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The effects of light quality, nitrate concentration and presence of bracteoles on germination of different fruit types in the heterocarpous *Atriplex sagittata*

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Summary

1 We investigated the effect of light quality, nitrogen supply, fruit size and age on germination of the three types of fruit produced by *Atriplex sagittata*.

2 Regardless of fruit type, seed germination was significantly reduced in the dark. Light quality had no significant effect on germination of seeds from fruit types A and B, both of which are dormant, but seeds from fruit type C, which are non-dormant, germinated better in green light (low photon flux and red : far-red ratio, simulating conditions in the canopy) than in white light.

3 Optimum nitrate concentration differed between seed types but, for all, germination was reduced at the highest concentration used.

4 The effects of cold stratification and its interaction with light and nitrogen effects were also studied. Strong interactions between stratification and light were found in all seed types but other interactions were less frequent.

5 Three size classes of type C fruit showed similar final germination percentages but large seeds germinated more slowly.

6 The effect of seed age was highly significant: over a 3 year period, the germinability of dormant seeds (types A + B) increased while that of non-dormant seeds (type C) fell.

7 The salt concentration in bracteoles of freshly ripened fruits was too low to mediate an inhibitory effect on germination. Moreover, the first autumn rain would be sufficient to remove all the salt from bracteoles.

8 Differences between fruit types in depth of dormancy, and in response to the quality of light and to nitrate concentration in the soil, allows *A. sagittata* to respond to the spatial and temporal variation in environmental conditions encountered by this annual of disturbed habitats.

Key-words: *Atriplex sagittata*, bracteoles, germination, heterocarpy, Chenopodiaceae, nitrate, red : far-red ratio, fruit size

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Introduction

Production of two or more morphologically and ecologically distinct types of diaspores by an individual plant is common in such families as Asteraceae, Chenopodiaceae and Poaceae (Harper 1977; Mandák 1997) and is typical for habitats where the environment is highly variable in either time (Stebbins 1974; Harper 1977) or space, e.g. deserts and salt marshes (Ellner & Schmida 1984; Ungar 1987).

Seed heteromorphism may be a bet-hedging strategy (Venable 1985b), or allow escape from the negative effects of density (Levin *et al.* 1984; Ellner 1985) or sib competition (Lloyd 1984; Schoen & Lloyd 1984; Cheplick 1992; Venable & Brown 1993). If there are several types of seed, at least some are likely to survive whatever the conditions. *Amphicarpum purshii* for instance, partitions limited resources mainly into a few large seeds, allocating any above a threshold value into as many small seeds as possible (Cheplick & Quinn 1982, 1983). Variable progeny may also allow seeds to be spread out in space (i.e. dispersive vs. non-dispersive) or time (dormant vs. non-dormant) (Venable *et al.* 1995) or in such a fashion that they tend to interact less with relatives (Venable & Brown 1993; Venable *et al.* 1995).

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Germination of *Atriplex* spp. (Chenopodiaceae) is sensitive to many factors but the response to light gives particularly ambiguous results (e.g. Beadle 1952; but see Koller 1972). Gap-detection may be important for the regeneration of many plants from seeds (Grubb 1977) and leaf canopy-induced dormancy is very frequently found in species of temperate deciduous woodlands (Stoutjesdijk 1972). Canopy-filtered light (characterized by low photon flux and/or low red : far-red ratio) may also stimulate germination (although not to the same extent as unfiltered light), as seen in the ruderal species *Amaranthus retroflexus* and *Potentilla norvegica* (Taylorson & Borthwick 1969). *Atriplex sagittata* occurs in later stages of succession on ruderal sites and its germination may be affected by canopy-filtered light (Mandák & Pyšek 1998).

Most *Atriplex* species occur in nitrate-rich habitats (Ellenberg 1988) but little is known about the effects of nitrate concentration on germination and its interaction with light quality. In other species, nitrate may promote germination (Williams & Harper 1965; Bewley & Black 1982) or alter light requirements of seeds (Hilhorst & Karssen 1988). The presence of bracteoles may also significantly affect germination in *Atriplex* (Beadle 1952; Koller 1957; Osmond *et al.* 1980), due to their high salt concentration, or by diminishing diffusion of oxygen or changing red : far-red ratios.

Baar (1912) identified two ecologically distinct types of fruits in *A. sagittata*, but a third has since been characterized. Kopecký & Lhotská (1990) showed that these differences allowed *A. sagittata* to germinate across a wide range of temperatures, but they did not test the influence of light or nitrates.

We tested whether seeds produced by the three fruit types of *A. sagittata* differed in their germination response to light and nutrients or in the presence of dormancy breaking mechanisms. We also examined whether fruit size or age affected the pattern of germination and whether chemical substances present in the bracteoles leach at a rate consistent with acting as inhibitors of germination.

STUDY SPECIES

Atriplex sagittata Borkh. (syn. *A. acuminata* W. et K., *A. hortensis* L. ssp. *nitens* (Schkuhr) Pons, *A. nitens* Schkuhr) (Chenopodiaceae) is one of three annual species of the section *Dichosperma* Dumort., all of which bear three types of achenes (Aellen 1960). *Atriplex sagittata* has spread from its native Central Asia, Asia Minor and eastern Europe to central and western Europe where it is abundant in urban areas, on disturbed sites, and along railways and roads (Kirschner & Tomšovic 1990; Mandák & Pyšek 1998). It prefers nitrogen-rich soils and tolerates a high content of KCl and NaCl (Kopecký & Lhotská 1990).

In the Czech Republic, flowering starts in July and fruits mature from mid-October. Type A fruits originate from female or bisexual ebracteate flowers and consist of small, black, lens-shaped achenes with a glossy, smooth testa enclosed within a 5-lobed perianth. Type B fruits are produced by female bracteate flowers. Although its achenes are larger than type A, they have a similar appearance, but are covered by extended bracteoles. Type C is also produced by female bracteate flowers but its achenes are brown and rather large, covered by extended bracteoles that are bigger than those of type B fruit (see Fig. 1 and Table 1)

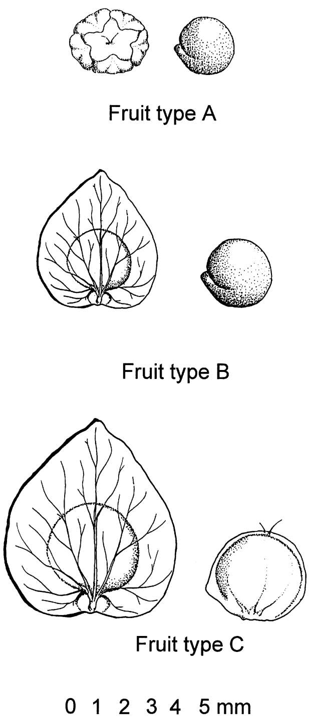

Fig. 1 The three types of fruits produced by *Atriplex sagittata*. The complete dispersal unit of each type (i.e. fruit enclosed in bracteoles in the case of types B and C, and in perianth in the case of type A) is shown on the left, and separated fruits (achenes) on the right.

Methods

Fruits were collected in November 1993, 1994 and 1995 from a population of *A. sagittata* on waste ground at Praha-Trója, Czech Republic (50.05° N, 14.27° E).

For each collection, the fruits were stored in paper bags in the dark at laboratory temperature for up to 3 months before the experiments, which were carried out between November 1995 and April 1996. Fruits were surface sterilized with 2% calcium hypochlorite, then placed in 100 mm diameter Petri dishes on a single layer of filter paper, wetted with 20 mL of water (or treatment solution) and incubated at 22 °C during a 14-h light period and at 15 °C during 10-h dark period each day (Hendry & Grime 1993). Germination was monitored at 3-day intervals for 21 days. Each experiment consisted of 5 replicate dishes of 50 seeds for each seed type and each treatment.

Table 1 Characteristics of fruits and bracteoles in *Atriplex sagittata*. Mean ± SE is shown for particular fruit types A, B and C (see text for description); $n = 2400$ for fruit weight, $n = 480$ for other measured characteristics (see Mandák & Pyšek 1999 for details on sampling). Means within a column followed by different superscript letter were significantly different at $P < 0.05$ in multiple range Tukey's test

Fruit type	Fruit weight (mg)	Bracteole weight (mg)	Dispersal unit weight (mg)	Bracteole area (cm^2)	Bracteole : fruit weight ratio
A	0.837 ± 0.011^a	–	0.827 ± 0.011^a	–	–
B	1.521 ± 0.014^b	0.656 ± 0.009^a	2.167 ± 0.021^b	0.420 ± 0.013^a	2.426 ± 0.027^a
C	3.760 ± 0.060^c	1.211 ± 0.020^b	4.974 ± 0.076^c	0.662 ± 0.010^b	3.166 ± 0.033^b
Pooled	2.034 ± 0.021	0.933 ± 0.011	2.656 ± 0.027	0.541 ± 0.008	2.796 ± 0.021

EFFECTS OF DORMANCY, LIGHT AND NUTRIENTS

Seeds harvested in autumn 1995 were used in a factorial design. Seeds were tested for germination after stratification (2 weeks storage followed by 4 weeks in the dark at 5 °C) and compared with control (unstratified) seeds kept at room temperature for 6 weeks.

Light treatments were imposed by incubating dishes under a fluorescent tube (Mini Fluo – 13 W) (white light), under the same tube but with a single layer of green plastic (green light), thus simulating canopy shade by reducing the red : far-red ratio by 69% and the photon flux density by 56% of white light levels (Skálová & Krahulec 1992), or by wrapping in aluminium foil (dark).

Potassium nitrate solution (10^{-1}, 10^{-2} and 10^{-3} M, respecitvely, for high, medium and low nitrate) or distilled water were used to give four nutrient levels.

Three-hundred and sixty dishes were used (3 seed types × 2 dormancy treatments × 3 light levels × 4 nutrient treatments × 5 replicates).

EFFECT OF SEED AGE

Unpublished data (B. Mandák & P. Pyšek) strongly suggest that weather conditions prior to collection do not cause maternal preconditioning in this species. The possible effect of density and nutrient status of the site (Mandák & Pyšek 1999) on germination was eliminated by using seeds from a locality where the population density was constant. Seeds collected in 1993, 1994 and 1995 were stratified prior to being tested in 1995 in distilled water under white light.

EFFECT OF FRUIT SIZE

Type C fruit, which exhibit the greatest variation in size (Mandák & Pysek 1999), were divided into three classes (≤ 0.220, 0.221–0.270 and ≥ 0.271 mg). Germination of seeds collected in 1995 was tested under white light in distilled water.

ROLE OF BRACTEOLES AS GERMINATION INHIBITORS

Salt may affect seed germination, and chloride ion concentrations were therefore determined immediately after seed maturation and at peak germination (i.e. when germination inhibitors are supposed to have been leached from bracteoles onto the soil surface). Bracteoles were collected from waste ground in Kostelec nad Černými lesy, on 24 October 1995 and 20 April 1996, separated from fruits, and gently blot-dried and weighed.

Five oven-dried samples from each harvest were ashed in a Thermolyne type 1400 muffle furnace for 24 h at 450 °C, and Cl^- concentration was determined by argentometric titration.

Precipitation data were obtained from the Prague-Libeň meteorological station to determine the amount of water available for leaching. Five replicates each of 200 bracteoles were put into 500 mL of distilled water and shaken for 25, 45, and 55 min, before analysis of the remaining chloride concentration.

Mathematical simulation showed that the experimental curve was very well fitted by the relationship:

$$c = \sqrt[x-1]{\frac{-c_0^{x-1}}{1 - ktc_0^{x-1}}}$$

Where c is the concentration of chloride ions in the solid phase in bracteoles, t is the time of leaching, k is the rate constant and c_0 is the initial concentration, with values of k (0.036) and x (2.40) optimized by regression.

The amount of water which can be imbibed was determined by incubating 10 dried bracteoles in distilled water and this value was combined with bracteole chloride concentration after 0, 25, 45 and 55 min to give four decreasing salt concentrations (simulating the gradual leaching of salt from bracteoles by rain in the course of the season). Only type C has fruits with a permeable testa and these were therefore used to test the effect of salt concentration.

STATISTICAL ANALYSIS

Data from germination experiments were transformed (arcsine) before analysis to achieve normality. Multiple analysis of variance was used to test for differences between final germination percentages (Snedecor & Cochran 1956). The pattern of germination over time was determined by survival analysis with comparison of multiple samples. A score is first assigned to each

Table 2 Multiple analysis of variance showing the effect of particular factors on final germination (performed on pooled data, $n = 360$). Data were transformed (arcsine) to achieve normality. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, NS = not significant

Source of variation	d.f.	*F*-ratio	*P* level
Dormancy	1	3777.3	***
Light	2	187.6	***
Seed type	2	5972.1	***
Nutrient	3	42.1	***
Dormancy × light	2	20.0	***
Dormancy × seed type	2	504.2	***
Light × seed type	4	10.2	***
Dormancy × nutrient	3	3.1	NS
Light × nutrient	6	6.1	***
Seed type × nutrient	6	14.5	***

survival time using Mantel's procedure (Mantel 1967); next a chi-square value is computed based on the sums (for each group) of this score. These data were analysed using Statistica™ software (StatSoft 1998).

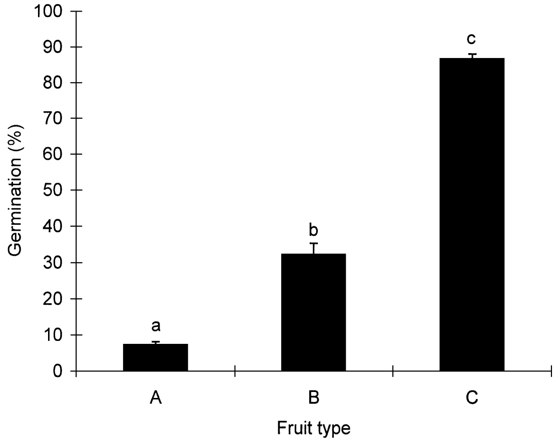

Fig. 2 Final percentage of germinated seeds (with SE) of particular types (pooled data from 1 year). Bars bearing different letters were significantly different in multiple range comparison (Tukey's test) at $P < 0.05$.

Results

EFFECT OF DORMANCY, LIGHT AND NUTRIENTS

Analysis of pooled data revealed significant differences in final germination percentages between seeds produced by particular fruit types (Table 2). The effects of dormancy-breaking, light and nutrients were also all significant, as were all two-factor interactions except that between dormancy-breaking and nutrients. Seeds produced by type C fruit germinated the best and those from type A the least (Fig. 2). Overall, stratified seeds germinated better then unstratified (Fig. 3d), and the

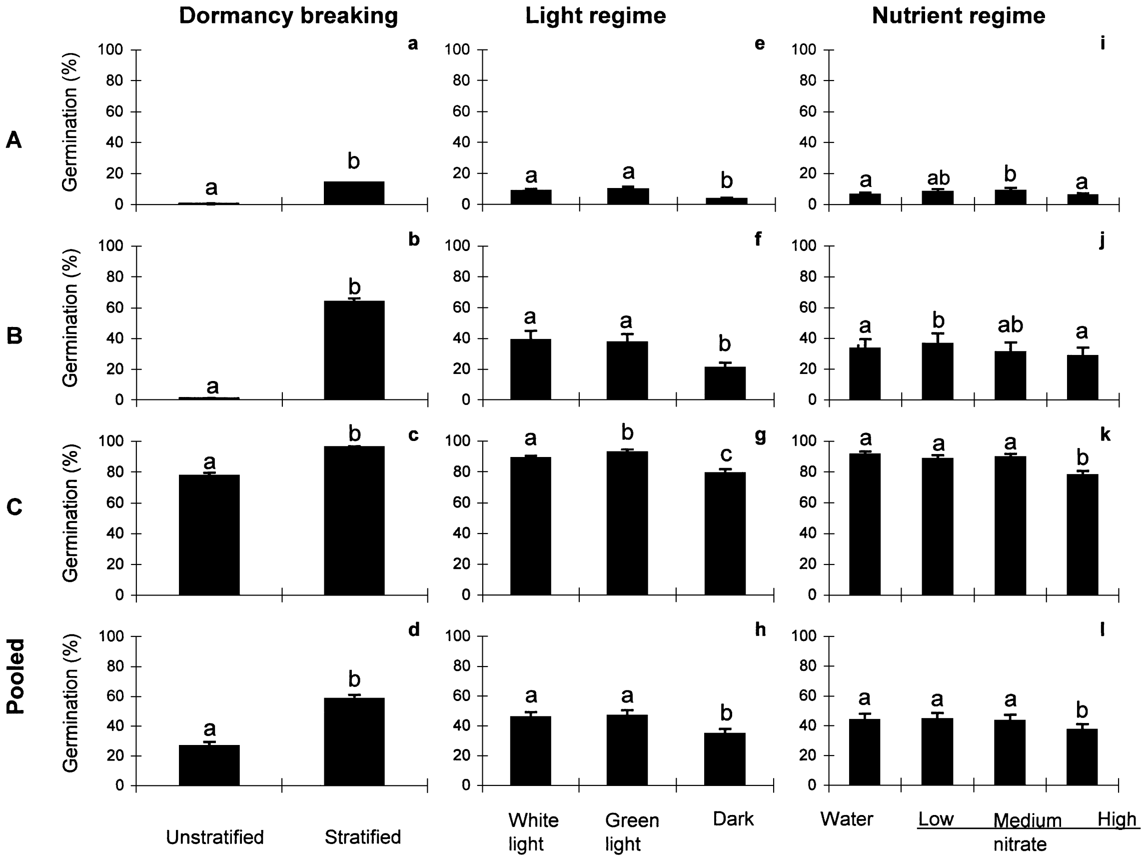

Fig. 3 Final percentage of germinated seeds pooled according to particular treatments or fruit types. Statistical conventions as in Figure 2.

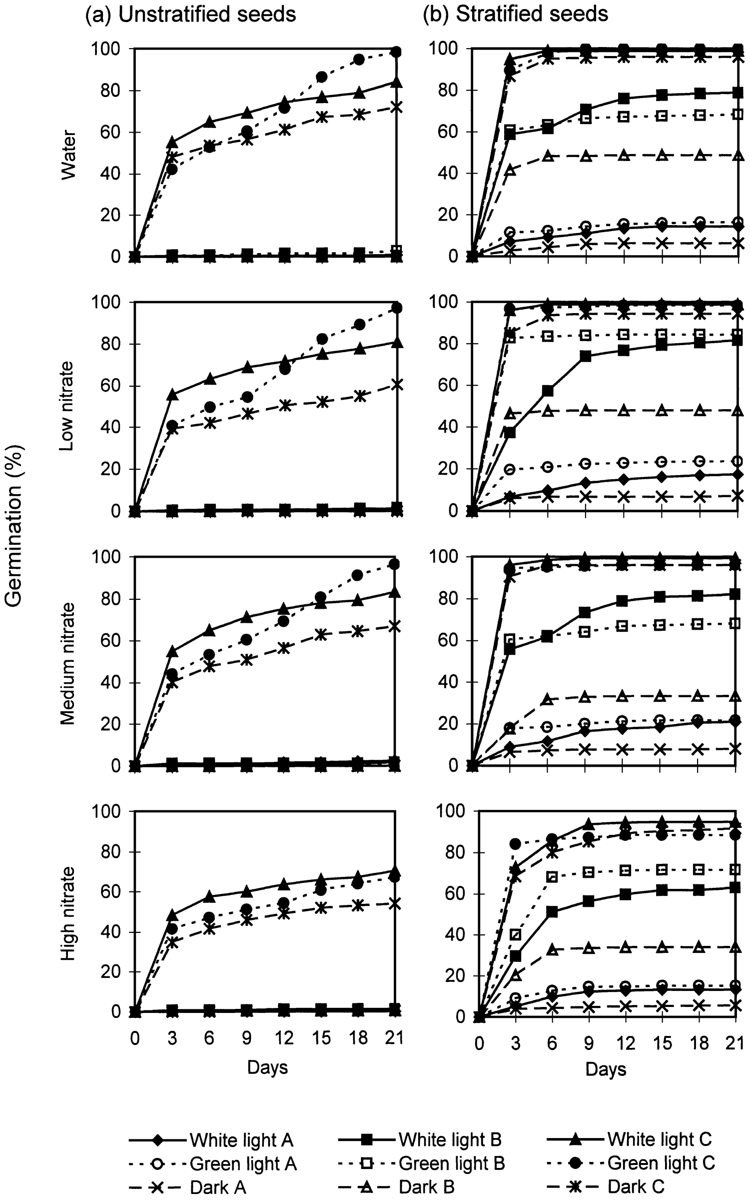

Fig. 4 The course of germination as recorded for (a) unstratified and (b) stratified seeds in 3-day intervals. Data points represent means from 5 replicates. See Tables 5 and 6 for the results of statistical analysis of the germination pattern.

final percentage was lower in the dark (Fig. 3h) and under high nutrients (Fig. 3l).

Survival analysis of pooled data revealed significant differences in the rate of germination with respect to all factors considered, i.e. seed type ($\chi^2 = 6991.6$, d.f. = 2, $P < 10^{-5}$), dormancy-breaking ($\chi^2 = 4.54$, d.f. = 1, $P < 10^{-5}$), light regime ($\chi^2 = 124.74$, d.f. = 2, $P < 10^{-5}$) and nutrient regime ($\chi^2 = 62.87$, d.f. = 3, $P < 10^{-5}$). Seeds from the type A fruit germinated most slowly, those from type C germinated fastest (Fig. 4a,b).

Breaking of dormancy, light and nutrient levels all had highly significant effects ($P < 0.001$) on the final percentage of germinated seed when fruit types were considered separately (Table 3). Interaction between dormancy-breaking and light was also highly significant for all types, but other interactions were only seen in one type.

Final germination percentages for each treatment are given in Table 4. Seeds from type A and B fruits were dormant and did not germinate without cold stratification (Fig. 3a,b); while seed from type C fruit were not dormant although stratification caused a further increase of germination (Fig. 3c).

Darkness significantly reduced germination in all seed types, whereas white and green light had a differential effect only on type C (Fig. 3e, f, g).

For all three fruit types, germination was low at high nitrate levels (Fig. 3i–k). Type A was stimulated by low and medium concentrations of nitrate, whereas type B germinated best at low nitrate levels. Type C fruit were unaffected except at high nutrient levels (Fig. 3k, Table 4).

Light and nutrient regimes had significant effects on the course of germination of seeds produced by particular fruit types, as revealed by survival analysis. Both light (Table 5, Fig. 4) and nutrients (Table 6, Fig. 4) affected seed from type C and (provided dormancy had been

Table 3 Multi-way analysis of variance showing the effect of particular factors on final germination (performed for seeds from particular fruit types, $n = 120$ for each type). Data were transformed (arcsine) to achieve normality. $***P < 0.001$, $**P < 0.01$, $*P < 0.05$, NS = not significant

		Seed type A		Seed type B		Seed type C	
Source of variation	d.f.	*F*-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*
Dormancy	1	769.9	***	3231.2	***	409.5	***
Light	2	32.3	***	81.2	***	82.1	***
Nutrients	3	7.3	***	7.5	***	52.2	***
Dormancy × light	2	18.4	***	44.5	***	43.1	***
Dormancy × nutrients	3	1.8	NS	4.0	*	2.0	NS
Light × nutrients	6	1.8	NS	1.9	NS	9.3	***

Table 4 Summary of final germination percentages recorded for particular treatments. Means ± SE are given ($n = 5$). The means followed by the same letter columnwise were not significantly different in multiple range comparisons within particular nutrient regimes (Tukey's test)

Treatments			Seed type		
Dormancy breaking	Light regime	Nutrient regime	A	B	C
Unstratified	White light	Water	0.8 ± 0.5^{a}	0.4 ± 0.4^{a}	84.0 ± 2.3^{a}
		Low nitrate	0.0 ± 0.0^{a}	1.2 ± 0.5^{a}	80.8 ± 1.5^{ab}
		Medium nitrate	2.4 ± 0.4^{b}	1.6 ± 0.8^{a}	83.2 ± 3.3^{a}
		High nitrate	0.0 ± 0.0^{a}	1.2 ± 0.8^{a}	70.4 ± 3.0^{b}
	Green light	Water	0.0 ± 0.0^{a}	2.8 ± 1.4^{a}	98.4 ± 0.8^{a}
		Low nitrate	0.4 ± 0.4^{a}	1.6 ± 1.0^{a}	97.2 ± 1.0^{a}
		Medium nitrate	1.2 ± 0.8^{a}	1.6 ± 0.8^{a}	96.4 ± 0.8^{a}
		High nitrate	0.0 ± 0.0^{a}	0.4 ± 0.4^{a}	67.2 ± 2.9^{b}
	Dark	Water	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	72.0 ± 1.7^{a}
		Low nitrate	0.0 ± 0.0^{a}	0.8 ± 0.5^{a}	60.4 ± 5.3^{ab}
		Medium nitrate	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	66.8 ± 3.4^{ab}
		High nitrate	0.4 ± 0.4^{a}	0.4 ± 0.4^{a}	54.0 ± 2.1^{b}
Stratified	White light	Water	14.4 ± 2.4^{a}	78.8 ± 4.5^{a}	98.8 ± 0.8^{ab}
		Low nitrate	17.2 ± 3.0^{a}	81.6 ± 1.6^{a}	98.8 ± 0.8^{ab}
		Medium nitrate	20.8 ± 2.5^{a}	82.0 ± 3.0^{a}	99.2 ± 0.8^{b}
		High nitrate	13.2 ± 3.1^{a}	62.8 ± 1.0^{b}	94.8 ± 1.6^{a}
	Green light	Water	16.4 ± 1.8^{a}	68.4 ± 4.4^{a}	100.0 ± 0.0^{a}
		Low nitrate	23.6 ± 0.1^{a}	84.4 ± 2.2^{b}	98.4 ± 1.6^{a}
		Medium nitrate	21.6 ± 3.9^{a}	68.0 ± 3.2^{a}	96.0 ± 0.6^{b}
		High nitrate	15.2 ± 2.8^{a}	71.6 ± 2.9^{a}	88.4 ± 1.5^{c}
	Dark	Water	6.4 ± 1.6^{a}	48.8 ± 2.5^{a}	96.0 ± 1.3^{a}
		Low nitrate	7.2 ± 1.7^{a}	48.0 ± 5.0^{a}	94.4 ± 0.8^{a}
		Medium nitrate	8.0 ± 1.1^{a}	33.2 ± 5.5^{a}	96.0 ± 1.4^{a}
		High nitrate	5.6 ± 2.3^{a}	34.0 ± 1.8^{a}	91.6 ± 2.1^{a}
Total			7.2 ± 0.3	31.9 ± 0.4	86.8 ± 0.4

broken by stratification) type B fruit; however, although stratified type A fruit responded to nutrient regime (Table 6, Fig. 4), they were not affected by light except for a weak response to green light.

EFFECT OF SEED AGE

Final germination percentage was significantly affected by fruit age ($F_{2,36} = 55.4$, $P < 10^{-7}$), fruit type ($F_{2,36} = 160.5$, $P < 10^{-7}$) and by their interaction ($F_{4,36} = 184.7$, $P < 10^{-7}$). Germinability of seeds from types A and B fruits increased with increasing age, but the reverse was seen in type C where germination was > 98% in the 2 two years but fell to 12.4% after 3 years (Fig. 5).

EFFECT OF FRUIT SIZE

Final percentage of germinated seeds did not differ among size classes (only tested for type C, $F_{2,12} = 3.8$, $P = 0.053$). However, survival analysis revealed highly significant differences in the course of germination ($\chi^2 = 61.9$, d.f. = 2, $P < 10^{-5}$), with largest seeds germinating significantly slower than those from the medium and small size classes (Fig. 6).

THE ROLE OF BRACTEOLES AS GERMINATION INHIBITORS

Immediately after maturation of seeds, the bracteoles

Table 5 Effect of nutrient regimes on the course of germination (i.e. the pattern of germination over time) as assessed by survival analysis (see Methods for details) in particular dormancy-breaking and light treatment combinations. Results are shown separately for seeds of particular fruit types (A, B and C) and for pooled data (ABC). Seeds in the analysis that did not germinate were considered as 'survivors'. A significant result means that a different pattern of germination over time was found in seeds of the given type under different nutrient regimes and given combination of dormancy-breaking and light regime

Treatments		A		B		C		ABC	
Dormancy breaking	Light regime	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Unstratified	White light	0.00	1.00	0.54	0.91	7.88	0.049	2.76	0.43
	Green light	0.00	1.00	1.77	0.62	19.55	0.001	2.64	0.45
	Dark	0.00	1.00	0.00	1.00	14.98	0.002	15.29	0.002
Stratified	White light	3.09	0.38	41.17	0.001	109.67	0.001	38.46	0.001
	Green light	9.04	0.03	65.47	0.001	30.68	0.001	48.40	0.001
	Dark	1.01	0.80	41.59	0.001	50.64	0.001	23.93	0.001

Table 6 Effect of light regime on the course of germination (i.e. the pattern of germination over time) as assessed by survival analysis (see Methods for details) in particular dormancy-breaking and nutrient treatment combinations. Results are shown separately for seeds of particular fruit types (A, B, and C) and for pooled data (ABC). Seeds in the analysis that did not germinate were consider as 'survivors'. A significant result means that a different pattern of germination over time was found in seeds of the given type under different light regimes and given combination of dormancy-breaking and nutrient regime

Treatments		A		B		C		ABC	
Dormancy breaking	Nutrient regime	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Unstratified	Water	0.00	1.00	0.00	1.00	7.70	0.02	0.746	0.689
	Low nitrate	0.00	1.00	1.19	0.55	32.33	0.001	18.19	0.001
	Medium nitrate	0.00	1.00	0.00	1.00	22.02	0.001	0.47	0.788
	High nitrate	0.00	1.00	0.49	0.78	14.08	0.001	7.53	0.02
Stratified	Water	11.43	0.003	29.52	0.001	9.76	0.008	24.07	0.001
	Low nitrate	27.22	0.001	92.76	0.001	30.48	0.001	65.79	0.001
	Medium nitrate	21.80	0.001	117.7	0.001	7.618	0.02	66.68	0.001
	High nitrate	13.67	0.001	59.16	0.001	12.43	0.002	38.75	0.001

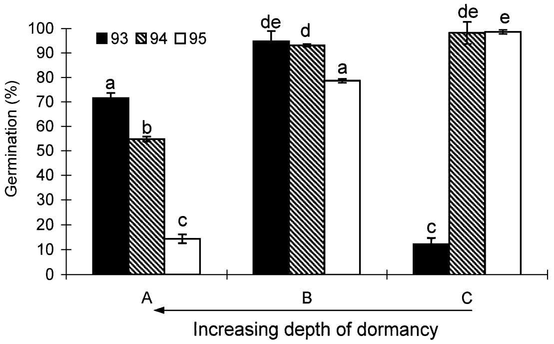

Fig. 5 Changes in germinability of particular seed types with seed age. Conventions as in Figure 2.

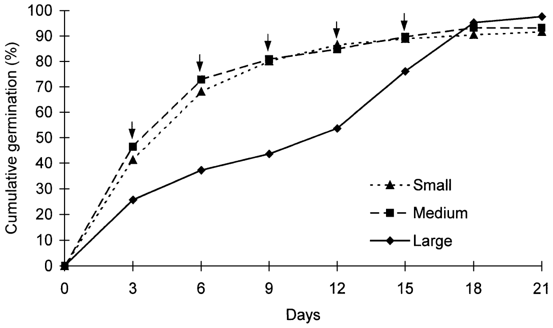

Fig. 6 The germination of seeds of fruit type C of different size classes. Arrows indicate sampling dates at which the cumulative percentage germination recorded in the two smaller size classes was significantly different from that recorded in large seeds (multiple range comparison, Tukey's test, $P < 0.05$).

contained 21.31 mg Cl^- per g dry weight. The ions were completely leached from bracteoles during autumn and winter so that the spring value (after dormancy had been naturally broken) was 0.007 mg g^{-1}.

Leaching of salt from bracteoles was extremely fast (Fig. 7). The model predicts that although it would take 28 000 min to reach the value recorded in bracteoles harvested in the spring, the concentration of salt dropped to approximately 5% of the starting value after only 25 min of shaking. If time reflects the amount of precipitation needed, then only 0.09% of the 172.6 mm of precipitation recorded in the study area for the period between fruit maturation and spring germination would be needed to wash out 95% of salt from the bracteoles. This 0.15 mm of precipitation would

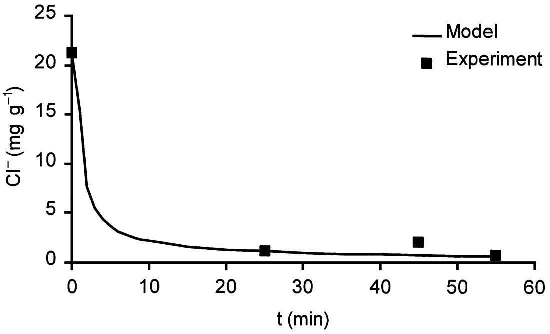

Fig. 7 Leaching of ions from bracteoles. Experimental data represent the concentration of ions (in mg per g of dry weight) recorded after the respective period of continuous shaking in distilled water simulating continuous rain. Theoretical values are based on the model described in the Methods section.

probably be achieved by the first autumn rain following fruit maturation.

Even the highest salt concentrations (i.e. that recorded immediately after fruit maturation) of NaCl (i.e. 1.484 g L^{-1}) did not significantly affect germination (type C fruit, $F_{5,24} = 0.84$, $P = 0.54$). The percentage germination pooled across all concentrations was high (96.30 ± 2.98%, mean ± SE, $n = 30$).

Discussion

DIFFERENCES IN GERMINATION BETWEEN SEEDS PRODUCED BY PARTICULAR FRUIT TYPES

In many heterocarpic species, dispersal abilities of diaspores are closely associated with germinability. Germination is rapid and dormancy low in far-dispersed diaspores and vice versa (Venable & Levin 1985; Kigel 1992). *Atriplex sagittata* appears to divide its reproductive effort between two strategies. Seeds from type C fruit are non-dormant and germinate as soon as conditions are favourable, thus ensuring survival in the short term (Wertis & Ungar 1986; Venable *et al.* 1987), but populations risk local extinction if conditions then become adverse (i.e. it is a high-risk strategy; Venable 1985a) because the seed bank is reduced to zero each summer (Mandák & Pyšek 2001). In contrast, the dormant seeds produced by types A and B fruits ensure long-term reproduction and survival in the field by protracted germination, albeit in low quantities (i.e. *A. sagittata* also adopts a low-risk strategy; Venable 1985b).

Differences in the pericarp or in the testa of fruit types are at least partly responsible for the differential germination (Baar 1912; Osmond *et al.* 1980; McEvoy 1984; Tanowitz *et al.* 1987). These structures may physically impede germination, block gas diffusion, restrict water intake, or contain chemical inhibitors. In a range of *Atriplex* species, including *A. hortensis* (Osmond *et al.* 1980), *A. sagittata* (Baar 1912) and *A. triangularis* (Khan & Ungar 1984, 1985), the pericarp of fruits producing non-dormant seeds is formed by flattened, relatively thin-walled cells, whereas that of dormant types is formed by densely packed cylindrical sclereids. In accordance with previous results, the germination of seeds from types A and B fruits in *A. sagittata* was strongly stimulated by scarification (Kopecký & Lhotská 1990).

Seed types also differ in their loss of germinability (recorded by observation of the number of germinated seeds, not by direct assessment of viability) over time. Non-dormant seeds (type C fruit) lose their germinability after 2 years, while dormant types (A and B) show increased germinability with age. The same phenomenon was observed in *A. semibaccata* and *A. inflata* (Beadle 1952), suggesting that the effect of the pericarp is only temporary. These patterns may ensure that emergence rates for seedlings of *A. sagittata* will be maintained even in years of strong disturbance, when all adult plants are destroyed.

The results for different sizes of the type C fruit indicate conspicuous variation in germination within as well as between fruit types. This is an example of the trade-off between seed size and emergence and subsequent size of seedlings and their competitive ability (Ross & Harper 1972; Ellison 1987). Final germination percentages did not differ but large seeds germinated more slowly. Seedlings from larger seeds are predicted to have a higher rate of root extension and thus to be more drought- and stress-tolerant and more competitive (Black 1958; but see Melzack & Watts 1982). However, seed size may have no effect in dense stands where seedling success is largely determined by order of emergence (Ross & Harper 1972).

EFFECT OF LIGHT ON GERMINATION

Seed germination is regulated by intensity, spectral composition and periodicity of light (Bewley & Black 1982; Fenner 1992). In all *A. sagittata* seeds there was a significant reduction of germinability in the dark, but the effect of spectral composition depended on fruit type. An overall stimulation by green light, seen only in type C, was due to an effect on unstratified seeds (i.e. there was a light × dormancy interaction). Light had no effect on stratified seeds. Thus, surrounding vegetation might act as a regulating factor in the autumn, in spring there is no reason to suggest that filtering of incoming light may influence germination.

Stratification, or possibly imbibition, is needed for a response of types A and B to light, with the resulting stimulation independent of spectral composition. The intensity may be partly determined by the hard, black testa of fruit types A and B, which is probably impermeable to far-red light in the same way as for *Hieracium pilosella* and *Silene nutans* (Silvertown 1980). *Atriplex sagittata* is found mostly in open, early successional habitats, but the absence of a gap-detection mechanism may explain why it is capable of persisting into later stages of ruderal succession (Mandák & Pyšek 1998).

EFFECT OF NITRATES ON GERMINATION

Nitrate stimulates germination in many weed species (Vincent & Roberts 1977; Williams 1983) but high levels reduced germination in *A. sagittata*. Different optima (medium nitrate for type A, low for type B) may enable *A. sagittata* to occupy a wide range of habitats and to cope with the remarkably variable NO_3^- concentration in ruderal soil (Ellenberg 1988; Osbornová *et al.* 1990; Kovář *et al.* 1997).

EFFECT OF BRACTEOLES ON GERMINATION

Leaching of salt from bracteoles has repeatedly been reported to stimulate germination in the genus *Atriplex* (*A. dimorphostegia*, Koller 1957; *A. hortensis*, Osmond *et al.* 1980; *A. nummularia*, *A. vesicaria*, *A. semibaccata*, *A. inflata* and *A. spongiosa*, Beadle 1952). In all these species, removal of salt from bracteoles by leaching stimulated germination. Possible explanations for the high concentration of salt in bracteoles was suggested by Khan *et al.* (1985), who found that the seed coat of *A. canescens* contained a very low concentration of sodium and chloride and speculated that bracteoles in *Atriplex* may serve as a salt-accumulation area. In contrast, the concentrations of the same ions reported for seed coats of other species, such as *A. triangularis* and *A. confertifolia* were not as low as in the case of *A. canescens* (Khan *et al.* 1987).

However, despite being characteristic of salt steppes, *A. sagittata* germination is not affected by salt contained in bracteoles. Beadle (1952) and Charley (1959, cited by Osmond *et al.* 1980) showed that 70–100 mm of precipitation were sufficient to leach about 95–100% of the chloride from bracteoles. Our model suggests that bracteole salt may not be important for *A. sagittata* in the field because the first autumn rain is probably sufficient to leach almost all their sodium and chloride. However, the bracteoles of *A. sagittata* are very leaf-like and the pattern of leaching may be different from some species with tightly fused or quite woody bracteoles.

Overall, therefore, heterocarpy may allow *A. sagittata* to respond to spatial and temporal variation in environmental conditions, allowing this annual species to perpetuate itself in a range of disturbed habitats.

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References

Aellen, P. (1960) *Atriplex. Illustrierte Flora Von Mitteleuropa* (ed. G. Hegi), 3/2, 664–693. München, Germany. (in German).

Baar, H. (1912) Zur anatomie und Keimumgsphysiologie heteromorpher Samen von *Chenopodium album* und *Atriplex nitens*. *Sitzber. Kais. Akad. Wiss. Wien. Math. Naturw*., **72**, 21–40.

Beadle, N.C.W. (1952) Studies on halophytes. I. The germination of the seeds and establishment of the seedlings of five species of *Atriplex* in Australia. *Ecology*, **33**, 49–62.

Bewley, J.D. & Black, M. (1982) *Physiology and Biochemistry of Seeds*, Vol. 2. Springer-Verlag, Berlin.

Black, J.N. (1958) Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular references to leaf area and the light microclimate. *Australian Journal of Agricultural Research*, **9**, 299–318.

Cheplick, G.P. (1992) Sibling competition in plants. *Journal of Ecology*, **80**, 567–575.

Cheplick, G.P. & Quinn, J.A. (1982) *Amphicarpum purshii* and the 'pessimistic strategy' in amphicarpic annuals with subterranean fruit. *Oecologia*, **52**, 327–332.

Cheplick, G.P. & Quinn, J.A. (1983) The shift in aerial/subterranean fruit ratio in *Amphicarpum purshii*: causes and significance. *Oecologia*, **57**, 374–379.

Ellenberg, H. (1988) *Vegetation ecology of Central Europe*, edn 4. Cambridge University Press, Cambridge.

Ellison, A.M. (1987) Effect of seed dimorphism on the density-dependent dynamics of experimental populations of *Atriplex triangularis* (Chenopodiaceae). *American Journal of Botany*, **74**, 1280–1288.

Ellner, S.P. (1985) ESS germination strategies in randomly varying environments. I. Logistic type models. *Theoretical Population Biology*, **28**, 50–79.

Ellner, S.P. & Schmida, A. (1984) Seed dispersal in relation to habitats in the genus *Picris* (Compositae) in Mediterranean and arid regions. *Israel Journal of Botany*, **33**, 25–39.

Fenner, M., ed. (1992) *Seeds – the Ecology of Regeneration in Plant Communities*. CAB International, Wallingford.

Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of regeneration niche. *Biological Review*, **52**, 107–145.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Hendry, G.A.F., Grime, J.P. (1993) *Methods in Comparative Plant Ecology. A Laboratory Manual*. Chapman & Hall, London.

Hilhorst, H.W.M. & Karssen, C.M. (1988) Dual effect of light on the gibberellin and nitrate-stimulated seeds of *Sisymbrium officinale* and *Arabidopsis thaliana*. *Plant Physiology*, **86**, 591–597.

Khan, M.A. & Ungar, I.A. (1984) The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. *American Journal of Botany*, **7**, 481–189.

Khan, M.A. & Ungar, I.A. (1985) The role of hormones in regulating the germination of polymorphic seeds and early seedling growth of *Atriplex triangularis* Willd. under saline conditions. *Physiologia Plantarum*, **63**, 109–113.

Khan, M.A., Weber, D.J. & Hess, W.M. (1985) Elemental distribution in seeds of the halophytes *Salicornia pacifica* var. *utahensis* and *Atriplex canescens*. *American Journal of Botany*, **72**, 1672–1675.

Khan, M.A., Weber, D.J. & Hess, W.M. (1987) Elemental compartmentalization in seeds of *Atriplex triangularis* and *Atriplex confertifolia*. *Great Basin Naturalist*, **47**, 91–95.

Kigel, J. (1992) Diaspore heteromorphism and germination in populations of the ephemeral *Hedypnois rhagadioloides* (L.) F. W. Schmidt (Asteraceae) inhabiting a geographic range of increasing aridity. *Acta Oecologica*, **13**, 45–53.

Kirschner, J. & Tomšovic, P. (1990) *Atriplex. Květena České Republiky* (eds S. Hejný & B. Slavík), Vol. 2, pp. 266–280. Academia, Praha. (in Czech).

Koller, D. (1957) Germination mechanism in some desert seeds. I. *Atriplex dimorphostegia* Kar. et Kir. *Ecology*, **38**, 1–13.

Koller, D. (1972) Environmental control of seed germination. *Seed Biology* (ed. T.T. Kozlowski), Vol. 2, pp. 1–101. Academic Press, London.

Kopecký, K. & Lhotská, M. (1990) K šíření druhu *Atriplex sagittata*. *Preslia*, **62**, 337–349.

Kovář, P., Kovářová, M., Bunce, R., Ineson, P. & Brabec, E. (1997) Role of hedgerows as nitrogen sink in agricultural landscape of Wensleydale, Northern England. *Preslia*, **68** (1996), 273–284.

Levin, S.D., Cohen, D. & Hastings, A. (1984) Dispersal strategies in patchy environment. *Theoretical Population Biology*, **26**, 165–191.

Lloyd, D.G. (1984) Variation strategies of plants in heterogenous environments. *Biological Journal of Linnean Society*, **21**, 357–385.

Mandák, B. (1997) Seed heteromorphism and the life cycle of plants: a literature review. *Preslia*, **69**, 129–159.

Mandák, B. & Pyšek, P. (1998) History of spread and habitat preferences of *Atriplex sagittata* (Chenopodiaceae) in the Czech Republic. *Plant Invasions: Ecological Mechanisms and Human Responses* (eds U. Starfinger, K. Edwards, I. Kowarik & M. Williamson), pp. 209–224. Backhuys Publishers, Leiden.

Mandák, B. & Pyšek, P. (1999) Effects of plant density and nutrient levels on fruit polymorphism in *Atriplex sagittata. Oecologia*, **119**, 63–72.

Mandák, B. & Pyšek, P. (2001) Fruit dispersal and seed banks in *Atriplex sagittata*: the role of heterocarpy. *Journal of Ecology*, **89**, 159–165.

Mantel, N. (1967) Ranking procedures for arbitrarily restricted observations. *Biometrics*, **23**, 65–78.

McEvoy, P.B. (1984) Dormancy and dispersal in dimorphic achenes of tansy ragworth, *Senecio jacobea* L. (Compositae). *Oecologia*, **61**, 160–168.

Melzack, R.N. & Watts, D. (1982) Variation in seed weight, germination and seedling vigour in the yew (*Taxus baccata* L.) in England. *Journal of Biogeography*, **9**, 55–63.

Osbornová, J., Kovářová, M., Lepš, J. & Prach, K. (1990) *Succession in Abandoned Fields. Studies in Central Bohemia, Czechoslovakia*. Kluwer Academic Publishers, Dordrecht.

Osmond, C.B., Björkman, O. & Anderson, D.J. (1980) *Physiological Processes in Plant Ecology – Towards a Synthesis with Atriplex*. Springer-Verlag, Berlin.

Ross, M.A. & Harper, J.L. (1972) Occupation of biological space during seedling establishment. *Journal of Ecology*, **60**, 77–88.

Schoen, D.J. & Lloyd, D.G. (1984) The selection of cleistogamy and heteromorphic diaspores. *Biological Journal of Linnean Society*, **23**, 303–322.

Silvertown, J. (1980) Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytologist*, **85**, 109–118.

Skálová, H. & Krahulec, F. (1992) The response of three *Festuca rubra* clones to change in light quality and plant density. *Functional Ecology*, **6**, 282–290.

Snedecor, G.W. & Cochran, W.G. (1956) *Statistical Methods*. Iowa State University Press, Ames.

Stebbins, G.L. (1974) *Flowering Plants: Evolution above the Species Level*. Belknap, Cambridge, MA.

StatSoft (1998) *Statistica for Windows*, edn 2. Tulsa.

Stoutjesdijk, P. (1972) Spectral transmission curves of some types of leaf canopies with a note on seed germination. *Acta Botanica Neerlandica*, **21**, 185–191.

Tanowitz, B.D., Salopek, P.F. & Mahall, B.E. (1987) Differential germination of ray and disc achenes in *Hemizonia increscens* (Asteraceae). *American Journal of Botany*, **74**, 303–312.

Taylorson, R.B. & Borthwick, H.A. (1969) Light filtration by foliar canopies: significance for light controlled weed seed germination. *Weed Science*, **17**, 48–51.

Ungar, I.A. (1987) Population ecology of halophyte seeds. *Botanical Review*, **53**, 301–334.

Venable, D.L. (1985a) Ecology of achene dimorphism in *Heterotheca latifolia*. III. Consequences of varied water availability. *Journal of Ecology*, **73**, 757–763.

Venable, D.L. (1985b) The evolutionary ecology of seed heteromorphism. *American Naturalist*, **126**, 577–595.

Venable, D.L. & Brown, J.S. (1993) The population-dynamic functions of seed dispersal. *Vegetatio*, **107/108**, 31–55.

Venable, D.L., Búrquez, A., Corral, G., Morales, E. & Espinosa, F. (1987) The ecology of seed heteromorphism in *Heterosperma pinnatum* in Central Mexico. *Ecology*, **68**, 65–76.

Venable, D.L., Dyreson, E. & Morales, E. (1995) Population dynamics consequences and evolution of seed traits of *Heterosperma pinnatum* (Asteraceae). *American Journal of Botany*, **82**, 410–420.

Venable, D.L. & Levin, D.A. (1985) Ecology of achene dimorphism in *Heterotheca latifolia* I. Achene structure, germination and dispersal. *Journal of Ecology*, **73**, 133–145.

Vincent, E.M. & Roberts, E.H. (1977) The interactions of light, nitrate and alternating temperatures in promoting the germination of dormant seeds of common weed species. *Seed Science and Technology*, **6**, 659–670.

Wertis, B.A. & Ungar, I.A. (1986) Seed demography and seedling survival in a population of *Atriplex triangularis* Willd. *American Midland Naturalist*, **116**, 152–162.

Williams, E.D. (1983) Effect of temperature, light, nitrate and pre-chilling on seed germination of grassland plants. *Annals of Applied Biology*, **103**, 161–172.

Williams, J.T. & Harper, J.L. (1965) Seed polymorphism and germination I. The influence of nitrates and low temperatures on the germination of *Chenopodium album*. *Weed Research*, **5**, 141–150.

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