crispus	0.43	Bakker et al., 1985
Ceratoides lanata	0.34	Workman & West, 1967
Cotula cornopifolia	0.34	Patridge & Wilson, 1987
Plantago maritima	0.34	Macke & Ungar, 1971
Sperglaria media	0.34	Ungar & Binet, 1975
Silene maritima	0.30	Binet, 1968
Spergularia rupicola	0.30	Okusanya, 1979
Samolus valerandi	0.25	Schat & 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 & Iyengar, 1982
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

2.4. Salinity tolerance during seed germination of monocotyledonous halophytes

Grass species which could tolerate above 0.6 M salinity but their germination was significantly reduced to 20% (Table 5)

2.5. Comparative salinity effects on seed germination.

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

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., 2004b
Cressa cretica	0.85	Khan, 1991
Tamarix pentandra	0.85	Ungar, 1967
Atriplex tornabeni	0.77	Binet, 1965
Atriplex laciniata	0.60	Ignaciuk & Lee, 1980
Atriplex nummularia	0.52	Uchiyama, 1987
Atriplex triangularis	0.51	Khan & 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 & Khan, 2004
Atriplex stocksii	0.35	Khan & Rizvi, 1994
Atriplex halimus	0.34	Zid & Boukhris, 1977
Atriplex patula	0.34	Ungar, 1996
Mesembryanthemum australe	0.34	MacKay & Chapman, 1954
Atriplex glabriuscula	0.24	Ignaciuk & 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 secreting monocotyledonous 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 & Miceli, 1975
Ruppia maritima	0.68	Koch & Seelinger, 1988
Puccinellia lemmoni	0.60	Harivandi et al., 1982
Puccinellia nuttalliana	0.51	Macke & Ungar, 1971
Aeluropus lagopoides	0.50	Gulzar & Khan, 2001
Sporobolus ioclados	0.50	Khan & Gulzar, 2003ab
Urochondra setulosa	0.50	Gulzar et al., 2001
Desmostachya bipinnata	0.50	Gulzar (unpublished data)
Hordeum marinum	0.45	Onnis & Bellattato, 1972
Distichlis spicata	0.43	Cluff & Roundy, 1988
Sporobolus airoides	0.38	Hyder & 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 & Ungar, 2001b

Fifty percent stem succulent species could germinate above seawater followed by 27% in leaf succulent and about 19% both in secreting and grass species (Table 6). It is also interesting to note that the salt tolerance of stem succulent halophytes at germination is 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).

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

Adaptations	*Number of species*	*<0.2*	*0.21-0.40*	*0.41-0.60*	*>0.61*
Stem Succulents	20	0	35	15	50
Leaf Succulents	30	26	13	24	27
Secreting	21	6	26	46	19
Grasses	16	0	31	50	19

3. RECOVERY

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 & 8).

3.1. Recovery of germination of temperate halophytes from salinity stress

Halophytes from the Great Basin desert (a cool temperate area) are highly salt tolerant to salinity (Table 7). Halophytes like *Allenrolfea occidentalis* (Gul & Weber, 1999), *Kochia scoparia* (Khan et al., 2001a), *Salicornia rubra* (Khan et al., 2000) and *Salsola iberica* (Khan et al., 2002c) had 80% or higher recovery of germination when exposed to 1000 mM NaCl (Table 7).

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., 2002a), *Suaeda moquinii* (Khan et al., 2001a) and *Triglochin maritima* (Khan & 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).

3.2. Recovery of germination of sub-tropical halophytes from salinity stress

Recovery of germination of sub-tropical halophytes also showed some variability (Table 8) and they appeared to be less salt tolerant while in the seed bank when compared with temperate desert species (Table 7).

Arthrocnemum macrostachyum showed a substantial recovery at 1000 mM NaCl (Khan & Gul, 1998) while all others recovered in up to 600 mM NaCl (Table 8). *Aeluropus lagopoides* (Gulzar & Khan, 2001), *Atriplex stocksii* (Khan, 1999), *Limonium stocksii* (Zia & Khan, 2004) and *Urochondra setulosa* (Gulzar et al., 2001) showed about 75% recovery at 600 mM NaCl (Table 8). While *Cressa cretica* (Khan, 1999), *Haloxylon stocksii* (Khan & Ungar, 1996), *Salsola imbricata* (Khan, unpublished data), *Suaeda fruticosa* (Khan & Ungar, 1998b) and *Sporobolus ioclados* (Khan & Gulzar, 2003a) showed poor recovery responses.

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	-	-

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

4. TEMPERATURE AND SALINITY EFFECT ON SEED GERMINATION

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, El-Keblawy and Al-Rawai 2005) and this variation could be due to ecological regions of the world where they belong.

4.1. Germination of sub-tropical halophytes under various temperature regimes under saline conditions

Sub-tropical halophytes predominantly showed optimal germination at 20-30°C (Table 9) and any further increase or decrease in temperatures affected seed germination (Khan & Rizvi, 1994; Khan & Ungar, 1996, 1997, 1998b, 1999, 2000, 2001a; Gulzar & Khan, 2001; Gulzar et al., 2001).

Table 9. *Percent 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 imbricata	++	++	+++	++
Sporobolus ioclados	++	++	+++	++
Suaeda fruticosa	+	+++	+++	++
Urochondra setulosa	+	++	+++	++
Zygophyllum simplex	+	+	+++	++

4.2. Germination of Great Basin desert halophytes under various temperature regimes under saline conditions

All halophytic species studied from the cold Great Basin desert progressively modified their seed germination with changes in temperature (Khan & Weber, 1986; Khan et al., 1987; Gul & Weber 1999; Khan et al., 2001abc). Germination increased with an increase in temperature (Table 10) and optimal germination was obtained at temperature regime of 25 – 35°C (Khan & Weber, 1986; Gul & Weber, 1999; Khan, 1999; Khan et al., 2000, 2001abc).

4.3. Germination of moist temperate region halophytes under various temperature regimes under saline conditions

Germination of halophytes from moist temperate regions usually shows better germination at lower temperature (5-15 °C) regime (Table 11, Khan & Ungar, 1984; Badger & Ungar, 1989; Khan & Ungar, 1998a; Ungar, 1977; Okusanya & Ungar, 1983; Ungar & Capilupo, 1969). Seed germination of halophytes under natural conditions is regulated by variation in soil salinity and ambient thermoperiod (Khan & Ungar, 1984; Badger & Ungar, 1989; Ungar, 1995). The salt tolerance of seeds appears to be affected by thermoperiod (Morgan & Myers, 1989; Khan & 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 are reduced (Khan & Ungar, 1996; Ungar, 1995).

Table 10. *Percent 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. *Percent 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	+	++	+++	-

5. TEMPERATURE EFFECTS ON THE RECOVERY OF SEED GERMINATION UNDER SALINE CONDITIONS

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 & Hannon, 1971; Ungar & Capilupo, 1969; Boorman, 1967; 1968; Woodell, 1985; Keiffer & 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).

5.1. Germination of Great Basin halophytes under various temperature regimes under saline conditions

Best seed germination of temperate desert halophytes occurred at 25 – 35°C (Khan & 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 & Weber, 1999), *Halogeton glomeratus* (Khan et al., 2001b), *Sarcobatus vermiculatus* (Khan et al., 2002a), *Salsola iberica* (Khan et al., 2002c) were reported in 25 – 35°C while at 10 – 20°C and 15 – 25°C temperature regimes seeds of *Suaeda moquinii* (Khan et al., 2001a), *Salicornia rubra* (Khan et al, 2000), *Kochia scoparia* (Khan et al., 2001b) recovered better while *Triglochin maritima* showed a better recovery at 5-25°C (Khan & Ungar, 1999). *Polygonum aviculare*, a native of moist temperate region showed best recovery at colder temperature regimes (5-15°C) (Khan & Ungar, 1998a).

Table 12. *Percent recovery of germination of temperate halophytes in 400 mM NaCl various thermoperiods (°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	-	-

5.2. Germination of Sub-tropical halophytes under various temperature regimes under saline conditions

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 & Khan 2001, Zia & Khan, 2004). *Atriplex stocksii* and *Suaeda fruticosa* showed about 70% recovery at 20-30°C and 15-25°C respectively (Khan & Ungar, 1998b; Khan, 1999), While most other halophytes showed a recovery response about 50% or less like *Arthrocnemum macrostachyum* (Gul & Weber, 1998), *Haloxylon stocksii* (Khan & Ungar, 1996), *Salsola imbricata* (Khan, unpublished data), while still other made little recovery at any temperature regime, *Cressa cretica* (Khan, 1999), *Sporobolus ioclados* (Gulzar & Khan, 2001), *Urochondra setulosa* (Gulzar et al., 2001). It appears from the published data that 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 (°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 imbricata	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

6. GROWTH REGULATORS

Growth regulator theory of dormancy has attracted a great deal of attention (Bewley & Black, 1994). This attributes the control of dormancy to various growth regulators – inhibitors, such as ABA, and promoters, such as gibberellins, cytokinins and ethylene. According to the theory, dormancy is maintained (or induced) by inhibitors such as ABA, and it can be released only when the inhibitors are removed or when promoters overcome it. A second concept is that important metabolic changes occur by the action of dormancy-breaking factors such as the synthesis of RNA, and protein or the operation of the pentose phosphate pathway (Bewley & Black, 1994). If all of the dormant conditions, including after-ripening, light or stratification requirements, and dormancies by endogenous inhibitors, are related to the balance of growth regulators (Khan, 1971, Ungar, 1991), this line of experimentation with halophytes should yield some basic information on the dormancy mechanisms of halophytes. Effect of various germination regulating chemicals like proline (Pr.), betaine (Bet.), gibberellic acid (GA), kinetin (Kin.), fusicoccin (Fc.), ethephon (Et.), thiourea (Tu.) and nitrate (Nit.) were studied on the innate and salinity induced seed dormancy of a number of sub-tropical and Great Basin halophytes.

6.1. Effect of germination regulating chemicals in alleviating innate dormancy of sub-tropical halophytes

The results presented in Table 14 show that except for proline all the germination regulating chemicals were effective in alleviating either partially or completely the innate dormancy in the annual *Zygophyllum simplex* and a perennial *Atriplex stocksii* (Khan & Rizvi, 1994, Khan & Ungar, 1997, 2000, 2002). Fusicoccin and Thiourea treatment caused a complete loss of seed dormancy (Khan & Ungar, 2002). Among seeds of perennial species like *Aeluropus lagopoides, Halopyrum mucronatum, Limonium stocksii*, *Salsola imbricata, Sporobolous ioclados*, and *Urochondra setulosa* germination regulating chemicals either had no effect or a negative effect on germination (Gulzar & Khan, 2002, Khan & Ungar, 2001b, Zia & Khan, 2004). *Arthrocnemum macrostachyum* (Bet., FA. and FC), *Haloxylon stocksii* (Bet. GA), *Suaeda fruticosa* (Pr. and Bet.) and *Sporobolous arabicus* (Fc, Et., Tu. and Nit.) have some effect (Khan et al., 1998, Khan and Ungar, 1996, 2000, 2001b).

Table 14.*Response of different germination regulating chemicals on the innate dormancy of sub-tropical halophytes*

Species	*Pr*	*Bet.*	*GA*	*Kin*	*FC*	*Et*	*Tu.*	*Nit.*
Aeluropus lagopoides	0	0	0	0	0	0	0	0
Arthrocnemum acrostachyum	0	+++	++++	0	++	0	0	0
Atriplex stocksii	+	+	++	+++	+	+	++	+
Halopyrum mucronatum	-	-	0	-	-	-	0	0
Haloxylon stocksii	-	+	++	-	?	?	?	?
Limonium stocksii	-	-	-	0	?	0	0	-
Salsola imbricata	0	0	0	0	0	0	0	0
Sporobolus ioclados	0	-	0	0	0	0	0	0
Suaeda fruticosa	+	++++	0	-	0	0	0	0
Urochondra setulosa	0	0	0	0	0	0	0	-
Zygophyllum simplex	0	++	+++	+++	++++	+++	++++	+++
Sporobolus arabicus	0	0	0	0	+++	+	+++	++

6.2. Effect of germination regulating chemicals in alleviating innate dormancy of Great Basin halophytes

Germination regulating chemicals have no effect on the innate dormancy of temperate halophytes like *Allerolfea occidentalis* (Gul & Weber, 1998) *Atriplex rosea* (Khan et al., 2004b). Whereas most of them have some effect on releasing innate dormancy in the case of *Ceratoides lanata, Kochia scoparia, Salicornia rubra, Salicornia utahensis*, *Suaeda moquinii,* and *Triglochin maritima* (Khan & Ungar, 2001c, Khan et al., 2002b; Gul & Khan, 2003; Khan et al., 2004a). Among chemicals, fusicoccin alleviated the innate dormancy of 80% of the temperate species studied while proline, betaine, kinetin, ethephon and thiourea alleviated 50% of the temperate halophytes (Table 15).

6.3. Effect of germination regulating chemicals in alleviating salinity effects on seed germination of sub-tropical halophytes

Effect of salinity on the seed germination of subtropical halophytes could not be alleviated by many chemicals (Table 16). *Halopyrum mucronatum, Haloxylon stocksii, Salsola imbricata, Sporobolous ioclados, Suaeda fruticosa* and *Urochondra setulosa* had little or no effect of the germination regulating chemicals in alleviating salinity induced dormancy (Khan et al., 1998, Khan & Ungar, 2000, 2001ab; Gulzar & Khan, 2002). Most chemicals had some effect on alleviating salinity induced effects on the germination of *Atriplex stocksii* and *Zygophyllum simplex*. Thiourea, Ethephon and Fusicocccin were most effective (60 %) in alleviating the salinity effects on germination, followed by GA, kinetin and nitrate (Table 16). Osmotica like proline and betaine alleviated seed germination of few species (Khan et al., 1998, Khan & Ungar, 2000, 2001abc, Gulzar & Khan, 2002).

Table 15. *Response of different germination regulating chemicals on the innate dormancy of Great Basin halophytes*

Species	*Pr*	*Bet.*	*GA*	*Kin*	*FC*	*Et*	*TU*	*Nit.*
Allenrolfea Occidentalis	0	0	0	0	0	0	0	0
Atriplex rosea	0	0	-	0	+	0	+	-
Halogeton glomeratus	+	+	0	+	++++	-	0	+++
Kochia scoparia	-	+	+	++	++	++	0	-
Salicornia rubra	0	-	0	0	++	+	+	0
Salicornia utahensis	++	++	-	++++	++++	0	++	-
Salsola iberica	+++	+	-	-	+++	+	0	-
Sarcobatus vermiculatus	0	0	0	0	0	0	0	-
Suaeda moquinii	+	++	++++	+++	+	++	++	+
Triglochin maritima	++	0	0	+	++	++	++	0

6.4. Effect of germination regulating chemicals in alleviating salinity effects on seed germination of Great Basin halophytes

Contrary to the sub-tropical halophytes, seed germination of Great Basin halophytes was substantially alleviated by the application of various chemicals (Table 17). All chemical used almost completely alleviated the salinity effects on the seed germination of *Allenrolfea occidentalis* (Gul & Weber, 1998, Gul et al., 2000). GA, kinetin, fusicoccin, ethephon, and thiourea had substantial effect in alleviating the salinity effects on seed germination. While Nitrate, proline and betaine were effective in some species (Gul et al., 2000, Khan & Ungar, 2001c,

Table 16. *Response of different germination regulating chemicals on the salinity induced dormancy of sub-tropical halophytes*

Species	*Pr*	*Bet.*	*GA*	*Kin*	*FC*	*Et*	*TU*	*Nit.*
Aeluropus lagopoides	+	-	0	++	+++	++++	+++	0
Arthrocnemum macrostachyum	+	+	+	+	+	+	+	0
Atriplex stocksii	++	+	+++	+++	++	0	+	+
Halopyrum mucronatum	-	-	+	0	?	?	+	+
Haloxylon stocksii	0	0	-	-	0	0	0	0
Limonium vulgare	-	-	-	-	?	++++	-	-
Salsola imbricata	-	-	-	-	-	-	-	-
Sporobolus ioclados	-	-	+	0	0	+	-	-
Suaeda fruticosa	0	+	-	0	+	++	0	-
Urochondra setulosa	0	0	0	0	0	0	0	-
Zygophyllum simplex	0	0	+++	+++	++++	++	++	+
Sporobolus arabicus	0	0	0	0	+++	0	+	+++

Table 17. *Response of different germination regulating chemicals on the salinity Induced dormancy of Great Basin halophytes*

Species	*Pr*	*Bet.*	*GA*	*Kin*	*FC*	*Et*	*TU*	*Nit.*
Allenrolfea occidentalis	+++	++++	+++	+++	++++	++++	+++	++++
Atriplex rosea	0	0	-	+	0	+	0	-
Halogeton glomeratus	+	0	+	++	+++	-	++	+++
Kochia scoparia	-	+	++	+++	+++	+++	+++	-
Salicornia rubra	0	-	+	+	+	++	+	+
Salicornia utahensis	+	0	0	+++	+++	+++	+++	0
Salsola iberica	+	0	+	0	+	0	+	-
Sarcobatus vermiculatus	0	-	+	++	++	++	+	-
Suaeda moquinii	0	0	++	+++	+	++	+	0
Triglochin maritima	+	0	0	+++	++	+	++	+++

Gul & Khan, 2003, Khan et al., 2000, 2002c, 2003, 2004ab). Physiology of halophyte seed germination is not properly understood. There is considerable variation in the seed germination responses with different factors involved. The physiological response of seed germination is perhaps evolved to make the particular halophyte adapt to specific environmental conditions.The clue for better understanding of the causes of seed dormancy would come from identifying environmental cues that are translated to specific physiological signals. The data based on seed germination at large and halophytic seed germination in particular is too small to make tangible ecological arguments for physiology and biochemistry of halophyte seed dormancy.

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