

Seed germination and dormancy of *Polygonum aviculare* L. as influenced by salinity, temperature, and gibberellic acid

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Summary

Germination of *Polygonum aviculare* L. seeds collected at a saline site near New England, Ohio was studied. Seeds that did not germinate after 20 days were subjected to a 90 day stratification treatment. Optimal germination percentages were obtained (about 100%) for stratified seeds in low and non-saline controls at the 5–15 °C thermoperiod. Increase in both salinity and temperature caused a decrease in both the percentage and rate of seed germination. Recovery of seed germination after twenty days of immersion in salt solution was complete at the low thermoperiod in high salinity treatments and it decreased with an increase in temperature. The salinity induced dormancy of *P. aviculare* seeds was alleviated by GA. Classification of germination recovery types from saline conditions was related to an interaction between salinity and temperature, and the need to study both of these factors simultaneously was confirmed in order to categorize a species response to salt stress.

Introduction

Polygonum aviculare L. was found growing in a brine spill site in southeastern Ohio. It has been previously reported to occur in disturbed areas and in some saline sites in North America (Ungar, 1974; Gleason and Cronquist, 1991; Hobbs, 1992). The primary purpose of this investigation is to determine the salt tolerance of seeds of *P. aviculare* and their ability to recover from exposure to salinity under different thermoperiods.

Woodell (1985) reported that the germination response of halophyte seeds could be placed into three categories based on their salt tolerance and their ability to germinate in freshwater after being exposed to saline conditions: Type 1. Seeds are inhibited by salinity and recovery of seeds was less than in the initial freshwater treatment, Type 2. Seeds are inhibited by salinity but recovery is equal to the initial freshwater treatment, and Type 3. Seeds are highly salt tolerant and all species showed a salt stimulation response in freshwater after a pretreatment in salt water. The effect of thermoperiod on the recovery germination of seeds after a pretreatment under salt stress has not been investigated and may complicate the ability to classify seeds into a particular germination response type. In this study the relative salt tolerance of *Polygonum aviculare* seeds and their ability to recover from immersion in salt solutions under different thermoperiods was investigated. Since *P. aviculare* is only moderately salt tolerant and is found on the

upper border of salt marshes, it is hypothesized to be a Type 1 species. The interaction between salinity and thermoperiod on the germination of seeds is not clearly understood, but it may have significant ecological implications in terms of when seeds germinate under field conditions (Ungar, 1995). Seeds of *P. aviculare* that do not germinate during the normal spring germination period may be inhibited from germinating by higher temperatures during the summer even though salinity levels are reduced by periods of precipitation (Foderaro, 1995).

Both Courtney (1968) and Baskin and Baskin (1990) indicate that low temperatures in the winter reduced dormancy in seeds of *P. aviculare*, but that an increase in temperature during the summer induced dormancy. These data indicate that achenes go through a dormancy cycle and may be capable of producing a persistent seed bank if conditions are not appropriate for germination during the spring. Achenes of *P. aviculare* are also reported to have a highly cutinized pericarp which restricts water uptake and prevents germination (Ransom, 1935; Justice, 1941; Courtney, 1968; Metzger, 1992).

Seed germination in annual halophytes usually occurs when soil salinity levels are low and soil moisture is relatively high (Ungar, 1991). Optimal germination of halophyte seeds is often under freshwater conditions and the germination of most species is inhibited by increasing the salinity concentration (Khan and Ungar, 1984; 1995; 1996a). Thermoperiod is reported to interact with salinity in affecting the germination response of seeds to salinity (Khan and Ungar, 1984; Berger, 1985; Agami, 1986; Ismail, 1990; Khan, 1991; Khan and Rizvi, 1994).

Seeds of halophytes have the ability to maintain their viability during exposure to hypersaline conditions and then to commence germination when salinity stress is reduced (Ungar, 1982; Woodell, 1985; Keiffer and Ungar, 1995; Khan and Ungar, 1995). However, seeds differ in their ability to recover and germinate after being exposed to hypersaline conditions. Variation in recovery germination responses of species after a pretreatment with salinity could be due to differences in the optimal thermoperiod for germination (Khan and Ungar, 1996c). Seeds of *P. aviculare* germinate during the moist and cool spring months when soil salinity levels are usually lowest (less than 0.5% total salts; Foderaro, 1995). Environmental factors such as high temperatures and high salinities may prevent seeds from germinating during the summer months. Seed germination early in the growing season is of survival value to annuals such as *P. aviculare* since surface soil salinities reach their peak during the summer and seedling mortality of later germinating seed cohorts is very high (Khan and Ungar, 1986). If seeds cannot germinate in the spring because of salt stress induced dormancy, they may be able to persist and form a seed bank that can germinate during the spring of the following season when soil salinity levels are reduced by the leaching effect of precipitation. The interaction between thermoperiod and salinity may provide a dual mechanism that is of survival value and assures persistence of populations of annuals in salt marsh habitats.

The role of gibberellic acid (GA) in breaking seed dormancy is well recognized (Bewley and Black, 1985). GA has been found to alleviate dormancy induced by salini-

ty in a number of halophyte seeds (Ungar, 1977; Khan and Ungar, 1985; Kabar, 1987; Khan et al., 1987; Khan, 1991; Khan and Rizvi, 1994). It may be that both salinity and thermoperiod are affecting seeds in a similar manner, causing either a reduction in the GA content in seeds or an increase in inhibitor substances under stressful conditions that inhibit germination, which can be alleviated by exogenous treatments with GA.

Materials and Methods

Seeds of *Polygonum aviculare* L. were collected from approximately 100 plants in a 0.1 hectare area, during August 1995, from a brine spill location in Athens County, Ohio (39°20'N and 81°57'W) situated on Rome Township road near New England, Ohio. Seeds were separated from the inflorescence and were stored at 4 °C. Germination studies were started in December 1995. Seeds were surface sterilized using the fungicide Phygon (2,3 dichloro-1,4-naphthol; U.S. Rubber). 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 emergence of the radicle.

Seeds of *P. aviculare* mature in the summer and are shed onto the soil. Newly produced seeds are dormant (Courtney, 1968). In the field they would be exposed to warm summer temperatures followed by cooling and cold stratification in the winter. To determine the effect of temperature on removal of dormancy and initiation of germination, seeds were first exposed to alternating temperature regimes of 5–15 °C, 5–25 °C, 10–20 °C, and 15–25 °C for 20 days. A 24-hr cycle was used, where the higher temperature (15, 20, and 25 °C coincided with the 12-hr light period (Sylvania cool white fluorescent lamps, 25 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 400–700 nm) and the lower temperature (5, 10, and 15 °C) coincided with the 12-hr dark period. Seeds were germinated in distilled water, 100, 200, 300, 400, and 500 mM NaCl solutions under the above mentioned temperature regimes. A second group of seeds were treated with gibberellic acid (0.3 and 3 mM) at all salinities and thermoperiods to determine if the dormancy or inhibition of germination by salinity and temperature could be alleviated by treatments with this growth regulator. Percent germination was recorded every alternate day for 20 days but no seeds germinated in any of the salinity, thermoperiod, or GA treatment at this stage. All of the petri dishes were then transferred to a 5 °C incubator for 90 days and then returned to their respective thermoperiod treatments for 20 days. Ungerminated seeds from the latter NaCl treatments were transferred to distilled water to study the recovery of germination, which was also recorded at 2 day intervals for 20 days. Rate of germination was estimated by using a modified Timson index of germination velocity = G/t , where G is the sum of percentage seed germination at 2-day intervals and t is the total germination period (Khan and Ungar, 1984). The maximum value possible using this index with our data was 50 (i.e., 1000/20). The higher the value, the more rapid the rate of germination.

Germination data were transformed (arcsine) before statistical analysis. These data

were analyzed using SPSS for windows release 6.1 (SPSS, 1994). To provide some method for determining which of the means are statistically different, all data were analyzed by a one-way ANOVA. A Bonferonni test was used ($P < 0.05$) to determine significant differences between means. A two and three way ANOVA was also used to demonstrate the interaction between various factors in affecting the rate and percentage germination.

Results

Germination Response

Seeds without a cold stratification pretreatment did not germinate in any salinity, thermoperiod, and GA treatment. Seeds required a pretreatment at 5 °C in the dark before germination was initiated. The cumulative germination percentage of *Polygonum aviculare* seeds decreased with an increase in salinity (Fig. 1). Maximum germination was obtained at 5–15 °C in the non-saline control but higher day temperatures inhibited germination. A two-way ANOVA of percentage germination indicated significant ($P < 0.0001$) main effects of salinity and temperature (Table 1). An interaction between salinity and temperature was also significant ($P < 0.002$). A one-way ANOVA of germination for each treatment revealed that salinity significantly affected the rate of germination of seeds at each thermoperiod (5 – °C, $F = 20.3$, $P < 0.0001$; 5–25 °C, $F = 19.3$, $P < 0.0001$; 10–20 °C, $F = 15.3$, $P < 0.0002$; 15–25 °C, $F = 9.2$, $P < 0.0019$).

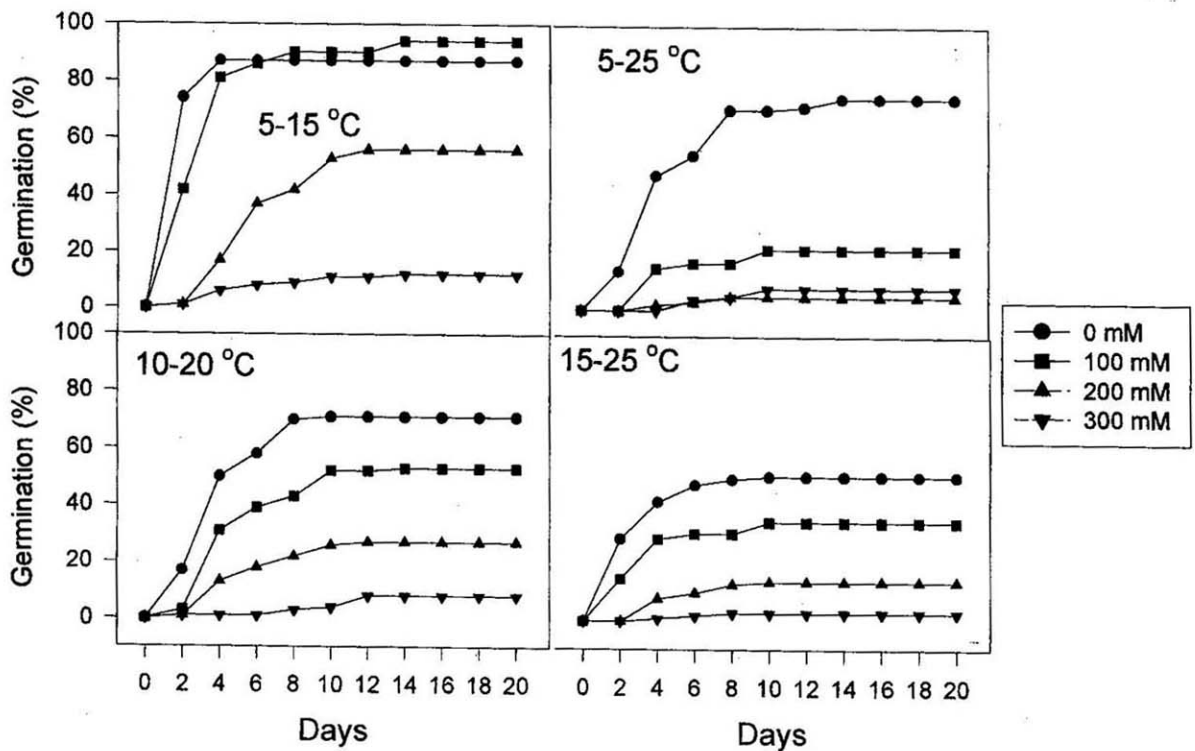


Fig. 1. Rate of germination of *Polygonum aviculare* seeds in 0, 100, 200, and 300 mM NaCl at thermoperiods of 5–15 °C, 10–20 °C, 10–30 °C and 15–25 °C.

Table 1. Results of two way analysis of variance of characteristics by Salinity (S), and Thermoperiod (T), treatments.

Dependent variable	S	T	S x T
Percent germination	55.4***	20.2***	3.5**
Rate of germination	71.3***	25.2***	3.7**
Recovery of germination	39.4***	24.5***	10.2***
Total germination	9.1***	48.1***	2.6*

Note: Numbers represent F values: * = $P < 0.01$; ** = $P < 0.001$; *** = $P < 0.0001$;
n.s. = non significant.

Rate of Germination

Rate of germination under non-saline conditions was highest at the 5–15 °C thermoperiod (Table 2), and decreased with an increase in salinity and temperature. A two-way ANOVA of rate of germination indicated a significant ($P < 0.0001$) main effect of salinity and temperature (Table 1). An interaction between salinity and temperature was also significant ($P < 0.001$). A one-way ANOVA indicated that salinity significantly affected the rate of germination of seeds at each thermoperiod (5–15 °C, $F = 27.6$, $P < 0.0001$; 5–25 °C, $F = 21.2$, $P < 0.0001$; 10–20 °C, $F = 22.2$, $P < 0.00001$; 15–25 °C, $F = 10.3$, $P < 0.0012$).

Recovery Germination in Distilled Water

After 20 days of salinity treatment, seeds were transferred to distilled water to determine the recovery of germination after salt inhibition. At low NaCl concentrations there

Table 2. Effect of GA₃, thermoperiod and salinity on the rate of germination (Timson Index, Max = 50) of *Polygonum aviculare* seeds.

NaCl mM	GA ₃ mM	Thermoperiod			
		5–15 °C	5–25 °C	10–20 °C	15–25 °C
0	None	42.9±4.7	31.6±3.6	31.1±1.20	23.8±3.1
	0.3 mM	46.3±0.9	10.3±3.1	20.8±3.1	12.8±4.9
	3.0 mM	47.7±0.9	41.0±1.6	31.0±5.9	25.5±2.2
100	None	42.8±1.1	9.1±2.9	21.6±3.3	15.8±4.2
	0.3 mM	38.4±3.8	7.9±4.3	21.5±9.4	12.5±3.1
	3.0 mM	42.5±1.1	24.1±9.1	13.4±4.2	17.3±4.3
200	None	21.5±4.5	2.0± 0.8	10.8±3.5	5.8±3.3
	0.3 mM	22.4±5.3	4.1± 2.1	5.7±1.8	3.4±1.8
	3.0 mM	15.8±6.0	19.7±10.1	20.6±7.8	18.9±3.8
300	None	4.7±1.9	2.9±1.0	2.5±1.7	1.2±1.2
	0.3 mM	3.1±2.3	1.2±0.6	1.4±0.9	1.1±0.7
	3.0 mM	24.5±4.3	22.5±7.7	7.2±3.7	10.8±4.8

Table 3. Mean percentage germination (\pm SE: N = 4) in treatments, initial salinity effect (S), germination recovery in distilled water (R), and total germination (T).

NaCl mM	5-15 °C			5-25 °C			10-20 °C			15-25 °C		
	S	R	T	S	R	T	S	R	T	S	R	T
0	87 \pm 10.0 ^a	0 \pm 0 ^a	87 \pm 10.0 ^a	75 \pm 7.9 ^a	2 \pm 2.0 ^a	76 \pm 6.8 ^a	71 \pm 3.0 ^a	8 \pm 8.0 ^a	74 \pm 2.0 ^a	51 \pm 5.2 ^a	0 \pm 0 ^a	51 \pm 5.2 ^a
100	94 \pm 1.6 ^{ab}	0 \pm 0 ^a	94 \pm 2.3 ^a	22 \pm 11.9 ^b	12 \pm 6.1 ^a	33 \pm 7.3 ^a	53 \pm 8.6 ^{ab}	13 \pm 6.5 ^{ab}	59 \pm 8.0 ^a	35 \pm 9.5 ^{ab}	2 \pm 2.0 ^{ab}	36 \pm 10.0 ^{ab}
200	56 \pm 11.7 ^a	83 \pm 4.8 ^b	94 \pm 2.1 ^a	5 \pm 1.9 ^b	25 \pm 5.4 ^a	29 \pm 4.4 ^b	27 \pm 9.2 ^{bc}	16 \pm 8.0 ^{ab}	37 \pm 12.5 ^a	14 \pm 8.1 ^{bc}	0 \pm 0.0 ^a	14 \pm 8.1 ^b
300	12 \pm 4.8 ^c	95 \pm 1.8 ^c	96 \pm 2.8 ^a	8 \pm 2.5 ^b	39 \pm 12.6 ^a	44 \pm 15.5 ^a	9 \pm 5.3 ^c	54 \pm 12.4 ^b	59 \pm 9.0 ^a	3 \pm 3.0 ^c	9 \pm 3.3 ^b	12 \pm 1.6 ^b

Values in each column having the same letter are not significantly different at $P > 0.05$, Bonferroni test.

was no recovery of germination (Table 3). Seeds exposed to high salinity at a lower or moderate thermoperiod had a significant recovery of germination. However at a warmer thermoperiod (15–25 °C) and high salinity recovery was reduced (9%). A two-way ANOVA of percent recovery germination indicated significant ($P < 0.0001$) main effects of salinity and temperature (Table 1). A one-way ANOVA revealed that salinity significantly affected the percent recovery of seed germination at each thermoperiod (5–15 °C, $F = 393.9$, $P < 0.00001$; 5–25 °C, $F = 2.6$, $P < 0.1011$; 10–20 °C, $F = 5.1$, $P < 0.017$; 15–25 °C, $F = 4.6$, $P < 0.0238$).

Total Germination Percentages

Total germination after a 20 day salinity treatment and subsequent transfer to distilled water for another 20 days was determined (Table 3). At the 5–15 °C thermoperiod the inhibitory effect of salinity was completely alleviated. With an increase in temperature (15–25 °C) total germination was reduced and only 12% of the seeds germinated in the high salinity (300 mM) and at the highest thermoperiod. A two-way ANOVA of total germination indicated a significant ($P < 0.0001$) main effect of salinity and temperature (Table 1). One-way ANOVA's revealed that except for 5–15 °C salinity significantly affected the total germination of seeds at each thermoperiod (5–15 °C, $F = 0.5389$, $P < 0.6646$; 5–25 °C, $F = 4.9$, $P < 0.0193$; 10–20 °C, $F = 5.1$, $P < 0.0170$; 15–25 °C, $F = 6.8$, $P < 0.0063$).

Response to Gibberellic Acid

A treatment with GA significantly alleviated salinity stress at all thermoperiods studied (Table 4). However, optimal recovery of germination was found at 300 mM NaCl. The

Table 4. Effect of GA₃, thermoperiod, and salinity on the percentage germination of *Polygonum aviculare* seeds.

NaCl mM	GA ₃ mM	Thermoperiod			
		5–15 °C	5–25 °C	10–20 °C	15–25 °C
0	None	87.0±10.5	75.0± 7.8	71.0± 3.0	51.0± 5.7
	0.3 mM	97.0± 1.9	26.0± 7.5	48.0± 7.8	28.0± 9.9
	3.0 mM	97.0± 1.9	94.0± 1.7	73.0±13.5	58.0± 5.3
100	None	94.0± 1.7	22.0±112.4	53.0± 8.6	35.0± 9.5
	0.3 mM	85.0± 7.7	23.0± 13.1	52.0±12.4	28.0± 7.1
	3.0 mM	92.0± 1.6	55.0± 9.5	36.0±11.2	42.0±10.1
200	None	56.0±13.4	5.0± 1.9	27.0± 9.8	14.0± 8.1
	0.3 mM	58.0±13.6	10.0± 5.3	17.0± 5.9	9.0± 5.0
	3.0 mM	35.0±13.6	51.0± 13.6	43.0±11.3	44.0± 7.1
300	None	12.0± 4.8	8.0± 2.8	8.0± 5.6	3.0± 1.8
	0.3 mM	9.0± 5.7	4.0± 2.3	4.0± 2.8	3.0± 1.4
	3.0 mM	52.0± 9.8	50.0± 17.5	33.0±16.2	23.0±11.2

Table 5. Results of three way analysis of variance of characteristics by Salinity (S), Thermoperiod (T), and Gibberellic acid (G) treatments.

Dependent variable	Independent variable						
	G	S	T	G x S	G x T	S x T	G x S x T
Percent germination	25.1***	65.8***	35.3**	4.9***	4.1**	3.9***	1.11 ^{n.s.}
Rate of germination	30.5**	81.4***	46.6**	6.0***	4.1**	5.4***	1.11 ^{n.s.}

Note: Numbers represent F values: ** = $P < 0.001$; *** = $P < 0.0001$; ^{n.s.} = non significant.

rate of germination of *Polygonum aviculare* seeds also increased with the application of GA (Table 4) and was more substantial at higher salinities. A three-way ANOVA of rate and percentage of germination indicated a significant ($P < 0.0001$) main effect and two-way interactions, but the three-way interactions were not significant ($P > 0.05$; Table 5).

Discussion

Freshly harvested seeds of *Polygonum aviculare* were dormant and required a stratification period before they germinated (Justice, 1941; Hammerton, 1964), but during the autumn and winter seeds became non-dormant (Baskin and Baskin, 1990). Baskin and Baskin (1990) also reported that *P. aviculare* seeds germinated from 95 to 100 % at all thermoperiods. Seeds remained non-dormant during spring, but during summer the seeds germinated from 17 to 53% in light at 30–15 °C and 35–20 °C but from 0 to 10% in all other test conditions (Baskin and Baskin, 1990). A similar seasonal pattern was also reported by Courtney (1968).

Polygonum aviculare populations were found growing at a brine contaminated site in southeastern Ohio where soil specific conductivity varied from 10 to 40 mS/cm (Foderaro, 1995). This corroborates the report of Hobbs (1992) which indicated that this species can grow in saline habitats. Data from these experiments indicate that seeds of *P. aviculare* were initially dormant. They did not germinate in any of the first 20 day thermoperiod treatments, but had optimal germination (100%) after 90 days of cold (5 °C) stratification at a thermoperiod of 5–15 °C. This pattern mimics field conditions, where seeds remain dormant in the summer and fall, are exposed to cold stratification in the winter, and germinate the following spring (Foderaro, 1995). However, even following stratification an increase in temperature inhibited germination in the nonsaline control. These data support the findings of Baskin and Baskin (1990), indicating that high summer temperatures maintain the dormancy of *P. aviculare* seeds. An increase in salinity inhibited germination but some seeds germinated at 300 mM NaCl. *Polygonum aviculare* had a cold stratification requirement and germinated well at lower thermoperiods in low to moderate salinity conditions. Interaction of salinity and temperature is also reported for germination of other halophytes (Badger and Ungar, 1989; Khan, 1991; Khan and Rizvi, 1994; Khan and Ungar, 1996ab).

Seeds of *P. aviculare*, when transferred to distilled water after a 20 day treatment at various salinity concentrations, responded differentially under different thermoperiods. Seeds exposed to higher salinity and more moderate thermoperiods showed a substantial recovery in germination but little recovery was recorded at the highest thermoperiod (15–25 °C). *Polygonum aviculare* would fit into the Type 3 germination category at 5–15 °C but is a Type 1 species at other thermoperiods (Woodell, 1985). The type varied with the germination temperature.

Previous reports classifying seed germination and the recovery of seeds from salt treatments were done at a single thermoperiod (Woodell, 1985; Keiffer and Ungar, 1995). Responses reported for the effects of salinity pretreatment on seed germination may have been at an optimal temperature for some of the species investigated but not for others, which would affect the category a species would be placed into (Type 1–3). Seeds of other inland halophytes have been placed in various categories based on their initial germination and recovery responses; Type 1 – *Atriplex prostrata*, Type 2 – *Salicornia europaea* and *Spergularia marina*, Type 3 – *Suaeda calceoliformis* (Keiffer and Ungar, 1995).

Seeds of salt desert species had varied responses to hypersaline conditions when they were transferred to distilled water. Seeds of *Suaeda fruticosa* recovered quickly from salt immersion at all thermoperiods when they were transferred to distilled water, but only those seeds exposed to salinity at a lower thermoperiod were salt stimulated (Khan and Ungar, 1996a). Thermoperiod beyond the optimal range inhibited the germination of other salt desert species that were exposed to high salinity pretreatments (Khan and Ungar, 1996bc).

Our data indicate that seed germination in *P. aviculare* is significantly affected by an interaction between salinity and thermoperiod. High day temperatures were inhibitory to germination at all salinities. Similar results were obtained in the recovery germination treatments, in which recovery from 300 mM NaCl ranged from 95% at 5/15 °C down to 9% in 15/25 °C. These results indicate that there is a dual mechanism, salinity and thermoperiod, that is inhibitory to germination of *P. aviculare* seeds during the summer months. The combined inhibitory effect of salinity and thermoperiod is of ecological significance because it prevents seeds from germinating and causes high seedling mortality during the summer months when surface soil salinities are extremely high. Environmentally triggered seed dormancy also produces a persistent seed bank that can germinate and establish a new population of *P. aviculare* during the following spring if salinity stress is alleviated. Since an interaction between temperature and salinity determines the recovery germination response of seeds, it will be difficult to classify most species into a particular recovery type category unless the interactions between these factors are investigated.

Effect of salinity on the rate and percentage germination of *P. aviculare* was alleviated by the application of GA and optimal recovery occurred at 300 mM NaCl. Dormancy induced by high salt concentrations was alleviated by GA in other halophytes (Ungar and Binet, 1975; Boucaud and Ungar, 1976; Ungar, 1977, 1984; Khan and Ungar, 1985; Khan and Weber, 1986; Khan, 1991; Khan and Rizvi, 1994).

Polygonum aviculare has an innate dormancy which could be broken by a 90 day cold and wet pretreatment. Seeds are moderately tolerant to salinity (300 mM NaCl) at the germination stage. Salinity induced seed dormancy in *P. aviculare* was alleviated with an application of GA. Highest germination was at a cooler thermoperiod (5–15 °C) and it decreased with an increase in temperature and salinity. Seeds were able to recover from salt stress when they were transferred to distilled water, but germination was severely inhibited by an increase in temperature.

Distribution of *P. aviculare* in moderately saline habitats on the border of salt marshes may be related to their ability to germinate and establish during a particular season of the year. The major limiting factors to seed germination in these saline habitats are hypothesized to be salinity and thermoperiod. Effects of a range of salinities, thermoperiods, and their interactions on the germination of *P. aviculare* seeds was investigated. The influence of pretreatment with salinity on recovery germination in freshwater was determined to be significantly affected by thermoperiod. GA was found to alleviate the salinity and thermoperiod induced dormancy of seeds.

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