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Alleviation of salinity and dark-enforced dormancy in *Allenrolfea occidentalis* seeds under various thermoperiods

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Abstract. The effect of germination-regulating chemicals on the alleviation of salinity-enforced germination inhibition of *Allenrolfea occidentalis* (S.Wats.) Kuntze at various thermoperiods in complete darkness was investigated. There was poor germination at cool temperatures and germination-regulating chemicals were ineffective in alleviating this effect. Germination in the dark increased progressively with increase in temperature and maximum germination was obtained at 25–35°C thermoperiod. Ethephon and fusicoccin (FC) substantially reverted dark-induced inhibition at moderate thermoperiods. All other germination-regulating chemicals were more effective at moderate temperature, while germination was not specifically different from control at higher temperature. Salinity-enforced germination inhibition was partially alleviated by all growth regulators at the higher temperature regime (25–35°C). Best reversal was obtained with the application of ethephon and FC. Our results suggest that temperature is the most critical factor influencing the germination of *Allenrolfea* seeds. *Allenrolfea occidentalis* seeds germinated better at higher than at lower temperatures in the dark and all of the growth-promoting compounds showed their maximum reversal effect at higher temperatures.

Introduction

Germination of halophytes could be regulated by a variety of environmental factors (water, temperature, light and salinity) and may even interact with the seasonal variation in photoperiod and thermoperiod to determine the temporal pattern of germination (Gutterman 1993). Germination of various halophyte seeds occurs at times when there is an optimal combination of day length, temperature and salinity (Ungar 1995). The interactions between salinity, light and temperature on seed germination have been studied in a number of species: *Atriplex dimorphostegia, Fouqieria splendens, Zygophyllum dumosum, Salicornia pacifica* var. *utahensis, T. hulhosa, Triglochin striata, Zygophyllum simplex* and *Allenrolfea occidentalis* (Koller 1957; Freeman 1973; Young *et al*. 1980; Agami 1986; Khan and Weber 1986; Naidoo and Naicker 1992; DeVillier *et al*. 1994; Gutterman *et al*. 1995; Khan and Ungar 1997; Gul and Weber 1999).

Germination-regulating chemicals are known to alleviate the stress caused by light, temperature and salinity (Copeland and McDonald 1995). Salinity effects on halophyte germination could be alleviated by using gibberellic acid (GA₃) and kinetin (Villiers and Wareing 1960; Khan and Ungar 1985; Khan and Weber 1986; Kabar 1987; Khan *et al*. 1987; Ismail 1990; Khan 1991; Khan and Rizvi 1994; Plummer and David 1995; Khan and Ungar 1997; Gul and Weber 1998; Khan *et al*.

1998), ethephon (Kepczynski and Karssen 1985; Kepczynski 1986; Kepczynski and Kepczynska 1997; Gul and Weber 1998), fusicoccin (FC) (Ismail 1990; Khan and Ungar 1997; Gul and Weber 1998), compatible osmotica (proline and betaine) (Khan and Ungar 1997; Khan *et al*. 1998; Gul and Weber, unpubl. data), nitrate and thiourea (Esashi *et al*. 1979; Kabar and Baltepe 1990; Bewley and Black 1994; Egely 1995; Noor and Khan 1995; Gul and Weber 1998; Khan and Ungar 1998). Thiourea, GA₃, cytokinins, ethylene and nitrate can substitute for light and temperature in promoting germination (Koller *et al*. 1962; Rao *et al*. 1975; Vincent and Roberts 1977; Eshashi *et al*. 1979; Khan and Weber 1986; Bewley and Black 1994; Corbineau and Come 1995; Noor and Khan 1995; Sutcliffe and Whitehead 1995).

Allenrolfea occidentalis, a stem-succulent halophytic shrub, is commonly distributed in inland playas of the Great Basin Desert in western North America, where soil salinity during summer reaches up to 1027 mM NaCl (Hansen and Weber 1975). Seeds produced during late autumn are dispersed around the parent plants and remain dormant until the next spring (Gul and Weber 1998). Seeds begin to germinate during late spring when temperatures are moderate and salinity is low due to high moisture from snowmelt from the adjacent mountains. *Allenrolfea occidentalis* seeds germinate better in light and many seeds can germinate in high salinity

(800 mM NaCl) at warm (25–35°C thermoperiod) (Gul and Weber 1998). The effect of high salinity in light could be partially or completely alleviated by the application of germination-regulating (proline, betaine, kinetin, ethephon, FC, nitrate and thiourea) chemicals (Gul and Weber 1998).

The effect of dormancy-relieving chemicals in light has been extensively reported. However, little information exists on the ability of these chemicals to alleviate germination inhibition at various salinity and thermoperiod regimes in the dark. The purpose of this investigation was to determine the role of these chemicals in alleviating dark- high salinity- and temperature-enforced germination inhibition of *A. occidentalis* seeds.

Materials and methods

Seeds of *A. occidentalis* were collected during autumn 1995 from a salt playa located half a mile (*c.* 1 km) east of Goshen, north-western Utah, USA. Seeds were randomly collected in order to get an adequate sampling of the genetic diversity of the population. The flowering spikes and seeds were stripped as the seeds matured and the inflorescence dried. The seeds were air dried and threshed by hand through screens. A small fanning mill was used to separate the seeds from chaff. Seeds were stored in sealed plastic jars at 4°C.

Germination studies were started in the spring of 1996. Seeds were surface sterilised with the fungicide, Phygon (Phygon had no effect on seed germination). Then 25 seeds were placed directly in 50 × 9-mm (Gelman No. 7232) tight-fitting plastic petri dishes and submerged in 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 of each test were prepared. The petri dishes were wrapped in aluminum foil for 20 days to prevent light exposure. Percentage germination was recorded after 20 days. Seeds were considered to have germinated with the emergence of a radicle. The seeds were germinated at six alternating temperature regimes of 5–15, 10–20, 10–30, 15–25, 20–30 and 25–35°C in controlled-temperature chambers for 20 days. Four replicates of 25 seeds were used for each temperature and salinity treatment. GA_3 (0.3 mM), kinetin (0.05 mM), fusicoccin (5 mM), ethephon (10 mM), nitrate (20 mM), thiourea (10 mM), proline and betaine concentrations of 0.1 mM and NaCl (0, 200, 400, 600 and 800 mM) solutions were used to enhance germination in salinity treatments. Preliminary experiments indicated that the concentration used were the optimal concentrations of these chemicals.

Germination data were transformed (arcsine) before statistical analysis in order to ensure homogeneity of variances before analysis. These data were analysed using SPSS, V.7 (SPSS Inc. 1996). A two-way ANOVA was used to determine whether significant differences were present among means. A Bonferonni test was used to determine significant differences ($P < 0.05$).

Results

A three-way ANOVA of *A. occidentalis* seed germination indicated significant ($P < 0.0001$) effects of salinity, dormancy regulating chemicals, temperature and their interactions (Table 1). Variation in one factor caused variation in other factors. Thermoperiod significantly affected the germination of *A. occidentalis* seeds in dark (Fig. 1). Seeds failed to germinate at 5–15°C in the non-saline control and germination was progressively increased with increasing temperatures. Maximum germination percentage (58%) in the non-saline control was obtained at 25–35°C thermoperiod.

Table 1. Results of a three-way analysis of variance of the effect of salinity, regulators and temperature on germination of *Allenrolfea occidentalis*

| Source	d.f.	SS	F	P
Salinity (S)	4	203830	2152	0.0001
Regulator (R)	11	48717	187	0.0001
Temperature (T)	5	47528	401	0.0001
S × R	44	40975	39	0.0001
R × T	55	31237	24	0.0001
S × T	20	52756	111	0.0001
S × T × R	220	35111	7	0.0001
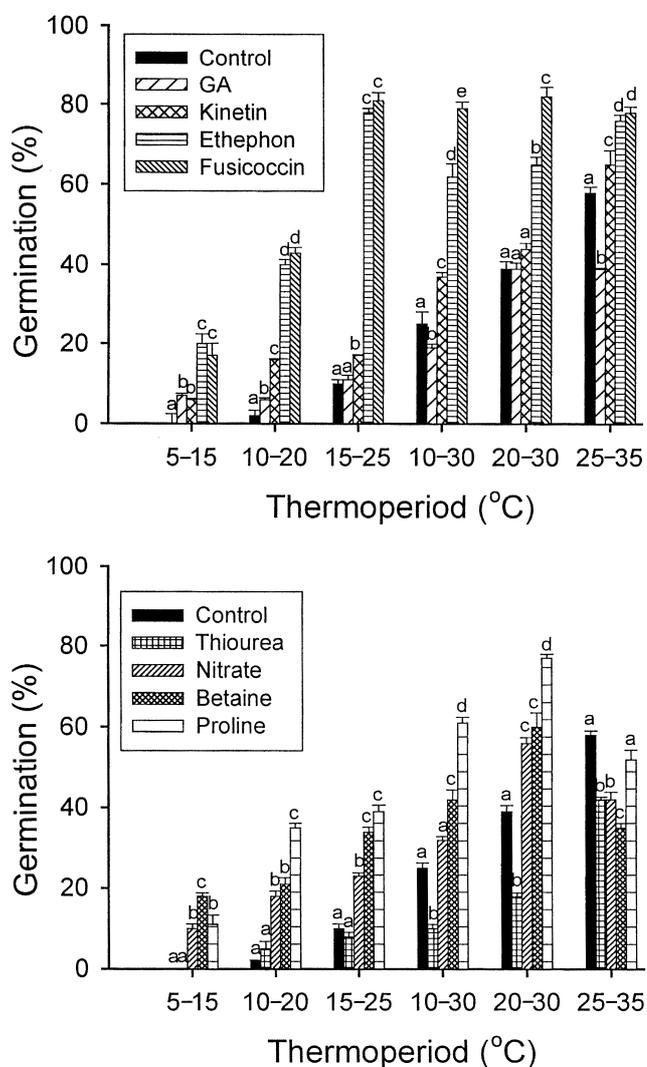
Fig. 1. Final germination percentages (mean ± s.e.) of *Allenrolfea occidentalis* seeds in water (control), betaine, fusicoccin, GA_3, ethephon, kinetin, nitrate, proline and thiourea. Values at each thermoperiod having the same letter are not significantly different ($P > 0.05$) from the control.

Germination-regulating chemicals were least effective below the 15–25°C thermoperiod (Fig. 1) in alleviating dark-induced germination inhibition. They were usually more successful in alleviating dark-enforced inhibition at the highest thermoperiod (25–35°C). Ethephon and FC were the most successful and they increased germination at 15–25°C in non-saline control from 10 to 78% followed by proline. Gibberellic acid, kinetin and thiourea failed to overcome the dark effects (Fig. 1).

Salinity substantially inhibited germination at all thermoperiods in the dark and no seeds germinated above 400 mM. Only 3% of the seeds germinated at optimal temperature (15–25°C) at 400 mM NaCl (Fig. 2). Ethephon partially alleviated the adverse effect of darkness on germination (Fig. 2). Ethephon reversal of dark-induced germination inhibition increased with increases in temperature, germination reaching 78% at the higher thermoperiod. At 15–25°C, the ethephon treatment resulted in up to 78% germination in comparison to 8% in the non-treated control. Ethephon also

alleviated salinity- enforced inhibition in the dark, this effect increasing with increase in temperature. At 5–15°C, no reversal of inhibition occurred above 200 mM NaCl, while ethephon partially alleviated inhibition of germination at 600 mM at higher thermoperiod (Fig. 2). FC had a similar pattern of germination alleviation and was generally more effective than ethephon. At 25–35°C, FC partially alleviated the effect of 800 mM NaCl on germination (Fig. 2).

Proline and betaine were more effective in alleviating dark-enforced dormancy in the 0 and 200-mM NaCl treatments and this reversal effect increased when the day temperature was equal or higher than 30°C (Fig. 3). Few seeds germinated with the proline and betaine treatment at 600 mM NaCl at higher thermoperiod (Fig. 3). Few seeds germinated at thermoperiods where higher temperatures were less than 20°C with the application of GA₃ and kinetin (Fig. 4). At the 25–35°C thermoperiod, both GA₃ and kinetin substantially stimulated the germination at low salinity but showed little effect at high salinity (Fig. 4). Thiourea promoted germination
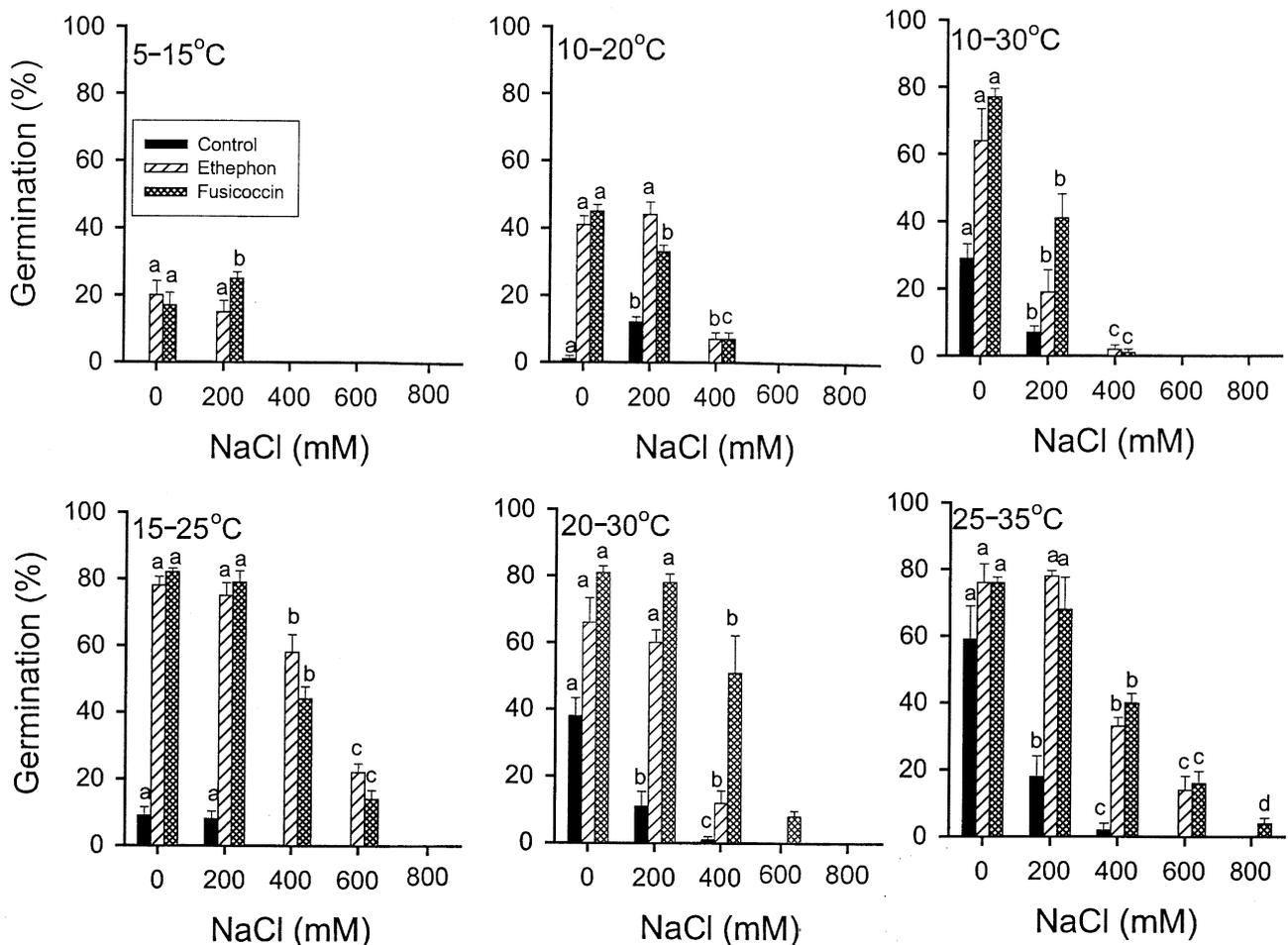
Fig. 2. Final germination percentages (mean ± s.e.) of *Allenrolfea occidentalis* seeds in 0, 200, 400, 600, 800 and 1000 mM NaCl and ethephon and fusicoccin at 5–15, 10–20, 10–30, 15–25, 20–30 and 25–35°C. Values at each thermoperiod having the same letter are not significantly different (*P* > 0.05) from the control (Bonferroni test).
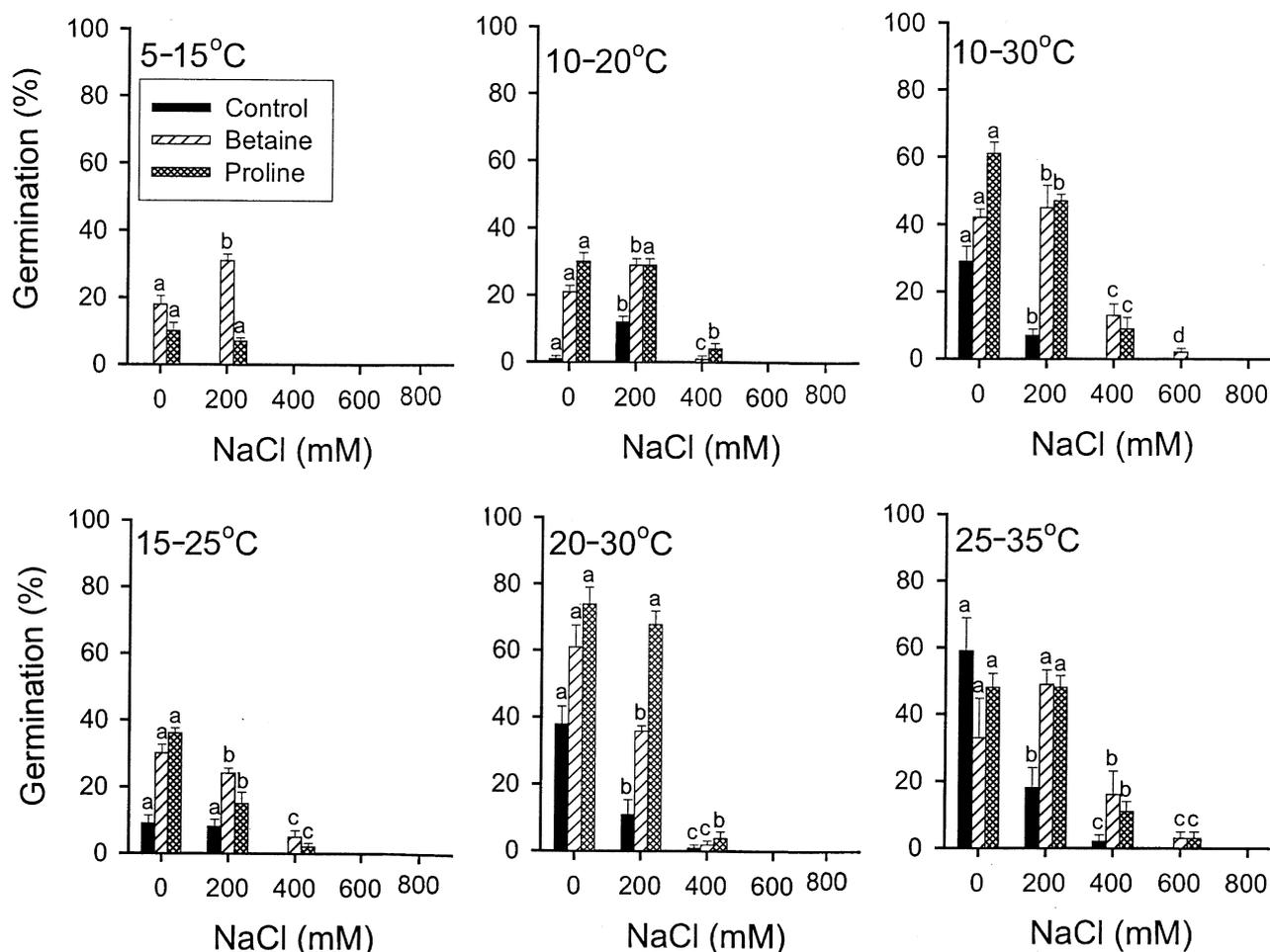
Fig. 3. Final germination percentages (mean ± s.e) of *Allenrolfea occidentalis* seeds in 0, 200, 400, 600, 800 and 1000 mM NaCl and betaine and proline at 5–15, 10–20, 10–30, 15–25, 20–30 and 25–35°C. Values at each thermoperiod having the same letter are not significantly different (*P* > 0.05) from the control (Bonferroni test).

only to a limited extent at low salinity (200 and 400 mM NaCl) at 25–35°C (Fig. 5). Nitrate was more effective in promoting germination at higher thermoperiods (Fig. 5).

Discussion

Light, temperature, water and salinity are the most important factors affecting germination of halophyte seeds under natural conditions. *Allenrolfea occidentalis* seeds showed no sign of dormancy when germinated under a 12-h photoperiod when the day temperature was higher than 30°C (Gul and Weber 1999). Lower day temperatures inhibited the germination under non-saline controls. Seeds that were germinated in total darkness showed lower germination percentages than light-germinated seeds in all salinity and temperature treatments (Gul and Weber 1999). Highest germination in the dark was obtained at 25–35°C in the control and lower salinity treatments. No seed germination occurred at or above 400 mM NaCl. In contrast, at the same temperature light-germinated seeds showed 3% germination at 800 mM NaCl (Gul and Weber 1999). No seeds germinated at 5–15°C.

The present study indicated that varied responses were obtained when various germination-regulating chemicals were applied to alleviate a combined effect of darkness, salinity and temperature. The best seed germination was obtained from growth-regulating compounds when the day temperatures were higher than 30°C. Seed germination was significantly decreased at lower thermoperiods. Betaine, proline, FC and ethephon partially alleviated the dark-induced dormancy in the control and 200-mM NaCl treatment. At higher thermoperiod, all the growth-regulating chemicals alleviated seed germination in the non-saline control and in low-salinity treatments. Ethephon and FC were the most effective. At higher salinity (800 mM NaCl), only FC treatment was able to stimulate seed germination. The FC completely reversed salinity-induced germination inhibition in the light (Gul and Weber 1998).

Compatible osmotica (proline and betaine) have been reported to alleviate innate dormancy in halophytes (Khan and Ungar 1997; Khan *et al.* 1998) and partial alleviation of the effect of salinity was reported in *Zygophyllum simplex*
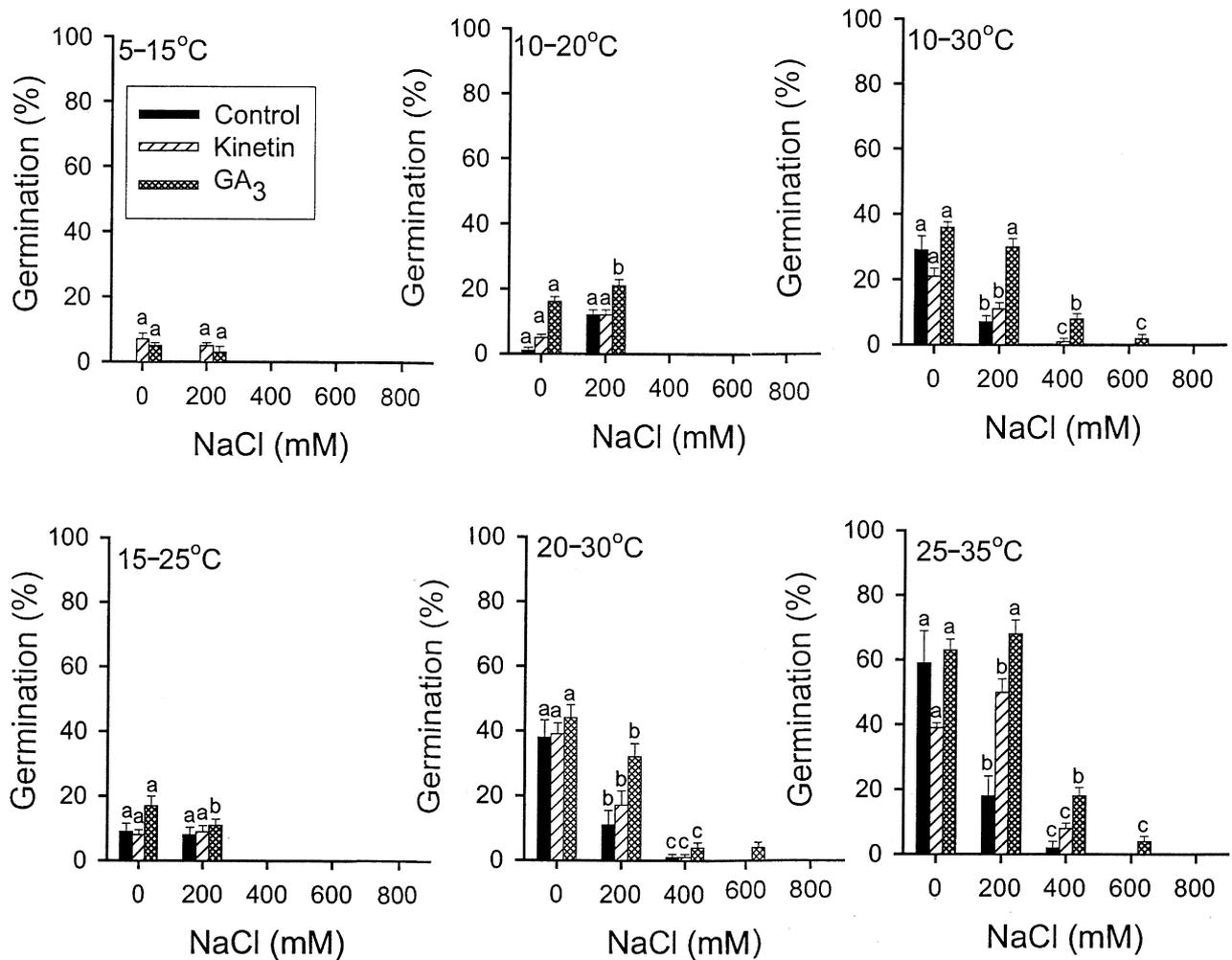
Fig. 4. Final germination percentages (mean ± s.e.) of *Allenrolfea occidentalis* seeds in 0, 200, 400, 600, 800 and 1000 mM NaCl and GA$_3$ and kinetin at 5–15, 10–20, 10–30, 15–25, 20–30 and 25–35°C. Values at each thermoperiod having the same letter are not significantly different ($P > 0.05$) from the control (Bonferroni test).

(Khan and Ungar 1997) and almost complete alleviation reported in *Allenrolfea occidentalis* (Gul and Weber 1998). Little is known about the reversal of dark- and temperature-induced germination inhibition by compatible osmotica. Proline and betaine partially alleviated the dark and low-salinity effect on the germination of *A. occidentalis* seeds at higher thermoperiods (Gul and Weber 1998).

Potassium nitrate is the most widely used chemical for promoting seed germination (Copeland and McDonalds 1995). Most seeds that respond to potassium nitrate are also sensitive to light, with this chemical completely counteracting light inhibition of rice grass seed germination. Potassium nitrate may interact with temperature in influencing seed germination in some species (Toole 1938). Germination inhibition caused by salinity was partially alleviated by nitrate in summer seeds of *Halopyrum mucronatum*, *Sporobolus arabicus* and *Atriplex griffithii* (Khan and Ungar, unpubl. data) and completely alleviated in *A. occidentalis* (Gul and Weber 1998).

Similar results are reported for *A. occidentalis*, where nitrate alleviated low-salinity effects at all the thermoperiods but was more effective at the higher thermoperiods.

Thiourea is able to substitute for the light and temperature requirements of germination, perhaps replacing the light and temperature requirements for the physiological processes that occur naturally during after-ripening (Villiers and Wareing 1960). Thiourea has been reported to replace growth promoters that develop naturally during stratification. Thiourea is also known to alleviate partially and sometimes completely the salinity-induced germination inhibition (Gul and Weber 1998; Khan, unpubl. data; Khan and Ungar unpubl. data). Thiourea, however, failed to alleviate the light effect in *A. occidentalis* seeds at low temperatures and at high salinities. Thiourea showed some promotion at low salinities at 25–35°C.

Kinetin and GA$_3$ can substitute for light and temperature in promoting germination (Copeland and McDonalds 1995;
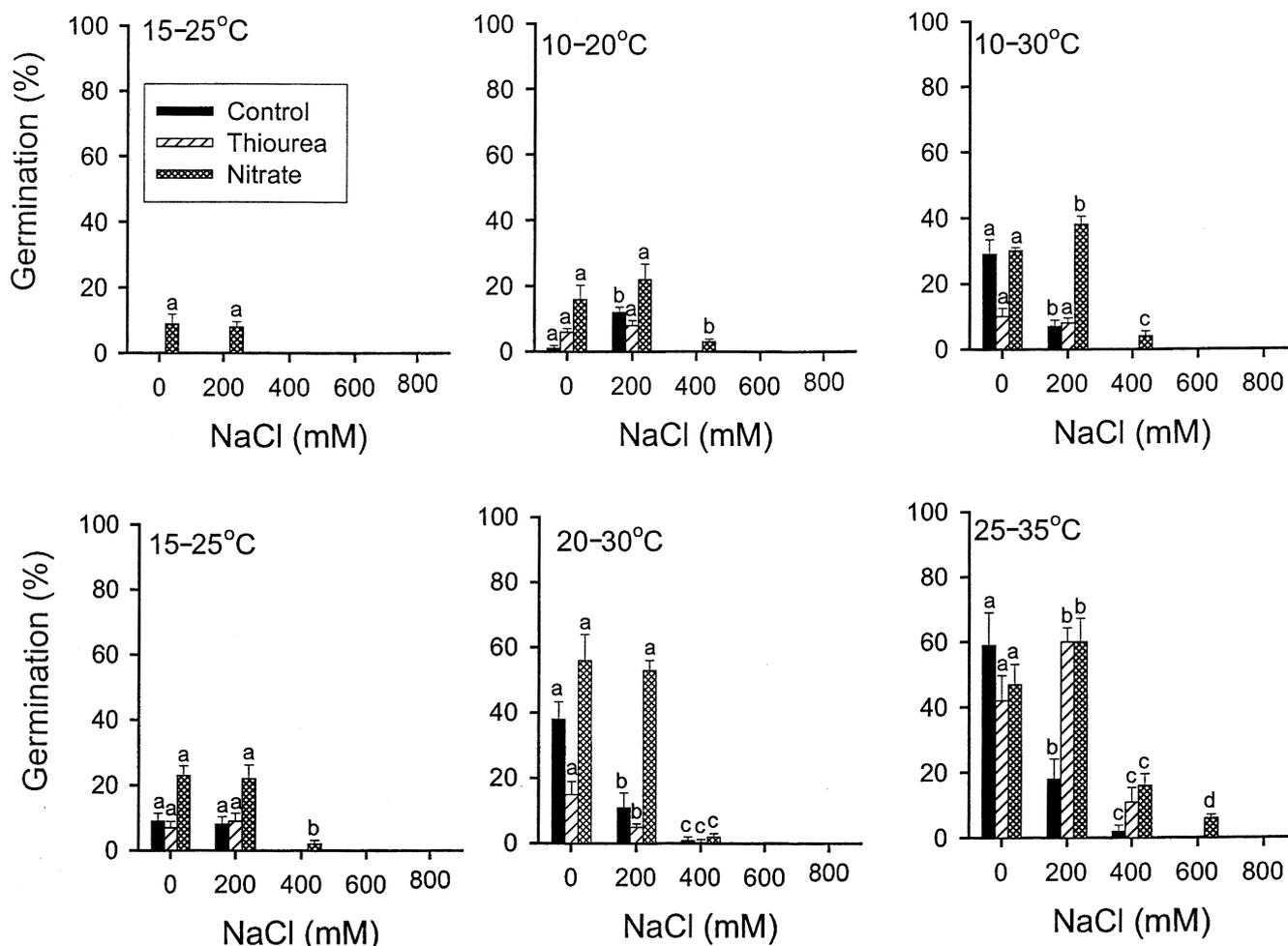
Fig. 5. Final germination percentages (mean ± s.e.) of *Allenrolfea occidentalis* seeds in 0, 200, 0, 600, 800 and 1000 mM NaCl and nitrate and thiourea at 5–15, 10–20, 10–30, 15–25, 20–30 and 25–35°C. Values at each thermoperiod having the same letter are not significantly different ($P > 0.05$) from the control (Bonferroni test).

Plummer and David 1995; Plummer *et al.* 1997). They can also promote germination of seeds not having these requirements. Gibberellins are believed to be important in controlling the germination of seeds in nature (Koller *et al.* 1962). Seed dormancy enforced by high salt concentrations could be alleviated by the application of GA_3 and kinetin (Khan and Ungar 1985; Khan and Weber 1986; Khan *et al.* 1987; Khan *et al.* 1998; Kabar and Baltepe 1990; Khan 1991; Khan and Rizvi 1994; Khan and Ungar 1997). Both growth regulators failed to compensate for light and temperature in *A. occidentalis* but kinetin and GA_3 partially alleviated the effect of low salt (200–400 mM NaCl) on seed germination in dark.

Ethylene is known to stimulate germination of dormant and non-dormant seeds both in the presence and absence of light (Suzuki and Taylerson 1981; Sutcliffe and Whitehead 1995). Ethylene increased seed germination in those species that were stimulated by far-red light (Taylorson 1979) but in those species that responded to both light and ethylene, the response was additive. Germination inhibition caused by salinity in halophytes was partially alleviated by ethephon in *Zygophyllum simplex*, *Sporobolus arabicus* and *Atriplex griffithii* (Khan and Ungar 1998) and completely alleviated in *A. occidentalis* (Gul and Weber 1998). Ethephon partially alleviated darkness, temperature and salinity effects on the seed germination of *A. occidentalis*.

FC was the most successful in alleviation of the salinity- and temperature-enforced germination inhibition in the dark. FC is reported to alleviate innate dormancy in *Zygophyllum qatarensis* (Ismail 1990), partially alleviated the salinity effect on germination of *Sporobolus arabicus* (Khan and Ungar 1998) and *Atriplex griffithii* (Khan and Ungar 1998) or completely alleviated the salinity effect on *Zygophyllum simplex* (Khan and Ungar, unpubl. data) and *Allenrolfea occidentalis* (Gul and Weber 1998). It appears that seed germination of *Allenrolfea occidentalis* is primarily regulated by endogenous growth regulators. An imbalance caused

by the absence of light, low temperature and high salinity can cause this imbalance, which at least can be partially alleviated by germination-regulating chemicals.

Dormancy-regulating chemicals were least effective at lower thermoperiods in alleviating germination inhibited by either the dark or salinity. At higher thermoperiod, however, they were more effective in alleviating both. Ethephon and FC were more effective in alleviating both dark and salinity effects on the germination of *A. occidentalis*. It appears from our study that temperature is a more important factor for the germination of the seeds buried under soil. No buried seed would germinate earlier in the growing season but they would germinate when temperature gets warmer during late spring and early summer. Growth-regulating chemicals failed to compensate for the effect of low temperature but most of them could partially or completely overcome the light effects. Seeding recruited in the early part of spring could be devastated or destroyed by the occasional severe frost. Fresh seedlings could be recruited through these buried seeds later in the season to maintain the continuity of the species. This information should be useful in the restoration of saline areas.

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