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How does seed heteromorphism influence the life history stages of *Atriplex sagittata* (Chenopodiaceae)?

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Abstract

Atriplex sagittata is an annual, heterocarpic species producing three types of fruits, (i) dormant ebracteate (further termed type A), (ii) dormant bracteate (type B) and (iii) non-dormant bracteate (type C). In this study, we investigated populations grown from particular fruit types under different density regimes, and assessed their fate in particular life stages throughout a complete growing season. Differences in germination date among populations grown from seeds of the three fruit types were found, followed by differences in population density and plant size. Low population density and total biomass was recorded in populations of types A and B fruit (which are smaller and exhibit less germination), but the low density was not associated with faster growth of individual plants. Type C fruit, with bigger seeds and higher germinability, generated populations with higher densities and higher total biomass than populations generated from type A and B. There was a significant effect of plant density on dry weight of individual plants, regardless of the fruit type from which they were grown. Under both density regimes, plants grown from types A and B fruit were lighter than those grown from type C fruit. Plants grown from different fruit types produced dispersal units (fruits + bracteoles) of different mean weight which increased from A to B to C. However, the total fruit weight was not significantly different when plant size was used as a covariate. Maternal effect on seed germinability, exhibited by plants grown from the three fruit types, was not significant. However, a remarkable trend was found. Lower germination was recorded in type A and B fruits produced by plants which grew under higher densities. It is concluded that plants derived from different fruit types differ in growth characteristics and population parameters which can have pronounced effect on the life cycle and population regeneration in successive years.

Keywords: *Atriplex sagittata*; Bet-hedging; Chenopodiaceae; Competition; Czech Republic; Germination; Maternal effect; Seed heteromorphism

Introduction

Seed heteromorphism is common in the Asteraceae, Chenopodiaceae, Poaceae and Brassicaceae (Harper et al., 1970; Mandák, 1997; Imbert, 2002), and among annuals, often pioneer species or plants faced with stochastic environments such as deserts or semideserts (Mandák, 1997). In the genus *Atriplex,* it is confined to annual species of salt marshes, semideserts and deserts, and there is a strong tendency for functional divergence of particular seed types, each being specialized on some

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aspect of temporally and spatially heterogeneous environment (Mandák and Pyšek, 1998, 1999a, 2001a, b, see also Donohue, 1997; Koller and Roth, 1964; Venable and Levin, 1985a, b).

Seed heteromorphism is probably an adaptive feature. Various seed functions are usually related to the bet-hedging, i.e. reducing temporal variance in fitness (Venable, 1985b; Philippi and Seger, 1989; Philippi, 1993a, b). Alternatively, it is explained as an escape from the negative effect of density, i.e. delayed germination prevents mortality under high densities (Ellner, 1985; Levin et al., 1984; Venable, 1989) or associated with sib-competition if dormancy of a fraction of seeds is favoured by intensive sibling competition (Ellner, 1986, 1987; Schoen and Lloyd, 1984; Venable and Brown, 1993).

In seed heteromorphic species, fruit types usually differ in seed mass, which is a crucial feature during early stages of seedling establishment (Baskin and Baskin, 1998). Fruit size in seed heteromorphic plants is usually associated with differences in shape, colour or presence of various appendages (Mandák, 1997) and with marked differences in ecological properties. These differences may reflect within- or between-year timing of germination (Baker and O'Dowd, 1982; De Clavijo, 1994, 1995; Mandák and Pyšek, 2001a; McEvoy, 1984; Kigel, 1992; Tanowitz et al., 1987; Yamaguchi et al., 1990), dispersal (Koller and Roth, 1964; Mandák and Pyšek, 2001b; McEvoy and Cox, 1987; Rocha, 1996; Sorenson, 1978), seed bank dynamics (Mandák and Pyšek, 2001b; Wertis and Ungar, 1986), dormancy patterns (Brändel, 2004), competitive abilities (Flint and Palmblad, 1978; Imbert et al., 1997; Venable, 1985a), survival and fecundity schedules (Cheplick and Quinn, 1982), or vulnerability to predation (Cook et al., 1971).

Some differences in life history stages of plants grown from different fruit types of seed heteromorphic species were previously reported (Imbert, 2002; Mandák, 1997) but some gaps in our knowledge remain. Because only some aspects of life cycles (e.g. germinability, dispersability, competitive ability) were addressed in previous studies, the complex effect of seed heteromorphy and its manifestation in different life history stages is not well understood (see Mandák and Pyšek, 1998, 1999a, b, 2001a, b). Data illustrating how plants grown from different fruit types perform throughout the whole life cycle are missing. In the few studies available, it was shown that plants derived from heavier seeds are more vigorous (Ellison, 1987; Gardocki et al., 2000; Imbert et al., 1996; Weiss, 1980) or have higher reproductive output (Cheplick and Quinn, 1982; Venable, 1985a). This is usually explained by different fruit size and timing of germination. However, Donohue (1997) found that seed types of *Cakile edentula* var. *lacustris* may differ in genetic composition due to the differences in probability of inbreeding.

In the present study, we focused on comparison of populations grown from seed produced by particular fruit types. Our objectives were (1) to compare germination under field conditions; (2) to determine how germination pattern influenced subsequent population development; (3) to assess the fecundity of plants grown from particular fruit types, and (4) to determine maternal effect on fruits produced by plants grown from different fruit types.

Materials and methods

Study species

Atriplex sagittata Borkh. (syn. *A. acuminata* W. et K., *A. hortensis* L. subsp. *nitens* (Schkuhr) Pons, *A. nitens* Schkuhr) is a tall (1–2 m), annual herb of the Chenopodiaceae. The species is monoecious, with non-Kranz anatomy, $2n = 18$. Flowers are borne in terminal and axillary inflorescences. They are dimorphic and produce three types of fruits differing both morphologically (mainly in colour and presence/absence of bracteoles), and ecologically (Kopecký and Lhotská, 1990; Mandák, 1997, 2003; Mandák and Holmanová, 2004; Mandák and Pyšek, 1998, 1999a, 2001a, b):

- The first fruit type (further termed type A) originates from female or bisexual ebracteate flowers. It is small, black and lens-shaped with a glossy, smooth testa, and five-lobed perianth. This fruit type is undispersed, deeply dormant, with a low level of germinability. It forms a persistent seed bank (according to Thompson and Grime, 1979).
- The second fruit type (type B) is produced by female bracteate flowers. It is medium in size and has a similar appearance to the previous type, but it is covered by extended bracteoles. It is easily dispersed and dormant, with intermediate germinability between fruit types A and C, forming a persistent seed bank.
- The third fruit type (type C) produced by female bracteate flowers is rather large, brown, covered by extended bracteoles which are larger than those of type B fruits. This type of fruit is easily dispersed, is non-dormant and forms a transient seed bank (type II, Thompson and Grime, 1979).

In general, the production of type A fruit favours later germination and restricted dispersal with less survival risk, in contrast to the type C which favours earlier germination and a more efficient dispersal with associated survival risk (Mandák and Pyšek, 2001a, b). The type B fruit has intermediate properties between types A and C, forming an ecological continuum between the contrasting strategies (Mandák and Pyšek, 1999a, b, 2001a, b).

A. sagittata is distributed widely from Siberia across Central Asia into western Europe, and it was recently introduced into South Africa. The native distribution covers Central Asia, Asia Minor and Eastern Europe where it occurs in salt steppe and riparian habitats. From the area of native distribution, the species has spread across south-eastern and eastern Europe to western Europe (Aellen, 1960). It is alien to Central Europe where it was introduced probably in the Bronze Age, i.e. 2000–1500 BC (Mandák and Pyšek, 1998).

A. sagittata is an early successional species, often dominating in the first 2 or 3 years of succession in disturbed sites. It is frequently found in ruderal habitats, namely in villages and cities, and along railways and roads. It prefers nitrogen-rich and saline soils (with KCl and NaCl) (Mandák and Pyšek, 1998).

Garden experiment

Fruits of *A. sagittata* were collected at the end of October 1997 from a population growing in a waste place in Praha, Czech Republic (50°07′27″N, 14°30′29″E). The fruits were separated from bracts, sorted according to fruit type, i.e. A, B, and C, and stored in the dark at room temperature in paper bags.

The experiment was carried out in the Experimental Garden of the Institute of Botany in Průhonice near Praha, Czech Republic (49°59′41″N, 14°33′56″E) in 1998. A randomized block design with ten replicates was used in a seedbed filled with potting soil. Each block consisted of seven experimental plots (25×25 cm). Three were occupied by a single plant each, grown from seeds produced by the three fruit types (termed "low density treatment"). Each of the remaining four plots (termed "high density treatment") received 313 fruits sown regularly to achieve the density one fruit per 2 cm^2. The three fruit types (A, B, C) occupied one plot each. The fourth plot was used for a mixture of the three fruit types (termed "fruit mixture"); the ratio of A: B: C was 1:1:8, and corresponded to the ratio in which the fruits are produced in nature (Mandák and Pyšek, 1999a). In addition, a supplementary plot was established next to each block for destructive sampling.

Seeds were sown on 16 March 1998 and germination was recorded daily in experimental plots until 10 April 1998. Later, it was recorded every 2–3 days until 11 May. After this date, no new seedlings were produced.

On 8 April (13 days since the first observed germination – Time 1), five seedlings were harvested from each supplementary plot, i.e. 50 seedlings in total, and epicotyl length, and length and width of cotyledons were recorded. Seedlings were oven-dried at 60 °C for 2 days and their dry mass was recorded (±0.0001 g). Mean values ($n = 5$) were used for analysis.

On 12 May (day 47 – Time 2), five plants of each fruit type were harvested from supplementary plots, their basal diameter, height, leaf number, length and width of the longest leaf was recorded, and dry mass obtained.

On 11 and 12 August (day 139–140 – Time 3), all plants from low-density plots and those from the inner 20×20 cm part of high-density plots (to account for possible border effects) were harvested. Harvested plants were weighed individually. In high-density plots, one plant was randomly selected and left to provide material for later fruit harvest.

The garden experiment was finished after 203 days on 12 October (Time 4) when the remaining single plants were harvested from high-density plots to evaluate fruit production and seed germinability. The mass of stem (without leaves that were drop off at this time) and that of reproductive structures was recorded separately (±0.0001 g). Stems were oven-dried for 2 days at 60 °C while reproductive structures were weighed without oven drying to make germination tests possible. This is justified because at harvest time, reproductive structures of *A. sagittata* are dry. Reproductive effort (RE) was determined according to the following formula:

$$\mathrm{RE} = \text{total reproductive mass}/\text{dry vegetative mass}.$$

Germination

Germination experiments were carried out to test for differences in germination between the three fruit types produced by plants grown from the particular fruit types. Five replicates of 25 fruits each were used in all experiments, representing nine possible combinations: AA (i. e. A type produced by plant grown form A type), AB, AC, BA, BB, BC, CA, CB, CC. Fruits were placed in 50 mm diameter Petri dishes on a single layer of filter paper, wetted with 5 ml of water and cold-stratified for 21 days in the dark at 5 °C. All experiments ran at one alternating temperature treatment (22/15 °C) based on a 24-h cycle, where the higher temperature (22 °C) coincided with a 14-h light and the lower temperature (15 °C) coincided with 10-h dark period (Hendry and Grime, 1993). Percentage of germinated seeds was recorded at 3-day intervals for 21 days.

Statistical analysis

Data analysis was performed using Statistica™ software (StatSoft, 1998). Growth data and RE were analyzed using ANOVA, ANCOVA and MANCOVA. If a significant difference between means was found, Tukey's multiple range test was used to perform pairwise comparisons between individual treatments.

Increase in mass over time was tested by using repeated measures ANOVA. Where necessary, logarithmic transformation was used to meet the assumptions of ANOVA. When assumptions of ANOVA were not satisfied we used non-parametric Kruskal–Wallis ANOVA.

Data from germination experiments were transformed (arcsine$\sqrt{\%}$) before analysis to achieve normality. Multi-way analysis of variance was used to test for the differences between final germination percentages (Snedecor and Cochran, 1956). To determine differences in the course of germination, survival analysis by comparing multiple samples was used. The multiple-sample test implemented in survival analysis is an extension of Gehan's generalized Wilcoxon test, Peto and Peto's generalized Wilcoxon test, and the log-rank test. A score is first assigned to each survival time using Mantel's procedure (Mantel, 1967); next a χ^2 value is computed based on the sums (for each group) of this score.

Results

Germination in the garden experiment

There were significant differences in final germination percentages between seeds produced by particular fruit types and fruit-type mixture (one-way ANOVA, d.f. $= 3$, MS $= 1.41$, $F = 152.70$, $P < 10^{-6}$). Germinability of seeds increased from type A to B to C fruits (Fig. 1). The fruit mixture had a significantly lower final germination percentage than type C, but the opposite was true during the first 5 days following the onset of germination (Fig. 1). Survival analysis revealed significant differences in the rate of seed germination from particular fruit types, i.e. A<B<C ($\chi^2 = 5874.03$, $P < 10^{-6}$, d.f. $= 3$) (Fig. 1). Seeds also differed in the time needed to start germination; those from type C fruit and fruit mixture germinated fastest followed by seeds from types A and B fruit (Fig. 1).

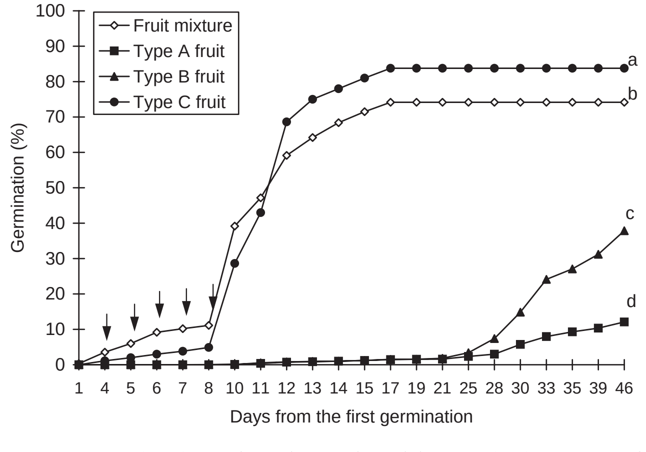

Fig. 1. Germination of seeds produced by particular types of fruit of *Atriplex sagittata*. Each data point represents the mean of 10 replicates. Arrows indicate sampling dates at which the percentage of germinated seeds of type C fruit was significantly different from those germinated in the mixture (Kruskal–Wallis test, $P < 0.05$). Significant differences in final germination percentages are indicated next to germination curves of particular fruit types; those followed by the same letter were not significantly different (Tukey HSD test, $P < 0.05$).

Growth of plants derived from various fruit types

In high-density treatments, the differences in the time of germination (Fig. 1) were maintained over the seedling stage. MANCOVA, using germination date as a covariate, showed a significant effect of the time of measurement (Time 1, Time 2) and fruit type (A, B, C and mixture) on seedling height, cotyledon length and width, and mass (two-way MANCOVA, Time of measurement: d.f. $= 4$, Wilks' $\lambda = 0.06$, $P < 0.001$; Fruit type: d.f. $= 12$, Wilks' $\lambda = 0.45$, $P < 0.001$; Time of measurement × Fruit type: d.f. $= 12$, Wilks' $\lambda = 0.06$, $P < 0.001$). Whereas seedlings of type C fruit produced 1.47 ± 0.15 mg of dry mass and were 7.8 ± 0.28 mm tall after 13 days (Time 1), seeds of type A and B fruit did not yet start to germinate (Table 1). Significant differences in the measured characteristics were maintained after 47 days (Time 2) (Table 1), and the difference between particular fruit types in cotyledon length and mass increased with time as indicated by significant (Time of measurement × Fruit type) interaction.

There was a significant effect of both density and fruit type on seedling height, leaf length and leaf width as recorded after 47 days (Time 2) (two-way MANOVA, Density: d.f. $= 3$, Wilks' $\lambda = 0.64$, $P < 0.001$, Fruit type: d.f. $= 6$, Wilks' $\lambda = 0.23$, $P < 0.001$, Density × Fruit type: d.f. $= 6$, Wilks' $\lambda = 0.56$, $P < 0.001$). At this growth stage, plants from particular fruit types growing under low density were not significantly different from those growing under high density, but in both density treatments, those derived from type C fruit were significantly taller and had larger cotyledons than those derived from type A and B fruits (Table 2).

Repeated-measures ANOVA revealed significant effects of plant density, fruit type and time on growth parameters (Table 3). Density had a highly significant effect on the majority of characteristics measured. The interaction between density and time was highly significant, indicating that plants derived from type C fruit grew faster than those from types A and B fruit and this difference was increasing over time (pairwise comparisons at $P < 0.05$, Tukey's test) (Table 3).

A significant effect of fruit type on the mass of the whole population (calculated as the sum of mass of all

Table 1. Total mass and other biometric characteristics of *Atriplex sagittata* plants as recorded after 13 (Time 1) and 47 (Time 2) days since the onset of germination in seedlings resulted from three fruit types (A, B, C) and mixture

Time of measurement	Fruit type	Plant height (cm)	Leaf length (cm)	Leaf width (cm)	Mass (mg)
Time 1	A	n. p.	n. p.	n. p.	n. p.
	B	n. p.	n. p.	n. p.	n. p.
	C	7.80 ± 0.28b	8.76 ± 0.45d	1.54 ± 0.10c	1.47 ± 0.15a
	Mixture	8.64 ± 0.41bc	10.22 ± 0.58e	1.77 ± 0.13cd	2.30 ± 0.31a
Time 2	A	1.75 ± 0.09a	1.34 ± 0.11b	0.66 ± 0.06b	19.47 ± 9.77a
	B	2.24 ± 0.10a	1.78 ± 0.13b	0.86 ± 0.07b	21.60 ± 3.32a
	C	11.86 ± 0.95c	4.09 ± 0.24c	2.29 ± 0.16e	204.24 ± 32.35b
	Mixture	10.33 ± 0.89bc	3.70 ± 0.22c	2.03 ± 0.15de	190.75 ± 34.01b

Means ± S. E. ($n = 10$) are shown; those followed by the same letters column-wise were not significantly different in pairwise comparisons at $P<0.05$ (Tukey HSD test). n.p. = not present.

Table 2. Mean plant height, and length and width of the largest leaf (cm) of *Atriplex sagittata* recorded after 47 days (Time 2)

Plant density	Fruit type	Plant height	Leaf length	Leaf width
Low	A	1.80 ± 0.12a	1.56 ± 0.23a	0.86 ± 0.13a
	B	2.28 ± 0.23a	2.04 ± 0.25a	1.04 ± 0.14a
	C	7.34 ± 1.20b	5.06 ± 0.44b	2.80 ± 0.27b
High	A	1.75 ± 0.09a	1.34 ± 0.11a	0.66 ± 0.06a
	B	2.24 ± 0.10a	1.78 ± 0.13a	0.86 ± 0.07a
	C	11.86 ± 0.95c	4.09 ± 0.24b	2.29 ± 0.16b

Mean ± S.E. ($n = 10$) are shown for particular density/fruit type combinations. Means followed by the same letters column-wise were not significantly different in pairwise comparisons at $P<0.05$ (Tukey HSD test).

Table 3. Effect of density (*D*), fruit type (*F*) and time of measurement (*T*) tested by repeated measure ANOVA on particular biometric parameters

	d.f.	Basal diameter			Plant height			Number of branches			Branches length			Leaf length			Leaf width		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Density	1	2.09	28.31	***	2162.09	2.88	NS	840.67	24.50	***	138,101.10	10.80	**	102.14	19.61	***	101.20	18.31	***
Fruit type	2	0.84	11.39	***	14,913.19	19.87	***	278.49	8.11	***	50,223.21	3.93	*	121.23	23.28	***	94.88	17.17	***
Time	2	1.49	82.82	***	117,347.2	268.60	***	844.44	44.20	***	131,509.90	13.06	***	208.74	107.60	***	365.05	194.60	***
$D\times F$	2	0.06	0.79	NS	684.73	0.91	NS	56.62	1.65	NS	38,212.04	2.99	NS	0.10	0.19	NS	1.22	0.22	NS
$D\times T$	2	0.45	24.80	***	4172.659	9.55	***	392.17	20.53	***	110,325.00	10.95	***	19.38	9.99	***	19.20	10.24	***
$F\times T$	4	0.01	0.60	NS	3248.96	7.44	***	144.09	7.54	***	39,698.34	3.94	**	1.70	0.88	NS	1.82	0.97	NS
$D\times F\times T$	4	0.02	0.96	NS	89.47	0.20	NS	18.22	0.95	NS	29,177.51	2.90	*	2.67	1.38	NS	4.05	2.16	NS

*$P<0.05$; **$P<0.01$; ***$P<0.001$; NS = non significant.

plants in a plot) was found at the end of experiment (Time 3) (one-way ANOVA, d.f. = 3, MS = 18.27, $F = 26.75$, $P<10^{-6}$). Mean final mass was also significantly affected by the type of fruit from which they originated (two-way ANOVA, d.f. = 2, MS = 1482.19, $F = 11.73$, $P<10^{-6}$), density (d.f. = 1, MS = 3262.70, $F = 25.82$, $P<10^{-6}$) and the interaction of fruit type and density (d.f. = 2, MS = 461.18, $F = 3.65$, $P<0.05$). Plants growing at low densities were heavier, and the mass increased from those grown from the type A to B to C (Table 4).

Mortality of populations derived from various fruit types

Mortality differed with respect to the fruit type, and the differences were highly significant (Kruskal–Wallis test, $H = 33.66$, $P<10^{-5}$, $n = 40$) (Fig 2). Significant reduction in density was found in populations of all three fruit types (Fig. 2). It was significantly lower in plants derived from types A (50.29 ± 2.01% of the initial density) and B (54.64 ± 3.62%) than from C (68.53 ± 2.25%) (see also Fig. 2).

Table 4. Mean total mass (g) of *Atriplex sagittata* plants recorded at the end of experiment (Time 3) for plants grow under different density (low, high) and derived from different fruit types (A, B, C)

Plant density	Fruit type	Total mass
Low	A	5.39 ± 1.80ab
	B	13.73 ± 4.69bc
	C	27.02 ± 9.48c
High	A	1.11 ± 0.25a
	B	1.83 ± 0.49a
	C	7.06 ± 2.08ab

Mean ± S.E. ($n = 10$) are shown; those followed by the same letters column-wise were not significantly different in pairwise comparisons at $P < 0.05$ (Tukey HSD test).

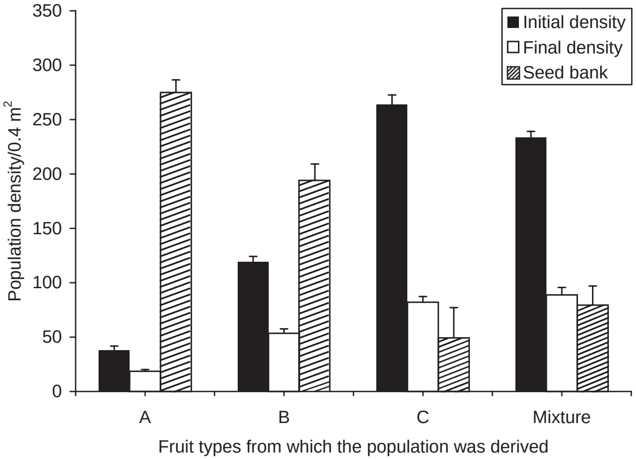

Fig. 2. Initial seedlings density and final plant density of *Atriplex sagittata* populations derived from different types of fruit (means from 10 plots, S.E. indicated). Seed bank is the number of seeds introduced into the soil at the beginning of the experiment replenished by those that germinated. Initial and final densities significantly differed for all types of fruit (Kruskal–Wallis ANOVA, $n = 10$, for type A fruit $H = 11.89$, $P < 0.001$; for type B fruit $H = 14.32$, $P < 0.001$; for type C fruit $H = 14.31$, $P < 0.001$) and for fruit mixture ($H = 14.33$, $P < 0.001$).

Fruit mass and fecundity

The origin of maternal plants (i.e. from which fruit type they originated) and the type of fruit they produced had a significant effect on the mass of fruits, bracteoles and dispersal units (Table 5). Mean mass increased from type A to B to C fruit (Fig. 3). We also found significant differences among plants originating from different fruit types; the fruits produced on plants grown from type C fruits were the heaviest (Fig. 3).

Total mass of fruits (i.e. A + B + C) produced by plants derived from different fruit types was not significantly different, if the stem mass was used as a covariate (ANCOVA, d.f. = 2, MS = 0.09, $F = 1.98$, $P = 0.16$; ANOVA for covariate was highly significant: d.f. = 1, MS = 3.49, $F = 76.38$, $P < 10^{-6}$). Comparison of REs yielded the same results (ANCOVA, d.f. = 2, MS = 41,175.82, $F = 2.83$, $P = 0.07$). In order to find whether the total fruit production was determined by plant size, expressed as stem mass in ANCOVA, we ran the analysis without the covariate. If the effect of total fruit production was significant in the re-analysis, the main factor influencing fruit production would be the plant size. The re-analysis revealed significant differences in fruit production with respect to the plant origin (one-way ANOVA, d.f. = 2, MS = 1.35, $F = 7.80$, $P = 0.002$). Hence, plants derived from different fruit types have different sizes and consequently also fecundity, which was probably evoked by different fruit sizes in the start of season.

Maternal effect

Seeds produced by plants grown from different fruit types were tested for germination in order to determine possible maternal effect. Significant differences in final germination percentages were found but they were not related to the origin of plants (Table 6). In general, seeds from type C fruit reached high germination percentages regardless of origin. However, there was a remarkable trend of types A and B fruit to germinate to lower

Table 5. Summary of ANCOVAs showing the effect of maternal plant (*M*), fruit type (*F*) and their interaction ($M \times F$) on total mass of fruits, bracteoles and dispersal units of *Atriplex sagittata* in the density treatments

	Fruit mass				Bracteole mass				Dispersal unit mass			
	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
Maternal plant	2	11.58	13.87	***	2	3.71	32.36	***	2	24.69	23.41	***
Fruit type	2	115.93	138.83	***	1	12.48	108.84	***	2	276.05	261.82	***
$M \times F$	4	1.50	1.79	NS	2	0.16	1.43	NS	4	2.91	2.76	*

Total mass of each pot was used as a covariate. *$P < 0.05$; ***$P < 0.001$; NS = non significant.

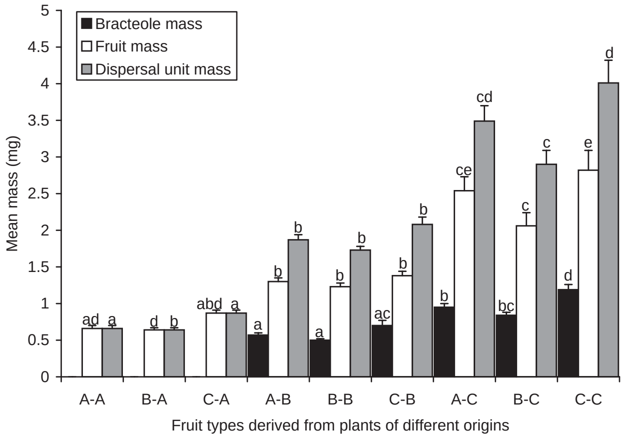

Fig. 3. Mean mass of fruits, bracteoles and dispersal units of *Atriplex sagittata* plants grown from different fruit types. The first letter in the code is the fruit type from which the maternal plant was grown, the second the fruit type it produced. Bars represent mean ± S.E. ($n = 10$); those bearing the same letter did not differ significantly in particular fruit characteristics (Tukey HSD test, $P < 0.05$).

Table 6. Summary of two-way ANOVA showing the effect of maternal plant (M) and fruit type (F) and their interaction ($M \times F$) on final germination percentage of seeds of *Atriplex sagittata*

	d.f.	MS	*F*	*P*
Maternal plant	2	0.03	2.93	NS
Fruit type	2	5.32	525.37	***
$M \times F$	4	0.04	3.82	*

*$P < 0.05$; ***$P < 0.001$; NS = non significant.

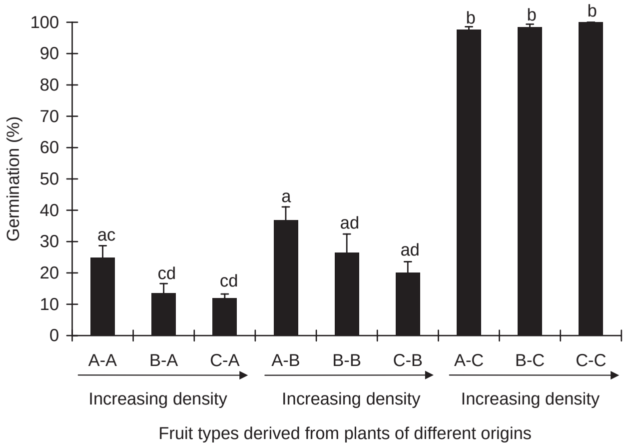

Fig. 4. Final germination percentages of particular fruit types produced by maternal plants of *Atriplex sagittata* derived from different types of fruit. Means ± S.E. are displayed ($n = 5$). Bars bearing the same letter were not significantly different in multiple range comparisons (Tukey's test, $P < 0.05$). In the two-letter coding of treatments, the first letter indicates fruit type from which the maternal plant grew, and the second letter the type of fruit it produced.

percentages if maternal plants grew under high density, i.e. in plants resulting from type C fruit (Fig. 4).

Discussion

Differences in germination are manifested in later life history stages

Pronounced heterocarpy of *A. sagittata* and its ecological meaning was studied in detail. In laboratory conditions, seed germinability increased from type A to B to C fruit, i.e. from small to large seeds (Mandák and Pyšek, 2001a). Similar results were reported for other *Atriplex* species (Khan and Ungar, 1984; Mandák, 2003). The present study confirmed this pattern under the conditions of a common garden. However, the early germination of type C fruit was higher when it was mixed with the other two types than in populations grown from the type C fruit alone. Murray (1998) found that leachates from seeds may inhibit germination under high seed densities and demonstrated the ability of seeds to predict environmental conditions of the habitat into which they will emerge, such as the potential competitive interactions from neighbouring seedlings. In some species, physiological differences may be involved; seeds of *Xanthium pensylvanicum* differ in production of ethylene (Katoh, and Esashi, 1975; Gorecki et al., 1991), which is considered to be a germination accelerator or dormancy-breaking compound (Saini et al., 1986; Taylorson, 1979). This would imply that in natural conditions, when particular types of *A. sagittata* fruits occur together, seed germination of the non-dormant C type might be accelerated by the presence of other fruit types which, to a large extent, do not germinate. Ecological meaning of this phenomenon could be in extending the germination period (some seeds germinate earlier than if they were alone) without increasing the interspecific competition (seedlings produced by the other two types do not compete because they germinate later and are weak competitors). Such a mechanism would ensure that part of the progeny is placed in most favourable conditions in the right time, while the rest is stored for the future (cf. Brändel, 2004).

The observed shift in the start of germination was further pronounced in the seedling stage and maintained until the end of the growing period. The difference in germination pattern of different fruit types has two important consequences:

(1) Delay in germination of seeds produced by type A and B fruits is reflected by differences in seedling size. Plant size is an important determinant of competitive ability (Gaudet and Keddy, 1988; Grace et al., 1992; but see Gerry and Wilson, 1995), so under natural conditions the late germinating

seedlings are exposed to a strong asymmetric competition from bigger seedlings derived from type C fruit. In mixed populations with a high seedling density and intense below- and above-ground competition, the contribution of seedlings derived from types A and B fruit is probably very low. In our opinion, this situation may change when the population is repeatedly destroyed over several generations and type C fruits with type II transient seed bank (Mandák and Pyšek, 2001b) are no longer present in the soil. In such a situation, dormant A and B fruits extend the germination period and may act as a source of the population regeneration. These results correspond to those of a previous study (Mandák and Pyšek, 2001b), where types A and B fruits occurred mainly in a seed bank, while the seed bank of type C fruit was replenished during spring and early summer.

(2) There was a very low density of individuals derived from types A and B fruit; a previous study showed that these two types germinate to lower percentages than type C (Mandák and Pyšek, 2001b). Surprisingly, the low density was not associated with faster growth of individual plants. Hence, competition was less intense than in populations derived from type C fruit (Fig. 2), and the mortality was markedly reduced. It can be assumed that the composition of populations (i.e. relative contribution of its members derived from particular fruit types) varies as a result of the number and frequency of strong disturbances which open the space for plants derived from A and B fruit types. These may appear if (i) mature plants are systematically removed from the community by disturbances, e.g. by building activity. The source of C type fruits is then eliminated so that they rapidly disappear from the seed bank. (ii) Occasionally, single *A. sagittata* plants may appear in older stages of succession, without a seed source in close vicinity (personal observation). Such plants are probably derived from dormant seeds which persisted in the soil long after the early successional stages retreated, and their development was made possible by opening of free space in relatively closed vegetation cover (Mandák and Holmanová, 2004).

The survival of individual plants in populations derived from different fruit types under natural conditions also depends on intraspecific competition. In this respect, the very slow increase in size observed in seedlings derived from A and B fruits may be a crucial disadvantage and these plants can probably complete the life cycle only under low levels of intraspecific competition.

Plants grown from different fruit types significantly differed in size and fruit production regardless of population density. Fecundity is probably always lower in populations evolved from dormant fruit types (A or B). However, low numbers of highly germinable seeds of type C fruit are probably enough to establish a new population. The rapid spread of *A. sagittata,* mainly in human-made habitats (Mandák and Pyšek, 1998) characterized by high levels of disturbance, may be taken as an indirect evidence of this phenomenon.

Maternal effect

Roach and Wulff (1987) predicted that the variation in seed, seedling, and adult traits caused by maternal effects could have important consequences for the ecology of an individual. Results of many ecological studies can be biased by the maternal effects due to our inability to separate it from direct environmental factors. Mandák and Pyšek (1999a) found that particular fruit types produced by *A. sagittata* responded to the conditions under which the maternal plants grew in a different way. Whereas type C fruit was not affected by the treatments imposed on the maternal plant, the germination of types A and B changed remarkably. The present experiment showed that the germinability of seeds from A and B fruits did not differ under different population densities. Nevertheless, a trend to produce better germinating seeds was recorded in plants grown under low population density, i.e. A and B (Fig. 4). A maternal effect might possibly decrease the germinable fraction of dormant seeds in plants derived from type C fruit and increase the germinable fraction in case of plants derived from types A and B fruits. We did not test the influence of nutrients as in the previous experiment (Mandák and Pyšek, 2001a) but it seems that the effect of maternal environment could be stronger under different nutrient regimes. For example, the nutrient content of seeds can be influenced by the soil nutrient level in which the mother plant is growing (Parrish and Bazzaz, 1985).

Ellison (1987) found, in an experiment with the heterocarpic species *Atriplex triangularis*, that differences in seed size primarily affected plant germination, and through the effect of seed size on germination, they may have affected plant mass and mortality. Hence through the interaction with germination date, seed size affected plant performance throughout the whole life of the plants. Differences between plants resulting from different fruit types have been rarely studied, but the results are consistent. The bigger seeds always produced bigger plants with greater reproductive outputs (Cheplick and Quinn, 1982; Ellison, 1987; Imbert et al., 1996; Venable, 1985b; Weiss, 1980). Comparison of different size classes of homocarpic species yields similar results, i.e. larger seeds tend to produce larger and more vigorous seedlings (Reader, 1993; Jurado and Westoby, 1992).

Conclusions

In unpredictably fluctuating environments, fractional seed release or germination is effective in reducing the risk of offspring mortality and variation in reproductive success. *A. sagittata* evolved in a desert environment (Aellen, 1960) and the bet-hedging strategy has been well studied in desert plants (Philippi and Seger, 1989; Philippi, 1993a, b; Venable and Levin, 1985b). By using the evolutionarily stable strategy (ESS) approach in a model for the evolution of seed size, Geritz (1995, 1998) showed that the single seed size is never evolutionarily stable. Variation in seed size within individual plants can be expected to increase in evolution if an environment is spatially or temporally unpredictable and there is a trade-off in the predator's attack rate for different seed sizes. Plant species capable of producing different seed types are extreme examples of variation in seed size since size is a parameter in which the particular types typically differ. Although many models predict how seeds of particular size classes would differ in their germination behaviour or dispersal, sufficient attention has not been paid to heterocarpy. However, as demonstrated in this study, this phenomenon can have even stronger effect on plant life, manifested throughout the entire life cycle and have an important impact on population regeneration in successive years.

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