Annals of Botany **87**: 233–239, 2001
doi:10.1006/anbo.2000.1321, available online at http://www.idealibrary.com on IDEAL®

Effect of Bracteoles on Seed Germination and Dispersal of Two Species of *Atriplex*

IRWIN A. UNGAR*† and M. AJMAL KHAN‡

†*Department of Environmental Plant Biology, Ohio University, Athens, Ohio 45701-2979, USA and*
‡*Department of Botany, University of Karachi, Karachi, Pakistan 75270*

Received: 28 June 2000 Returned for revision: 7 September 2000 Accepted: 13 October 2000

The influence of bracteoles on the germination response of a salt marsh annual, *Atriplex prostrata*, and a salt desert perennial, *A. griffithii*, was determined. Attached bracteoles did not inhibit germination of *A. prostrata* but completely inhibited germination of *A. griffithii* seeds. Germination of seeds of *A. griffithii* was also somewhat inhibited in the presence of detached bracteoles. The osmotic potential of dissolved substances in water-saturated bracteoles was $-4{\cdot}8 \pm 0{\cdot}05$ MPa for *A. griffithii* and $-2{\cdot}4 \pm 0{\cdot}15$ MPa for *A. prostrata*. Ash content of bracteoles on a dry weight basis was $28{\cdot}7 \pm 0{\cdot}37$ % for *A. prostrata* and $30{\cdot}0 \pm 0{\cdot}29$ % for *A. griffithii*. The presence of relatively high concentrations of dissolved salts in bracteoles may explain the reduced germination of *A. griffithii*. Germination of seeds of the perennial *A. griffithii* may also be inhibited mechanically by the presence of persistent bracteoles, whereas the annual *A. prostrata* has ephemeral bracteoles that may serve to limit germination in the autumn but are not present during the normal spring germination period. Bracteoles could affect the dispersal of seeds by water since some fruiting structures of *A. griffithii* and *A. prostrata* are able to float in 1·0 % NaCl solutions for 5 and >30 d, respectively, compared with a maximum of 4 and 3 d for seeds without bracteoles. Fruiting structures of *A. prostrata* floated for longer over a range of salinities than did those of *A. griffithii*; this may play a significant role in the dispersal of this salt marsh species.

Key words: *Atriplex*, bracteoles, dispersal, flotation, germination, salinity, temperature.

INTRODUCTION

Bracteoles on fruiting structures in *Atriplex* species may serve to control the timing of seed germination and also aid the wind or water dispersal of seeds (Osmond *et al.*, 1980). Inhibition of seed germination of *Atriplex* spp. by bracteoles has been reported in the literature (Beadle, 1952; Kadman-Zahavi, 1953; Osman and Ghassali, 1997). Inhibition of germination could occur through a number of different pathways: induction of a light requirement for germination, mechanical inhibition, osmotic stress, specific ion effects, negative effects of growth regulator substances, and the production of allelopathic compounds (Beadle, 1952; Koller, 1957; Cresswell and Grime, 1981; Giusti and Grau, 1983; Aiazzi and Arguëllo, 1992). Bracteoles of *Atriplex inflata* Muell. contained as much as 31 % NaCl on a dry weight basis or 0·9 M NaCl in saturated bracteoles (Beadle, 1952). Beadle (1952) concluded that the high ionic content of bracteoles inhibited germination and therefore protected seeds from unsuccessful establishment during periods when they were exposed to drought stress.

Sankary and Barbour (1972) reported that bracteoles probably did not contain inhibitors, and their presence was not responsible for a reduction in seed germination in *Atriplex polycarpa* S. Wats. In contrast, Osman and Ghassali (1997) determined that removal of the fruiting bracteoles of *Atriplex halimus* L. increased germination from 35 to 98 %, but no significant inhibition of germination was found when soluble bracteole leachates were tested. Giusti and Grau (1983) reported that bracteoles produced a water-soluble substance that inhibited germination of *A. cordobensis* Gandoger and Stuckert seeds. Fruiting structures of *Atripex repanda* Phil. accumulated 10 % saponins and these substances could cause a significant reduction in germination percentages of both *A. repanda* and *A. semibaccata* R. Br. seeds (Fernandez *et al.*, 1985, 1986). Another possibility reported by Beadle (1952) is that ion accumulation in bracteoles can retard seed germination, since soaking bracteoles for 24 h and removing excess salts increased germination in *A. spongiosa* Muell. from 6 % in unsoaked to 100 % in soaked and leached fruiting structures. Soaking of bracteoles and leaching did not increase germination of *Atriplex patula* var. *hastata* L. seeds, but this treatment did stimulate germination in two other species: *A. lentiformis* (Torn.) S. Wats. and *A. semibaccata* (Young *et al.*, 1980). Binet (1965) and Aiazzi and Arguëllo (1992) concluded that the chief inhibitory action of bracteoles in *A. tornabeni* Gandoger and Stucker and *A. cordobensis* was mechanical. In contrast, Springfield (1970) determined that the bracteoles of *Atriplex canescens* (Pursh.) Nutt. did not inhibit germination.

In this investigation we compare the effects of bracteoles on germination of two species: *Atriplex prostrata* Boucher, an annual salt marsh species, and *Atriplex griffithii* Moq. var. stocksii Boiss, a perennial salt desert species. It is possible that differences in germination response in the presence of bracteoles of *Atriplex* spp. is related to the habit

* For correspondence. Fax 00 1 740 593 1130, e-mail ungar@ohio.edu

0305-7364/01/020233+07 $35.00/00

and longevity of the species. Bracteoles are not usually present during the spring germination period of salt marsh *Atriplex* species, having decayed in the period between seed dispersal in the autumn and seed germination the following spring. We hypothesize that salt marsh species may be less affected by bracteoles, which are often ephemeral and not fused in these species, than are salt desert species that tend to have more persistent, fused bracteoles that may inhibit germination by some mechanical, allelopathic, or osmotic mechanism. The significance of bracteoles in the dispersal of seeds will be considered in flotation experiments. Because of its broad distribution in coastal marshes of North America and Europe, we hypothesize that seeds of the salt marsh species *A. prostrata* will have a longer flotation period than those of the salt desert species *A. griffithii*.

MATERIALS AND METHODS

Seeds (utricles) of *Atriplex griffithii* were collected during autumn 1994 from salt flats situated on the University of Karachi campus, Karachi, Pakistan. *Atriplex prostrata* seeds were collected in autumn 1998 at the Rittman salt marsh, Rittman, Ohio, USA. Germination tests were carried out in 50 × 9 mm (Gelman No. 7232) tight-fitting Petri dishes with 5 ml of test solution, and each dish was placed in a 10 cm diameter plastic Petri dish as an added precaution to avoid water loss from dishes by evaporation. Four replicates of 25 seeds each were used for each of the treatments and we considered seeds to have germinated after radicle emergence.

Germination

Seeds of *A. griffithii* and *A. prostrata* were germinated for 30 d in incubators with a 12 h photoperiod (Sylvania cool white fluorescent lamps, 25 μmol m^{-2} s^{-1}, 400–700 nm) and 12 h thermoperiods (dark : light) of 5 : 15, 5 : 25 and 15 : 25°C. The three seed treatments were a control with seeds and attached bracteoles, seeds in the presence of detached bracteoles, and seeds with bracteoles removed.

To determine whether bracteoles of *A. griffithii* limit germination, seeds with attached bracteoles were germinated for 20 d at 15 : 25°C (dark : light) before bracteoles were removed and seeds were left for another 20 d. To test the possibility that leachable soluble inhibitors present in bracteoles of *A. griffithii* prevent seeds from germinating, seeds with attached bracteoles were soaked in 100 ml of distilled water for 1, 24 and 48 h. Germination was then monitored for a 30 d period. The aqueous extracts were diluted from full strength 1·5 g bracteoles per 100 ml distilled water to 0·50, 0·25 and 0·125 strength, and seeds were germinated in these solutions.

Flotation

The floating capacity of seeds and dispersal units (seeds + bracteoles) of *A. griffithii* and *A. prostrata* was determined by using five replicates containing five seeds of each species. Five seeds or dispersal units were placed in individual beakers containing 100 ml 1·0 % NaCl solution to mimic inland salt marsh water and shaken on a platform shaker for 20 d to determine how many seeds or dispersal units remained afloat. Another flotation test was run using the above procedure to determine the effect of salt treatment (1·5, 3·0, 6·0 and 12·0 % NaCl) on the flotation of fruiting structures, because salinities higher than that of seawater may occur in salt marshes and salt deserts.

Bracteole water and salt status

The ash content of bracteoles was determined by placing dried bracteoles in a crucible and heating them in a muffle furnace for 24 h at 450°C. Aqueous extracts were made by placing the bracteoles in boiling water (100°C) for 1 h. Aqueous extracts were cooled at room temperature, filtered and centrifuged, and an estimate of the osmotic potential of soluble substances in the extracts was determined with a Wescor model 5520 vapour pressure osmometer, which measures the osmolarity of solutions.

Statistical analysis

A two-way analysis of variance (ANOVA) was used to determine if significant differences occurred among treatment means in the bract, soaking, and water leachate experiments. One-way ANOVA was used to identify significant differences among treatment means for the bracteole water, ash, and salt status data. If significant differences occurred among treatments, a Bonferroni *post hoc* test was used to determine if there were significant differences between individual treatments (Sokal and Rohlf, 1995).

RESULTS

Germination

A two-way ANOVA indicated that both the presence of bracteoles ($F = 14{\cdot}18$, $P < 0{\cdot}001$) and temperature treatment ($F = 212{\cdot}78$, $P < 0{\cdot}001$) significantly affected germination; there was a significant interaction ($F = 20{\cdot}2$, $P < 0{\cdot}001$) because of reduced germination in the bracteole treatment at low temperature. Seeds of *Atriplex prostrata* were not inhibited by the presence of bracteoles in the 5 : 25°C and 15 :25 °C treatments, and over 90 % of seeds germinated in all three bracteole treatments (i.e. bracteoles attached, bracteoles present, bracteoles absent) (Fig. 1B). At the suboptimal temperature 5 : 15°C, germination was generally lower and inhibited by the presence of bracteoles.

There was no significant effect ($F = 1{\cdot}28$, $P = 0{\cdot}29$) of soaking time on the germination of *A. prostrata* seeds. Soaking seeds with attached bracteoles for 1, 24 and 48 h completely alleviated the inhibitory effect of bracteoles on germination of *A. prostrata* seeds at the low temperature regime ($F = 0{\cdot}68$, $P = 0{\cdot}51$) and there was no significant interaction between temperature and soaking time ($F = 0{\cdot}44$, $P = 0{\cdot}78$) (Fig. 1A).

Germination of *A. griffithii* seeds with attached bracteoles was not significantly affected ($F = 1{\cdot}61$, $P = 0{\cdot}219$) by soaking for 1, 24, or 48 h, or by temperature ($F = 0{\cdot}68$, $P = 0{\cdot}51$) and there was no significant interaction between

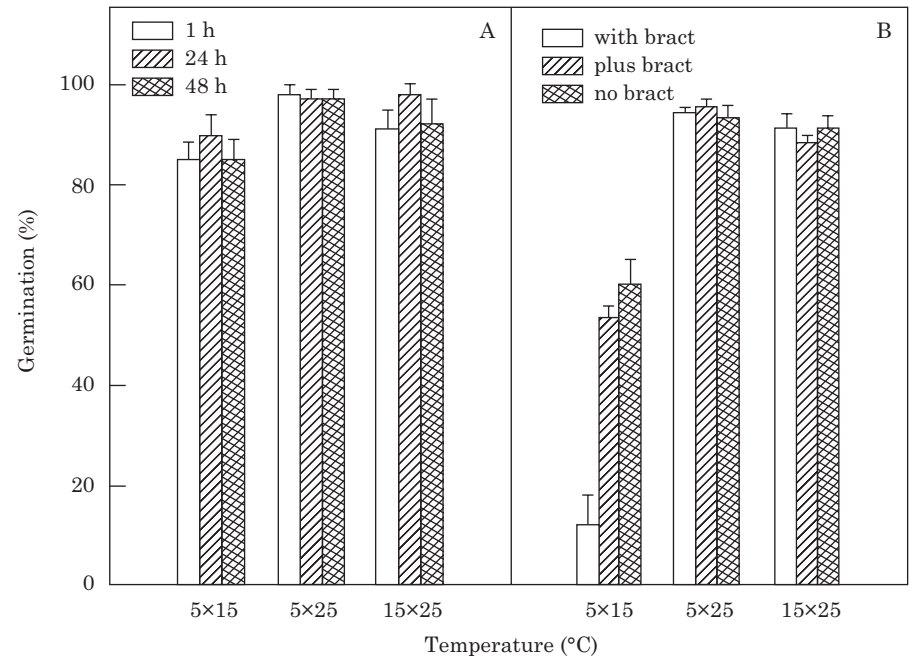

FIG. 1. A, The effect of soaking the fruiting structures for different time periods on the subsequent germination of *Atriplex prostrata* seeds at three temperature regimes. B, The influence of temperature and the presence or absence of bracteoles on the germination of *Atriplex prostrata* seeds. With bract, bracteoles attached to seeds; plus bract, bracteoles removed from seeds but placed in the Petri dish with seeds; no bract, bracteoles removed from seeds.

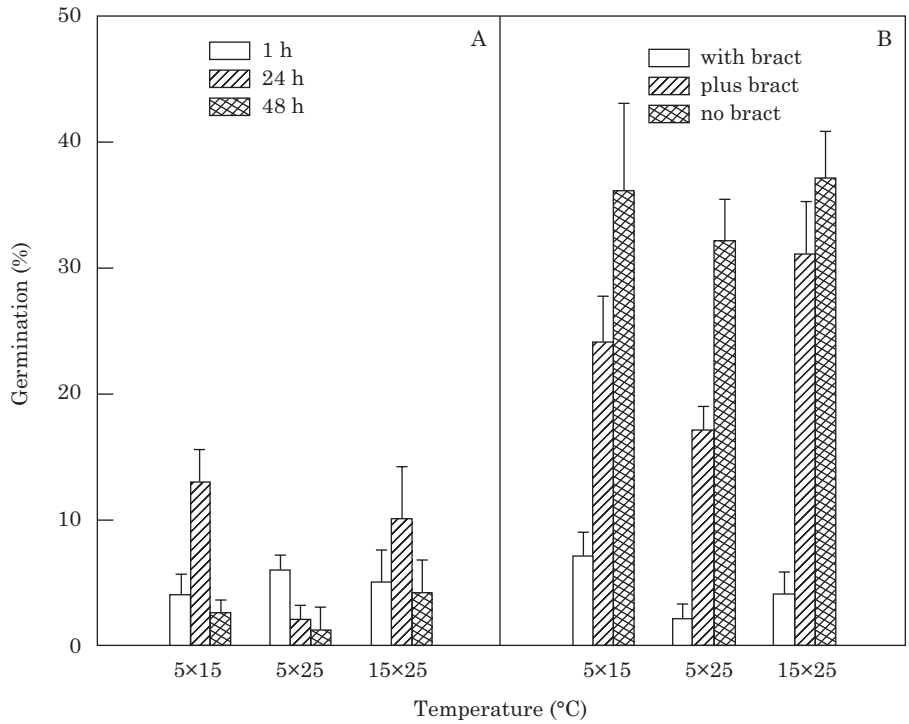

FIG. 2. A, The effect of soaking the fruiting structures for different time periods on the subsequent germination of *Atriplex griffithii* seeds. B, The influence of temperature and the presence or absence of bracteoles on the germination of *Atriplex griffithii* seeds.

temperature and soaking time ($F = 0{\cdot}44$, $P = 0{\cdot}78$) (Fig. 2A). Full strength aqueous extracts were inhibitory to seed germination at the three temperature regimes, averaging 7 % germination compared to 32 % germination in the quarter-strength treatment at 15 × 25°C (Fig. 3). A two-way ANOVA indicated a significant ($F = 15{\cdot}38$, $P < 0{\cdot}001$) effect of extract strength, but the effect of temperature ($F = 0{\cdot}61$, $P = 0{\cdot}55$) and the interaction

between extract strength and temperature were not significant ($F = 1{\cdot}17$, $P = 0{\cdot}34$).

Two-way ANOVA showed that both the presence of bracteoles ($F = 105{\cdot}80$, $P < 0{\cdot}001$) and temperature treatment ($F = 6{\cdot}92$, $P = 0{\cdot}004$) significantly affected germination of *A. griffithii* seeds, but there was no significant interaction between these factors ($F = 2{\cdot}02$, $P = 0{\cdot}12$). Germination was strongly inhibited in all temperature regimes when bracteoles were attached (Fig. 2B). Temperature did not significantly affect germination of *A. grifithii* seeds in treatments when bracteoles were removed.

After a 20 d germination period at 15 × 25°C, only $3{\cdot}0 \pm 1{\cdot}9$ % of the *A. griffithii* seeds with attached bracteoles had germinated. Removal of the bracteoles released the seeds from dormancy and after 1 d $19{\cdot}5 \pm 5{\cdot}1$ % of the seeds had germinated; at the end of the 20 d germination period this percentage had increased to $76{\cdot}0 \pm 9{\cdot}1$ % (Fig. 4), which was significantly different ($F = 125{\cdot}875$, $P = < 0{\cdot}001$) to the percentage germination in the 20 d pretreatment with bracteoles.

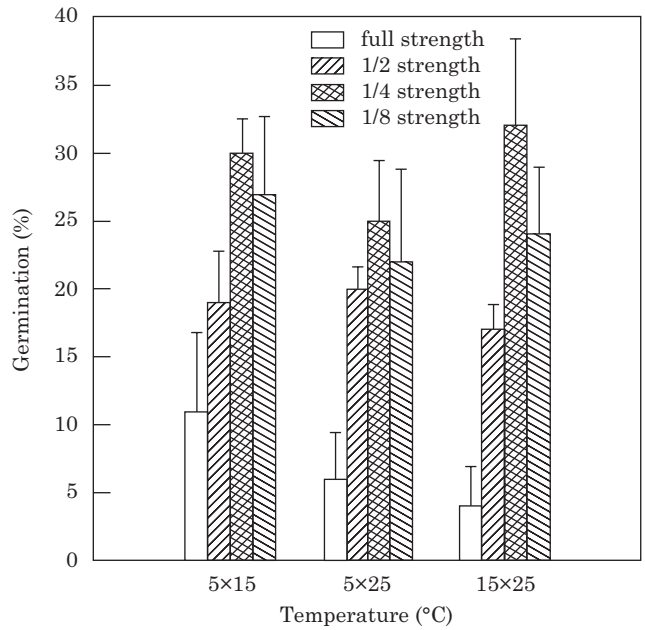

FIG. 3. The influence of full strength or diluted bracteole extracts on the germination of *Atriplex griffithii* seeds at three temperature regimes.

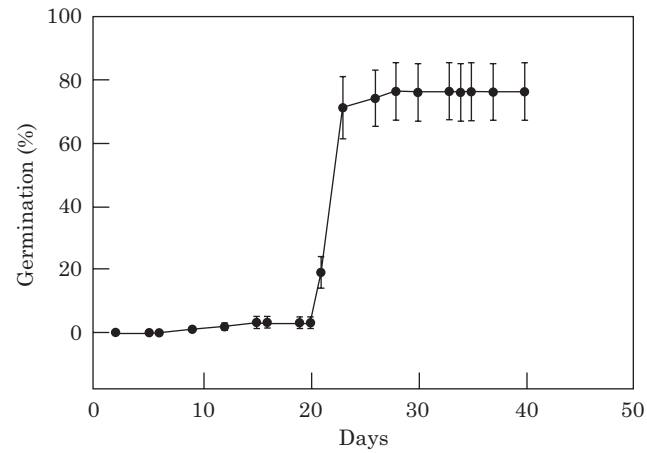

FIG. 4. The effect of bracteole removal after a 20 d germination period on the subsequent germination of *Atriplex griffithii* seeds.

Flotation

Seeds of both species with bracteoles removed floated for less than 5 d in 1·0 % NaCl, whereas fruiting structures of *A. griffithii* ($76{\cdot}5 \pm 15$ %) and *A. prostrata* (92 ± 5 %) remained afloat for 5 d. After 10 d, 0·0 % of *A. griffithii* and 24 ± 7 % of *A. prostrata* fruiting structures were still floating in 1·0 % NaCl. Fruiting structures of *A. prostrata* remained afloat for longer than did those of *A. griffithii* at higher salinities. This was especially apparent in the 3·0 % NaCl treatment in which 35 % of *A. prostrata* and 0 % of *A. griffithii* fruiting structures remained afloat after 30 d (Table 1). Fewer fruiting structures remained afloat at lower salinities than at higher salinities (Table 1). All of the *A. prostrata* and 50 % of *A. griffithii* fruiting structures were still floating after 30 d in the 10 % NaCl treatment in comparison to 25 and 0 %, respectively, in the 1·5 % NaCl treatment (Table 1).

Bracteole water and salt status

Mean dry weights of bracteoles were significantly different for *A. griffithii* ($3{\cdot}08 \pm 0{\cdot}05$ mg) and *A. prostrata* ($0{\cdot}68 \pm 0{\cdot}05$ mg) ($F = 1326{\cdot}7$, $P = < 0{\cdot}001$) (Table 2). The percentage water content of saturated bracteoles was 70 % for *Atriplex griffithii* and 80 % for *Atriplex prostrata*. Ash content of bracteoles was significantly different for *A. griffithii* ($30{\cdot}0 \pm 0{\cdot}58$ %) and *A. prostrata* ($28{\cdot}7 \pm 0{\cdot}37$ %) ($F = 7{\cdot}31$, $P = 0{\cdot}035$). The osmotic potential of dissolved substances in water-saturated bracteoles was $-4{\cdot}8 \pm 0{\cdot}05$ MPa for *A. griffithii* and $-2{\cdot}4 \pm 0{\cdot}15$ MPa for *A. prostrata*; these values were significantly different ($F = 16{\cdot}37$, $P = 0{\cdot}007$) (Table 2).

DISCUSSION

The two *Atriplex* spp., *A. prostrata* (a salt marsh species with ephemeral bracteoles) and *A. griffithii* (a salt desert species with persistent bracteoles), showed different germination responses when their bracteoles were attached to seeds. Germination of *Atriplex prostrata* seeds was not inhibited by the presence of attached or detached bracteoles at higher temperatures but showed some bracteole × temperature inhibitory interaction at the lowest temperature regime. It has been suggested that bracteoles inhibit germination via a number of different pathways, which include mechanical inhibition of germination, allelopathy, osmotic effects, specific ion effects, and change in the red : far-red ratio of incident radiation (Koller, 1957; Young *et al.*, 1980; Cresswell and Grime, 1981; Giusti and Grau, 1983; Aiazzi and Arguëllo, 1992).

Intact fruits of *A. griffithii* are dormant, and their bracteoles inhibited germination in this investigation: less

TABLE 1. *Percentage (±s.e.) of fruiting structures of* Atriplex griffithii *(Ag) and* A. prostrata *(Ap) that remained afloat in a range of saline solutions over a 30 d period*

	NaCl (%)							
	1·5		3·0		6·0		12·0	
Days	Ap	Ag	Ap	Ag	Ap	Ag	Ap	Ag
5	95 ± 5	100	100	100	100	100	100	100
10	80 ± 15	25 ± 12	65 ± 9	65 ± 17	65 ± 5	95 ± 5	100	100
15	35 ± 20	15 ± 5	40 ± 14	20 ± 14	40 ± 8	50 ± 10	100	90 ± 10
20	25 ± 5	5 ± 5	40 ± 14	0	40 ± 8	35 ± 5	100	90 ± 10
25	25 ± 5	0	40 ± 14	0	40 ± 8	10 ± 5	100	75 ± 9
30	25 ± 5	0	35 ± 12	0	40 ± 8	5 ± 5	100	50 ± 5

TABLE 2. *Mean dry weight, ash content, saturated water content and osmolarity of extracted sap in bracteoles of* Atriplex griffithii *and* A. prostrata

	Atriplex griffithii	*Atriplex prostrata*
Dry weight (mg)	3·08 ± 0·05	0·68 ± 0·05*
Ash content (%)	30·0 ± 0·58	28·7 ± 0·37*
Water content (%)	68·4 ± 0·94	79·9 ± 0·88*
Osmotic potential (MPa)	−4·8 ± 0·05	−2·4 ± 0·15*

Data are means ± s.e. * $P < 0{\cdot}05$.

than 3·0 % seeds with attached bracteoles germinated after 20 d but up to 76 % germinated when the bracteoles were removed from fruiting structures. Neither Sankary and Barbour (1972) nor Springfield (1970) found the presence of bracteoles inhibitory to the germination of seeds in *A. polycarpa* and *A. canescens* respectively. Other investigators have reported that bracteoles can inhibit the germination of seeds of *Atriplex* spp. (Giusti and Grau, 1983; Osman and Ghassali, 1997). Kadman-Zahavi (1953) reported that bracteoles or extracts from bracteoles inhibited germination of *A. rosea* L. He showed that bracteoles contained a substance that inhibited germination and that could be absorbed by charcoal, but NaCl concentrations equivalent to bracteole extracts did not inhibit germination. Full strength leachates from *A. griffithii* inhibited germination of seeds when bracteoles were removed, whereas the more dilute leachate solutions were not inhibitory. Leaching of bracteoles of *A. nummularia* Lindl. increased germination from 34 % in unleached to 52 % in leached fruiting structures, while bractless seeds showed 62 % germination (Uchiyama, 1981). Uchiyama (1987) determined that bracteoles contained 11·2 % NaCl and hypothesized that germination probably occurs after salts are leached by rainwater. However, leaching of bracteoles of *A. griffithii* alone did not stimulate seed germination; this may be because the seeds are mechanically inhibited from germinating by fused bracteoles. The presence of soluble salts or an organic inhibitor in the bracteoles of *A. griffithii* may explain, in part, the dormant nature of its fruiting structure, since the leaching of bracteoles, followed by their removal, stimulated germination greatly.

Seeds of *A. dimorphostegia* Kar. et Kir. in intact dispersal units did not germinate (Koller, 1957). The ash content of these bracteoles was 27·6 % of their air dry weight. Osmotic potentials of extracts from bracteoles of *A. dimorphostegia* averaged −0·6 MPa, which was sufficiently high to inhibit germination. Koller (1957) concluded that salts or inhibitory substances would be leached by precipitation, allowing seeds to germinate and providing sufficient moisture for plant growth. Soluble salt content of bracteoles of *A. cordobensis* was not considered sufficiently high to inhibit germination, and Giusti and Grau (1983) reported that an organic inhibitor, probably ABA, was present in the bracteoles. However, Aiazzi and Arguëllo (1992) reported that soaking fruiting structures in water did not promote seed germination, that bracteoles of *A. cordobensis* formed a mechanical barrier to water uptake, and that they required scarification to enhance germination. A similar mechanical effect was shown by Binet (1965) for *A. tornabeni* Tin. He concluded that only in less humid environments would an osmotic effect be significant, since salts in the bracteoles (12·7 % on a dry weight basis) would be leached out in high rainfall habitats. Ash content of bracteoles of *A. griffithii* was 30·0 % and that of *A. prostrata* was 28·7 %, which was in the same range found for the salt desert species *A. dimorphostegia* (27·6 %) (Koller, 1957). The osmotic potential of saturated bracteole extracts was higher in *A. prostrata* (−2·4 MPa) than in *A griffithii* (−4·8 MPa) because the former species imbibed a greater amount of water when their bracteoles were saturated with water.

Beadle (1952) found that three *Atriplex* spp. (*vesicaria* Heward, *inflata* Muell., and *spongiosa*) showed 95–100 % germination when bracteoles were removed, but only 6–38 % when bracteoles were attached. He showed that bracteoles contained high concentrations of NaCl but that soaking dispersal units for 24 h removed the inhibitory effect of bracteoles on germination. It has been suggested that the bracteoles maintain dormancy in seeds until conditions are favourable for germination (Beadle, 1952). Bracteoles may serve to maintain a bet-hedging strategy in some *Atriplex* spp. such as *A prostrata* and *A. griffithii*, determining the season and controlling the timing of germination. If all of the seeds germinated simultaneously in the unpredictable salt marsh or salt desert environments,

populations could go locally extinct whenever flooding occurred or salt stress increased during the period of seedling development (Ungar, 1987; Egan and Ungar, 1999).

Results for *A. prostrata* indicate that the presence of bracteoles may inhibit germination of seeds under the lower temperatures in late autumn and winter but they would not be inhibitory under warmer temperature regimes. Since *A. prostrata* is a summer annual and its seedlings are not frost tolerant, the presence of bracteoles in the autumn may serve to maintain dormancy in seeds before they are exposed to the freezing temperatures of winter. We have not observed bracteoles on seeds during the spring germination period, indicating that they probably begin decaying sometime between October–December (Ungar and Khan, unpubl. obs.). Binet (1965) also reported that the bracteoles of *A. tornabeni* were not present on seeds during the spring germination period in French coastal salt marshes.

Cresswell and Grime (1981) suggested that the presence of green bracteoles around seeds in *A. hastata* or photosynthetic fruiting structures in other species can alter the red : far-red ratio perceived by seeds and may be significant in inducing a light requirement for germination. In a seed burial experiment, Khan and Ungar (1986) showed that small black seeds of *A. prostrata* are more dormant in the soil than are the larger brown seeds. Since both seed types are produced with attached bracteoles, the influence of bracteoles may be differential, or exposure to cold stratification in the winter may have replaced the light requirement more readily in the large seed morph than in the small seed morph of *A. prostrata*. Baskin and Baskin (1998) reported that stratification can sometimes replace the light requirement in dormant seeds of some plant species.

Bracteoles may play a significant role in the dispersal of *Atriplex* seeds. Osmond *et al.* (1980) indicated that, in arid shrubland, *Atriplex* spp. bracteoles could possibly aid wind dispersal. Bracteoles may also be significant in determining the distribution of species through the flotation properties of dispersal units of salt marsh populations of *Atriplex* spp. (Gustafsson, 1973), especially if narrowly-limited species have short flotation times and widely-distributed species such as *A. glabriuscula* and *A. triangularis* have long flotation times. Gustafsson (1973) showed that flotation times of *Atriplex* species varied from up to 24 d for 71 % of the dispersal units in *A. glabriuscula* Edmonston to 0 % in 10 d for the more narrowly-distributed *A. calotheca* (Rafn.) Rafn. and Fries. However, he concluded that even though there was a correlation between the breadth of distribution and flotation time of dispersal units, this factor alone could not explain the cosmopolitan distribution of *A. triangularis* Willd. He suggested that human factors could have played a significant role in the widespread distribution of this species**.** *Atriplex griffithii* dispersal units are relatively heavy (5·6 mg) compared to those of *A. prostrata* (3·0 mg) and remained floating in 1 % NaCl for only 5 d compared to >30 d for the latter species. The fruiting structures of *A. griffithii* may play a more significant role in determining the timing of germination than in the dispersal of diaspores. Thirty-five percent of the fruiting structures of *A. prostrata* remained floating in 3 % NaCl after 30 d compared to 0 % for fruiting structures of *A. griffithii*, and their capacity to float for an extended period of time could play a significant role in the dispersal of diaspores in water as was suggested by Gustafsson (1973). Seeds of both species with their bracteoles removed remained floating for a shorter period of time in 1·0 % NaCl than did seeds enclosed in bracteoles (4 and 3 d for seeds and 5 and >30 d for fruiting structures of *A. griffithii* and *A. prostrata*, respectively).

Beadle (1952) indicated that bracteoles of salt desert species in Australia had high salt content, which could osmotically inhibit the germination of seeds contained in the bracteoles because of the low water potentials produced. This would inhibit germination until sufficient precipitation occurred to leach the soluble salts from bracteoles. Bracteoles of both *A. griffithii* and *A. prostrata* may play a significant role in determining the timing of seed germination. Only under low temperature conditions were bracteole-enclosed seeds of *A. prostrata* inhibited from germinating, and leaching of fruiting structures completely alleviated the effect of bracteoles. The inhibition of germination by the persistent bracteoles of *A. griffithii* is related to a combination of morphological and physiological factors. A soaking pretreatment of the dormant *A. griffithii* fruiting structures could have removed an osmotic or allelopathic inhibitor substance, which then permitted seeds to germinate when bracteoles were removed.

ACKNOWLEDGEMENTS

We thank the National Science Foundation for support of this project under NSF Research Grant INT-9730882. We sincerely thank Carolyn Reilly and Lorena Brown for the technical assistance they provided on this project with the support of an Ohio University PACE grant.

LITERATURE CITED

Aiazzi MT, Arguëllo JA. 1992. Dormancy and germination studies on dispersal units of *Atriplex cordobensis* (Gandoger and Stucker) (Chenopodiaceae). *Seed Science and Technology* **20**: 401–407.

Baskin CC, Baskin JM. 1998. *Seeds: ecology, biogeography and evolution of dormancy and germination*. San Diego: Academic Press.

Beadle NCW. 1952. Studies in halophytes I. The germination of the seed and establishment of the seedlings of five species of *Atriplex* in Australia. *Ecology* **33**: 49–62.

Binet P. 1965. Etude de quelques aspects physiologiques de la germination chez *Atriplex tornabeni* Tin. *Bulletin de la Société de Botanique du Nord de la France* **18**: 40–55.

Cresswell EG, Grime JP. 1981. Induction of a light requirement during seed development and its ecological consequences. *Nature* **291**: 583–585.

Egan TP, Ungar IA. 1999. The effects of temperature and seasonal change on the germination of two salt marsh species, *Atriplex prostrata* and *Salicornia europaea*, along a salinity gradient. *International Journal of Plant Sciences* **160**: 861–867.

Fernández G, Johnston M, Olivares A. 1985. Rol del pericarpio de *Atriplex repanda* en la germinación. III. Efecto histólogico y qimíco del pericarpio. *Phyton* **46**: 165–171.

Fernández G, Olivares A, Johnston M, Contreras P. 1986. Rol del pericarpio de *Atriplex repanda* en la germinación. IV. Efecto del NaCl y saponinas en la germinación de cuatro especies. *Phyton* **46**: 19–26.

Giusti L, Grau A. 1983. Inhibidores de la germinacion en *Atriplex cordobensis* Gand et Stucker (Chenopodiaceae). *Lilloa* **36**: 143–149.

Gustafsson M. 1973. Evolutionary trends in the *Atriplex triangularis* group of Scandinavia. I. Hybrid sterility and chromosomal differentiation. *Botaniska Notiser* **126**: 345–392.

Kadman-Zahavi A. 1953. Notes on the germination of *Atriplex rosea*. *Palestine Journal of Botany* **6**: 145–148.

Khan MA, Ungar IA. 1986. Life history and population dynamics of *Atriplex triangularis*. *Vegetatio* **66**: 17–25.

Koller D. 1957. Germination regulating mechanisms in some desert seeds. IV. *Atriplex dimorphostegia* Kar et Kir. *Ecology* **38**: 1–13.

Osman AE, Ghassali F. 1997. Effects of storage conditions and presence of fruiting bracts on the germination of *Atriplex halimus* and *Salsola vermiculata*. *Experimental Agriculture* **33**: 149–155.

Osmond CB, Björkman O, Anderson DJ. 1980. *Physiological processes in plant ecology*. Berlin: Springer-Verlag.

Sankary MN, Barbour MG. 1972. Autecology of *Atriplex polycarpa* from California. *Ecology* **53**: 1155–1162.

Springfield HW. 1970. Germination and establishment of fourwing saltbush in the southwest *USDA Forest Service Paper* RM-55: 1–48, Fort Collins.

Sokal RR, Rohlf FJ. 1995. *Biometry*. New York: W. H. Freeman and Company.

Uchiyama Y. 1981. Studies on the germination of saltbushes. 1. The relationship between temperature and germination of *Atriplex nummularia* Lindl. *Japanese Journal of Tropical Agriculture* **25**: 62–67.

Uchiyama Y. 1987. Salt tolerance of *Atriplex nummularia*. *Technical Bulletin of the Tropical Agriculture Research Center* **22**: 1–69.

Ungar IA. 1987. Population ecology of halophyte seeds. *Botanical Review* **53**: 301–334.

Young JA, Kay BL, George A, Evans RA. 1980. Germination of three species of *Atriplex*. *Agronomy Journal* **72**: 705–709.