

Effects of light, salinity, and thermoperiod on the seed germination of halophytes

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Abstract: Seed germination of desert shrubs (*Atriplex griffithii* Moq., *Haloxylon recurvum* (Moq.) Bunge ex Boiss, *Suaeda fruticosa* (L.) Forssk., *Triglochin maritima* L.), and a forb (*Zygophyllum simplex* L.) was studied under various light, temperature, and salinity regimes. Seed germination of *Atriplex griffithii*, *Z. simplex*, and *Suaeda fruticosa* was least affected by light, whereas, seeds of *H. recurvum* and *T. maritima* had a light requirement for germination. *Haloxylon recurvum* seeds did not germinate at 10–20°C in the dark, and no *T. maritima* seeds germinated in dark at all thermoperiod and salinity regimes studied. Seed germination was inhibited in all species with an increase in salinity, and this inhibition was more substantial in dark than in light.

Key words: *Atriplex griffithii*, halophyte, *Haloxylon recurvum*, light, seed germination, *Suaeda fruticosa*, *Triglochin maritima*, thermoperiod, *Zygophyllum simplex*.

Résumé : Les auteurs ont étudié sous différentes conditions de lumière, de température et de salinité, la germination des graines d'arbustes du désert (*Atriplex griffithii* Moq., *Haloxylon recurvum* (Moq.) Bunge ex Boiss, *Suaeda fruticosa* (L.) Forssk., *Triglochin maritima* L.) et une herbe non-graminéenne (*Zygophyllum simplex* L.). La germination des graines des *A. griffithii*, *Z. simplex* et *S. fruticosa* est la moins affectée par la lumière, alors que les graines des *H. recurvum* et *T. maritima* ont besoin de lumière pour germer. Les graines de l'*H. recurvum* ne germent pas à 10–20°C à l'obscurité, et aucune graine du *T. maritima* ne germe à l'obscurité, quels que soient les régimes de thermopériode ou de salinité étudiés. La germination des graines est inhibée chez toutes les espèces avec l'augmentation de la salinité, et cette inhibition est amplifiée par l'absence de lumière.

Mots clés : *Atriplex griffithii*, halophyte, *Haloxylon recurvum*, lumière, germination des graines, *Suaeda fruticosa*, *Triglochin maritima*, thermopériode, *Zygophyllum simplex*.

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Introduction

Seed dormancy is a significant factor in the ecophysiology of salt marsh species (Ungar 1991). It permits seeds to remain viable in the soil during periods when the environment is not suited for germination. Flooding, hypersaline conditions, and burial of seeds by tidal depositions or sand drift may make salt marsh and salt desert environments unsuitable for seed germination. Some seeds remain dormant because of a hard or impermeable pericarp, testa, or an immature embryo restricts germination, while in other cases the seeds are responding to some environmental factors (e.g., light, temperature, and salinity) when they become dormant (Ungar 1977).

Light is one of the most important regulatory environmental signals in the life cycle of desert plants and their seed germination (Gutterman 1993). Germination of various halophyte seeds occurs at times when there is an optimal combination of day length, temperature, and salinity. In *Pancre-*

atum maritimum L. (Keren and Evenari 1974) and *Calligonum comosum* L'Her. (Koller 1956) seeds germinate when the micropyle is aligned towards light and light penetrates through this structure. Light alone in some species controls germination, while in others it operates in combination with salinity and temperature (Gutterman 1993; Gutterman et al. 1995). The interaction between salinity, temperature, and light on germination has been studied (Koller 1957; Binet 1961; Datta 1965; Barbour 1968; Freeman 1973; Keren and Evenari 1974; Young et al. 1980; Agami 1986; Khan and Weber 1986; Khan et al. 1987; DeVilliers et al. 1994; Naidoo and Naicker 1992; Gutterman et al. 1995). The interaction between salinity and temperature has also been investigated (Khan and Ungar 1984; Khan and Weber 1986; Khan et al. 1987; Badger and Ungar 1989; Khan 1991; Gutterman 1993; Khan and Rizvi 1994).

There is little information available on the interaction between salinity, temperature, and light on the germination of halophytic species. The aim of this study was to investigate the presence of dark-inhibited seed germination under various salinity and thermoperiod treatments in halophytes.

Materials and methods

Seeds of *Atriplex griffithii* Moq., *Haloxylon recurvum* (Moq.) Bunge ex Boiss, *Suaeda fruticosa* (L.) Forssk., and *Zygophyllum simplex* L. were collected during the fall 1994 from salt flats situated on the Karachi University campus, Karachi, Pakistan. Seeds of *Triglochin maritima* L. were collected during the summer 1995

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Fig. 1. Percentage (\pm SE) of germination of *Atriplex griffithii* seeds in various light, salinity, and thermoperiods. (■), 24 h dark; (▨), 12 h dark : 12 h light.

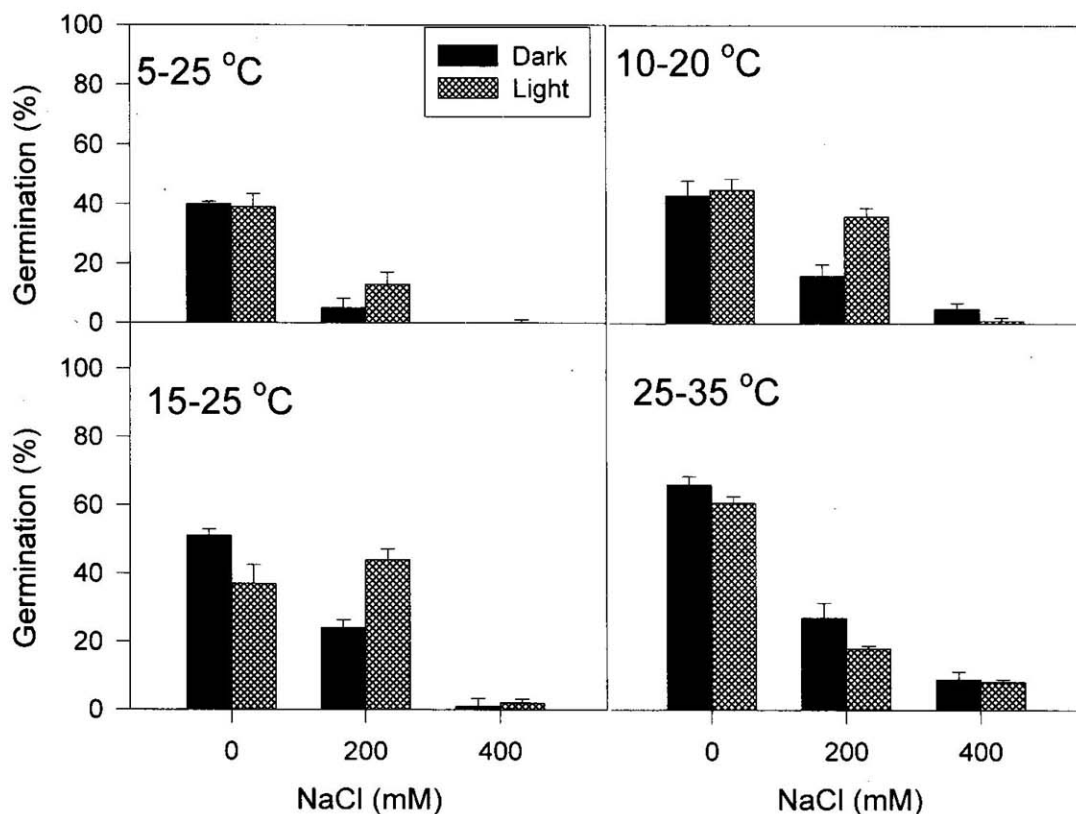


Table 1. Results of three-way analysis of variance of characteristics by species (Sp), salinity (S), thermoperiod (T) treatments.

Dependent variable	Independent variable						
	Sp	S	T	S × Sp	S × T	Sp × T	Sp × T × S
Germination in dark	217.9***	473.0***	47.5**	79.3***	10.7***	8.8**	4.0***
Germination in light	87.8***	550.8***	19.4***	8.8***	5.6***	21.6***	8.4***

Note: Values are *F* values: **, $P < 0.001$; ***, $P < 0.0001$.

from a salt marsh located 30 miles (1 mile = 1.6 km) south of the Great Salt Lake, at Faust, Utah. Seeds were separated from the inflorescence and then brought to Ohio University where they were stored at 4°C. Germination studies were started in September 1995. Seeds were surface sterilized by mixing them in the powder form of the fungicide Phygon (3-dichloro-1,4-naphthol, U.S. Rubber, Naugatuck, Conn.). Germination was carried out in 50 × 9 mm (Gelman No. 7232) tight-fitting plastic Petri dishes with 5 mL of test solution. Each dish was placed in a 10 cm diameter plastic Petri dish as an added precaution against loss of water by evaporation. Four replicates of 25 seeds each were used for each treatment. Seeds were considered to be germinated with the emergence of the radicle.

To determine the effect of temperature on germination, 12-h alternating temperature regimes were used 5–15°C, 5–25°C, 10–20°C, and 15–25°C for *T. maritima* and 10–20°C, 10–30°C, 15–25°C, and 25–35°C for *Atriplex griffithii*, *Suaeda fruticosa*, *H. recurvum*, and *Z. simplex*. A photoperiod of 12 h light : 12 h dark (25 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 400–700 nm) was used at the higher alternating temperature. Four replicates of 25 seeds were used for each temperature and salinity treatment. The seeds were kept in a metal box for 20 days to prevent any exposure to light. Seeds were germinated in distilled water; in 100, 200, 300, 400, and 500 mM NaCl for *Suaeda fruticosa*, *H. recurvum*, and *T. mari-*

tima; and in 0, 25, 50, 75, 100, and 125 mM NaCl for *Z. simplex* at the above-mentioned temperature regimes. The percentage germination was recorded for 20 days. Seeds were considered germinated when the radicle emerged.

Germination data was arcsine transformed before statistical analysis. These data were analyzed using ANOVA with SPSS for windows release 6.1 (SPSS Inc. 1994).

Results

Germination of *Atriplex griffithii* seeds in the nonsaline control varied from 38% in the 5–25°C to 65% in the 25–35°C treatments (Fig. 1). There was no significant difference ($P > 0.05$) between light and dark treatments in all thermoperiods studied. Increase in salinity affected dark germination more adversely than seeds germinated in the light (Fig. 1). Cooler thermoperiods were more inhibitory to germination. A three-way analysis of variance of germination indicated significant main effects of salinity, species, thermoperiod, and their interactions (Table 1).

Haloxylon recurvum seeds did not germinate in the dark at the 10–20°C regime, the only regime in which tempera-

Fig. 2. Percentage (\pm SE) of germination of *Haloxylon recurvum* seeds in various light, salinity, and thermoperiods. (■), 24 h dark; (▨), 12 h dark : 12 h light.

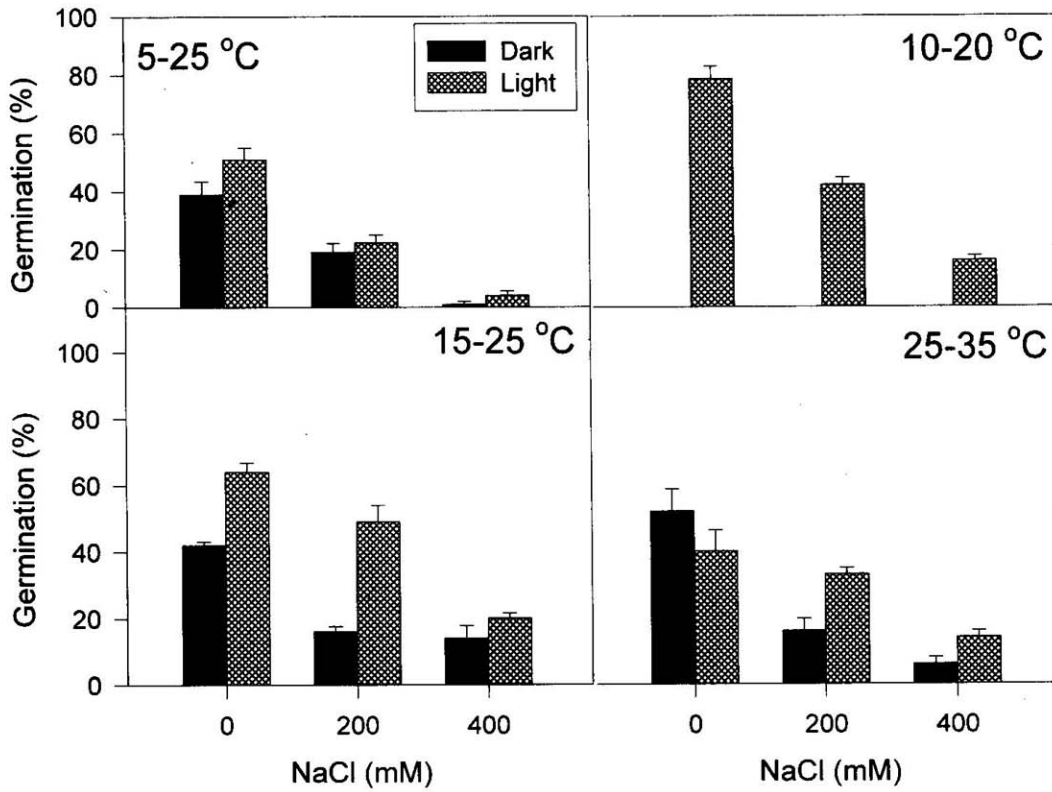
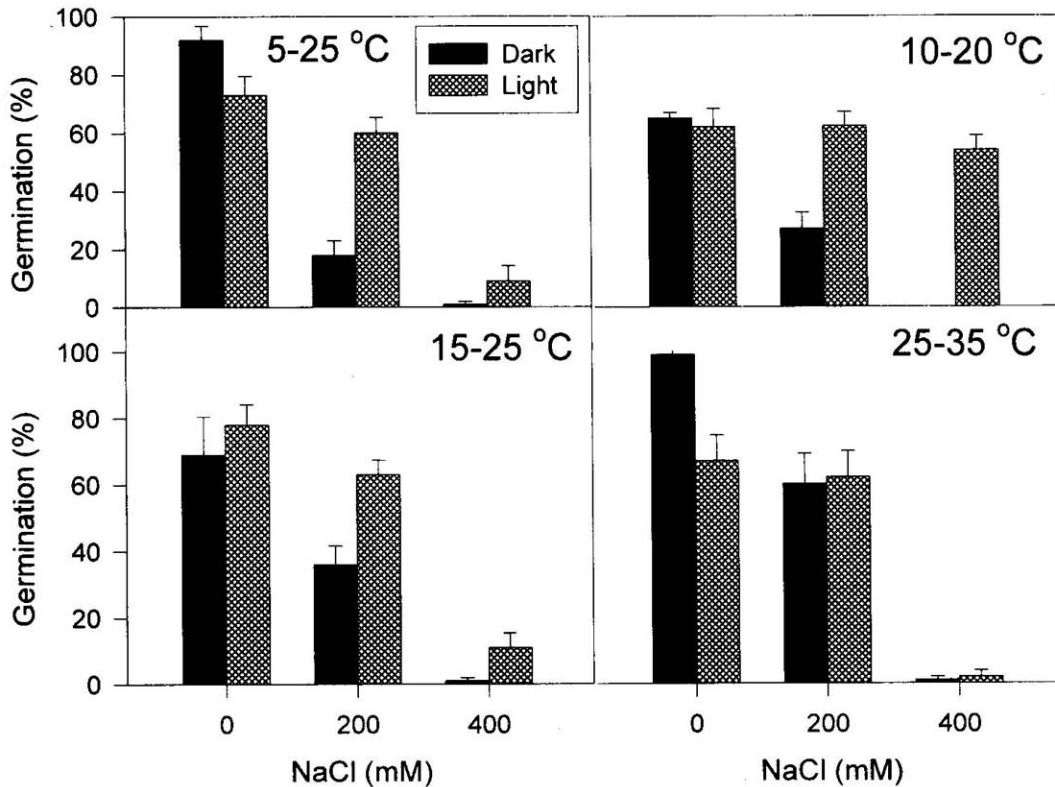


Fig. 3. Percentage (\pm SE) of germination of *Suaeda fruticosa* seeds in various light, salinity, and thermoperiods. (■), 24 h dark; (▨), 12 h dark : 12 h light.



ture was lower than 25°C (Fig. 2). However, about 80% of the seeds germinated in the 12-h light treatment at 10–20°C. In the dark, seeds germinated in the other thermoperiod regimes studied, but the percent germination was usually

lower than for light-germinated seeds. Increases in salinity significantly ($P < 0.0001$) inhibited germination, and this inhibition was greater in dark-germinated seeds.

Germination of *Suaeda fruticosa* reached 100% in the

Fig. 4. Percentage (\pm SE) of germination of *Triglochin maritima* seeds in various light, salinity, and thermoperiods. (■), 24 h dark; (▨), 12 h dark : 12 h light.

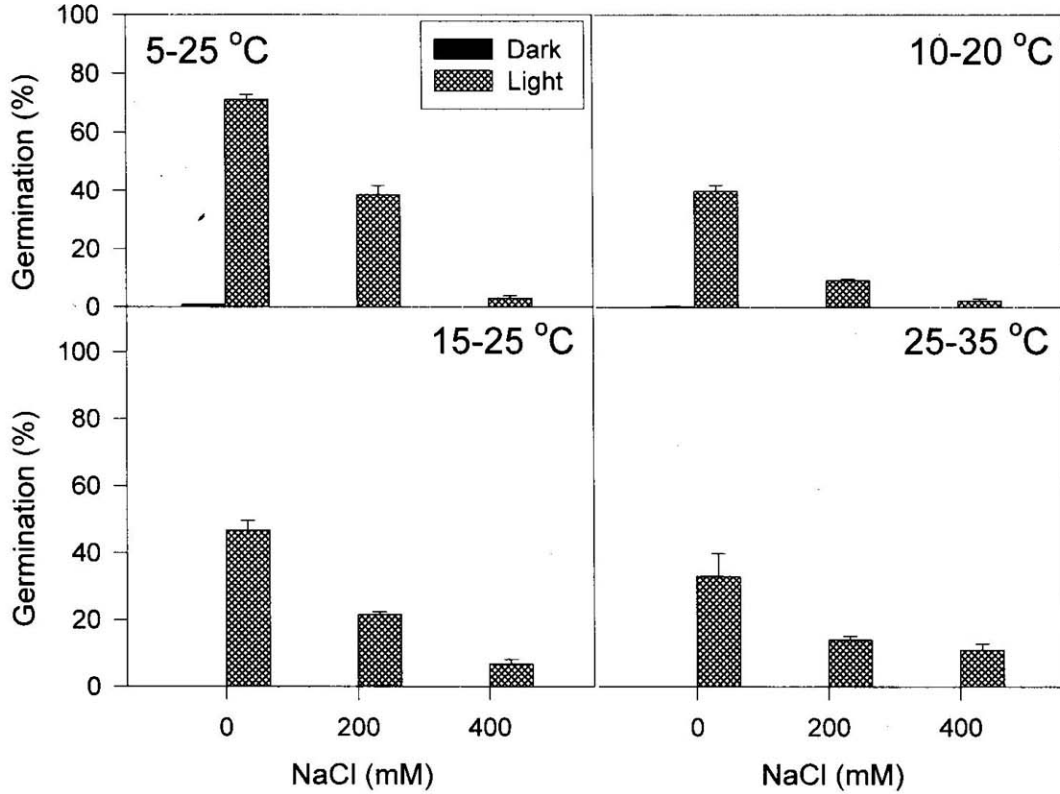
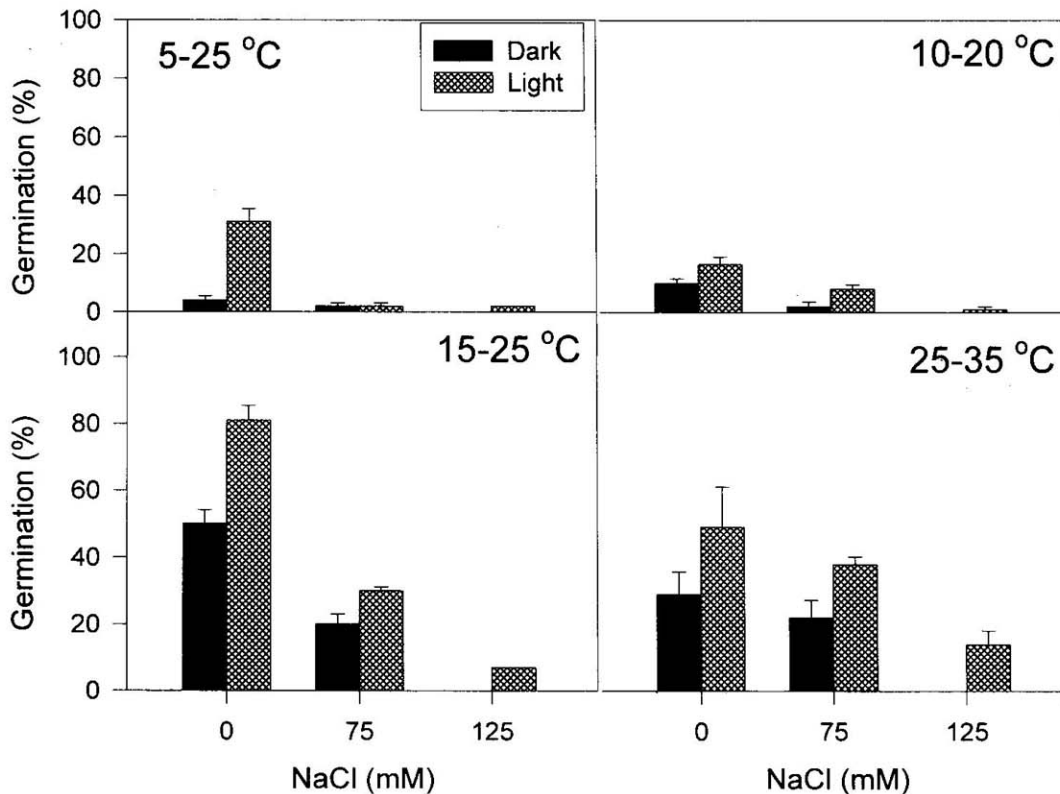


Fig. 5. Percentage (\pm SE) of germination of *Zygophyllum simplex* seeds in various light, salinity, and thermoperiods. (■), 24 h dark; (▨), 12 h dark : 12 h light.



nonsaline dark treatment at 25–35°C (Fig. 3), while only 70% of seeds germinated in 12 h light under similar conditions. In all other regimes there was no significant difference ($P < 0.001$) between light and dark germination in nonsaline controls. Increase in salinity inhibited germination more in

the dark. This inhibition was highest at 5–25°C and lowest at 25–35°C.

No seeds of *T. maritima* germinated in the dark at any salinity or temperatures studied (Fig. 4). However, germination in light varied from 70% at 5–25°C to 37% at 25–

Table 2. Results of four way analysis of variance of characteristics by species, salinity, thermoperiod, and light treatments.

Source of variation	SS	df	F	P
Main effects				
Light (L)	93 019.0	1	2618.1	0.0001
Salinity (S)	53 461.0	2	752.4	0.0001
Species (Sp)	19 767.7	4	139.1	0.0001
Thermoperiod (T)	2 454.3	3	23.0	0.001
Two-way interactions				
L × S	24 338.2	2	342.5	0.0001
L × Sp	6 810.4	4	47.9	0.001
L × T	1 943.2	3	18.2	0.0001
S × Sp	4 169.4	8	14.7	0.001
S × T	1 472.6	6	6.9	0.0001
Sp × T	8 853.3	12	20.8	0.001
Three-way interactions				
L × S × Sp	2 600.3	8	9.1	0.001
L × S × T	992.1	6	4.7	0.0001
L × Sp × T	9 121.8	12	21.4	0.001
S × Sp × T	7 093.2	24	8.3	0.0001
Four-way interaction				
L × S × Sp × T	6 851.6	24	8.0	0.0001

35°C. Increase in salinity significantly ($P < 0.001$) inhibited germination at all temperatures.

Few *Z. simplex* seeds germinated when exposed to the 5–25°C regime, and the highest germination was recorded at 15–25°C (Fig. 5). There was a significant ($P < 0.001$) difference between light and dark germination in controls at 5–25°C. Results of all other treatments showed no significant ($P > 0.05$) difference between light and dark.

A four-way analysis of variance of germination indicated significant main effects of light, salinity, species, thermoperiod, and their interactions (Table 2).

Discussion

The present study revealed a variety of germination syndromes, which would support plant population renewal at different periods when extreme desert conditions were alleviated. This occurs at least once in several years when rainfall coincides with other favorable factors, is well-distributed temporally as well as spatially, and is above average for the area (M.A. Khan, unpublished results). During the summer of 1994, many *Suaeda fruticosa* seedlings appeared after 865 mm rain at Karachi, Pakistan, but no seedlings appeared in 1992 and 1993 when mean precipitation was only 220 mm. The germination responses of three shrubs and a herb from the subtropical maritime region of Karachi, Pakistan, and a perennial herb *T. maritima* collected from the Great Basin Desert (Faust, Utah) are reported in this study.

Triglochin maritima did not germinate in dark at any of the temperature and salinity regimes tested and achieved optimal germination in the light at 5–25°C. Binet (1961) reported that seeds of *T. maritima* and *Triglochin palustre* L. germinated both in light and in dark. Germination in light was higher than in the dark at all of the seawater concentrations studied for both species. A 40-day cold treatment in either distilled water or seawater revealed that a cold pre-

treatment with seawater significantly stimulated the germination in dark. Binet (1961) also obtained germination of seeds at various temperatures (5, 10, 15, 20, 25, and 30°C) in the dark, with a maximum for both species at 25°C. Contrary to this result, Naidoo and Naicker (1992) reported only 10% germination in the dark as compared with 90% in the light for *Triglochin bulbosum* L. and *Triglochin striata* Ruiz and Paron, and dormancy was alleviated when dark-germinated seeds were transferred to light. They reported that a thermoperiod of 30–20°C was optimal for germination, and these species germinated even at 500 mM NaCl. The obligate requirement of light for germination in *T. maritima* collected from Faust, Utah, may be an ecological strategy for survival in a very competitive environment. Most of the young plants are recruited through rhizomes, and they grow very quickly, shading the area where seeds are stored. If seeds germinate early, plants can grow in full sunlight with less competition, but as the growing period progresses the light level decreases and competition intensifies. It is of selective advantage for a seed to germinate early and establish itself because delayed germination will result in high mortality of young seedlings. Absence of light, therefore, prevent seeds from germinating late in the growing season when they are shaded by mature plants.

Zygophyllum simplex, a succulent forb from Karachi, Pakistan, germinated well at the 15–25°C thermoperiod. At low salinity the absence of light reduced the germination percentages, and at high salinity (125 mM), no germination was recorded in dark. Ismail (1990) showed that germination of *Zygophyllum qatarense* Hadid: decreased with an increase in salinity and temperature. Agami (1986) studied the effect of temperature on the germination of *Zygophyllum dumosum* and reported that germination of seeds was independent of temperature in the range of 10–25°C but strongly inhibited at 30 and 35°C. At 20°C, germination was inhibited by salinity of the medium (85 mM) but still occurred even at a concentration of 500 mM NaCl. *Zygophyllum simplex* germinated well at moderate temperatures that are about similar to that which they will experience in natural conditions after monsoon rains, and low salinity facilitated seed germination. Light is abundant even at later stages of this population's life history, but buried seeds will fail to germinate if the area does not receive adequate rainfall.

Haloxylon recurvum, a shrubby perennial from salt deserts of Karachi, Pakistan, has higher seed germination in the light in comparison with the dark. However, at a thermoperiod of 10–20°C with low day temperature, no seeds germinated in the dark, whereas highest germination percentages were obtained in light at the same thermoperiod. Sharma and Sen (1989) reported that *H. recurvum* seeds germinate rapidly within 75–125 min in distilled water, and germination was inhibited with increased salinity. Rajpurohit and Sen (1977) reported that seed germination of *H. recurvum* was substantially inhibited at about 100 mM NaCl. From 5 to 20% of the seeds in our experiment germinated at 400 mM NaCl in the thermoperiods studied.

Germination of *Atriplex griffithii* and *Suaeda fruticosa* seeds were not significantly inhibited by light, but at higher temperatures, more seeds germinated in the dark in the non-saline control. Germination responses to salinity of *Suaeda fruticosa* was unaffected by changes in thermoperiod in the

light treatment at 10–20°C. Seeds in both species germinated in the 400 mM NaCl treatments.

Light is an important factor for seed germination (Baskin and Baskin 1995; Benvenuti 1995; Plummer and Bell 1995) because seeds may undergo transition from primary to secondary dormancy during the burial period, and light is frequently required to trigger germination. There are very few reports concerning the effect of light on the germination of halophyte seeds under various salinity and temperature regimes (De Villiers et al. 1994). Baskin and Baskin (1995) determined that of 41 species of halophytes, light promoted germination in 20 species; darkness, in 10; and 11 species germinated equally well in light or dark. There was a 50% reduction in dark germination of *Salicornia pacifica* var. *utahensis* seeds in comparison with that in the light in nonsaline controls, and increased salinity was more inhibitory in the dark than in the light (Khan and Weber 1986). Khan et al. (1987) reported that seeds of *Chrysothamnus nauseosus* were not affected by light when germinated at various salinity and thermoperiods. Photoinhibition of seed germination is reported for halophytes (*Allium stacticiforme*, *Brassica tournefortii*, *Cakile maritima*, *Matthiola tricuspidata*, and *Othanus maritimus*) inhabiting the sandy coast of the Mediterranean Sea (Thanos et al. 1991, 1994).

Seeds of desert halophytes are usually buried owing to sand accretion and could only germinate when salinity and temperature is reduced after monsoon rains, and light was not a very important factor. However, except for *Suaeda fruticosa* and *Atriplex griffithii*, seeds of the other halophytes germinated better in light than in dark conditions. Change in thermoperiod had an affect on the germination of these halophytes. Temperature, light, and salinity interact in their effect on germination of halophyte seeds. Further investigation is needed to determine how our laboratory results correlate with the germination behavior of these species in salt desert and salt marsh habitats.

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