

Fruit dispersal and seed banks in *Atriplex sagittata*: the role of heterocarpy

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Summary

1 *Atriplex sagittata*, an early successional, annual species of disturbed habitats in Central Europe, produces three types of fruits. We studied the differences in dispersal between the fruit types in order to investigate their ecological roles.

2 The typical positive relationship between dispersal ability and germinability is not found in this species. Type A (ebracteate) fruits produced deeply dormant seeds and had the lowest dispersal potential, but of the two fruits with bracts, type B, with dormant seeds, was better dispersed by both water and wind than type C, which produces non-dormant seeds.

3 Wind, temperature and precipitation have significant effects on fruit release but their effects differ between fruit types. The release of fruit types with bracts was positively correlated with wind whereas all fruit types tended to be negatively correlated with precipitation and temperature range.

4 Type C fruit, which contains non-dormant seed, are absent from the soil in summer and have a Type II transient seed bank. Type A and B fruits, containing dormant seeds, form a persistent seed bank.

5 Heterocarpy, where fruit types show distinct ecological behaviour, enables colonizing species such as *A. sagittata* to survive both major disturbance (by ensuring that some seeds persist) and unfavourable conditions (by spreading germination over a long period).

6 In *A. sagittata*, seed dynamics can be explained by the germination behaviour of seeds produced by the three types of fruit. All fruit types mature in autumn, but few of Type A fall from the mother plant until spring, when germination is probably inhibited because of insufficient stratification. Type C fruit, however, show peak dispersal in winter and the majority of these non-dormant seeds are able to germinate as soon as conditions become more suitable.

Key-words: *Atriplex sagittata*, Chenopodiaceae, morphology, seed bank, seed rain, terminal velocity

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Introduction

Atriplex sagittata (Chenopodiaceae) belongs to a family that contains many halophytes and species adapted to other rather specialized habitats such as deserts and semi-deserts or are confined to human-made sites (McArthur & Sanderson 1984). Under such stressful conditions, the varying dispersal distances and levels of dormancy associated with heterocarpy may enhance the probability of germination and/or seedling survival (Venable & Lawlor 1980; Ungar 1987). Reproductive allocation into different fruit morphs may also confer a selective advantage on this species (Harper *et al.* 1970; Venable 1985; Mandák & Pyšek 1999a).

Many studies of the ecological role of particular diaspore types concern the family Asteraceae (Mandák 1997). However, almost all annual species of *Atriplex* also show heterocarpy (Osmond *et al.* 1980; Mandák 1997), which like the presence of bladder hairs (Freitas & Breckle 1994) and/or the use of the C₄ photosynthetic pathway (Osmond *et al.* 1980) may enable them to grow in stressed, disturbed and unpredictable environments (McArthur & Sanderson 1984).

Particular types of diaspores differ in their dispersal ability (Sorenson 1978; Payne & Maun 1981; Baker & O'Dowd 1982). Easily dispersed diaspores usually germinate better and are less dormant, although the chances of seedling survival are low, while those with lower dispersal ability are often dormant but produce seedlings with increased chances of survival (Venable & Levin 1985a; Venable *et al.* 1995; Mandák 1997). Fruits

of the former (colonizer) type enable range expansion and facilitate gene flow while the latter maintain populations in environments of proven suitability (Koller & Roth 1964).

Detailed information on the pattern of seed rain is again mainly available for members of the Asteraceae (e.g. Sorenson 1978; Baker & O'Dowd 1982), although the light papery bracteoles or fruit wings of many *Atriplex* species may be involved in the wind dispersal of its seed (Osmond *et al.* 1980).

Fruit heteromorphism affects both within- and between-year dynamics of seed banks (Philippou & Ungar 1984; Venable & Levin 1985a,b; Wertis & Ungar 1986; Venable *et al.* 1987, 1995). For instance, the between-year seed banks of *A. triangularis*, differ between the large brown (easily germinable) and small black (less germinable) forms of its seeds (Wertis & Ungar 1986) (transient Type II and persistent Type IV, respectively, of the Thompson & Grime (1979) seed bank classification).

Seeds of other species, e.g. *Heterosperma pinnatum* (Asteraceae), do not over winter and, although overall ability to germinate may not differ between peripheral and central achenes, within-year timing of germination may be very important (Venable *et al.* 1995).

We investigated whether there are differences in overall seed dispersal ability, the rate and pattern of seed release and the role in seed bank dynamics of the three types of fruit produced by *A. sagittata*.

STUDY SPECIES

Atriplex sagittata Borkh. (Chenopodiaceae) is an annual characteristic of disturbed habitats which produces fruits that differ in germinability and which are either (i) small and black, lack bracteoles and contain dormant seeds (Type A fruits), (ii) medium sized and black, covered by small bracteoles and contain dormant seeds (Type B fruits), or (iii) have large bracteoles covering large, brown, non-dormant seeds (Type C fruits) (Mandák & Pyšek 2001). Seeds are not released or otherwise separated from the fruit, but 'seed rain' and 'seed bank' are used to refer to what is strictly speaking the complete achene. *Atriplex sagittata* produces 80–85%, 12–15% and 2–4% of types C, B and A fruit, respectively, depending on growth conditions (Mandák & Pyšek 1999b). In Central Europe, the species is an invasive alien of eastern European and Asian origin (Mandák & Pyšek 2001).

Methods

DISPERSAL POTENTIAL

Dispersal by water was analysed using primary data on the floatation of *A. sagittata* fruits (Kopecký & Lhotská 1990).

Terminal velocity was used as a measure of air dispersal assuming that the slower the rate of fall the greater the dispersal potential. Ten fruits of each type were weighed and the width and length of their bracteoles

(in types B and C fruit) was measured before release from a height of 120 cm in a dead air space in the laboratory. We assumed that fruits reached terminal velocity very quickly (Sheldon & Burrows 1973) and fall time was thus inversely related to terminal velocity (cm s^{-1}).

Correlation between terminal velocity and fruit weight, bracteole weight, dispersal unit weight and bracteole area were investigated. Regression equations were used to determine bracteole area for type B and C fruits (Area = $0.011 + 0.713 (\text{Width} \times \text{Length})$, $F_{1,48} = 135.5$, $R^2 = 96.6$, $P < 0.0001$ and Area = $0.009 + 0.713 (\text{Width} \times \text{Length})$, $F_{1,48} = 2918.7$, $R^2 = 98.4$, $P < 0.0001$, respectively).

FRUIT RELEASE FROM MOTHER PLANT

Ten plants were grown from seed and spaced at a distance of 5 m apart. As soon as any fruits had developed fully, each plant was surrounded by a wooden frame whose sides were covered with soft net to prevent loss of released fruits while not substantially affecting wind velocity.

The experiment was carried out in the experimental garden at Kostelec nad Černými lesy, Central Bohemia, Czech Republic (Latitude 50°00' N, Longitude 14°30' E). Fruits released onto a sheet of plastic placed on the soil surface within each frame were collected each week between 10 October 1995 and 24 June 1996 and sorted according to fruit type and counted.

The nearest meteorological Station (Praha-Libeň) provided data on the daily amount of precipitation, maximum daily wind velocity and maximum and minimum day and night temperatures. Maximum wind velocity, average wind velocity, maximum precipitation, range of temperatures, and sum of precipitation was calculated for the period between each pair of collection dates for correlation with fruit release data.

SEED BANK

Seed bank dynamics were studied in the field in Praha, Czech Republic (50°05' N, 14.27' E), on a large area of waste land which had been abandoned after construction work. Two parallel transects, each 60 m long, and 10 m apart, were established across a dense natural population of *A. sagittata*. Permanent plots 1 × 1 m ($n = 60$) were established along each transect at 2 m intervals.

Soil samples were taken monthly using a cork borer 2 cm in diameter to obtain soil from a depth of 0–10 cm at a random location in each plot. The samples were sieved under running water and fruits were extracted and divided according to type before being counted. It was not possible to distinguish between types A and B in soil samples since small bracteoles of type B had often been lost. Seed viability was not determined.

STATISTICAL ANALYSIS

To test for differences in the pattern of seed rain between fruit types, we analysed the effect of environmental

factors on fruit release by survival analysis, using a comparison of multiple samples (as for germination data in Mandák & Pyšek 2001) and proportional hazard (Cox) regression procedures. The proportional hazard model is the most general of the regression models because it is not based on any assumptions concerning the nature or shape of the underlying survival distribution. The model assumes only that the underlying hazard rate (rather than survival time) is a function of the independent variables (covariates). Thus, in a sense, Cox's regression model may be considered to be a non-parametric method (Cox 1972). The same statistical method was used for analysing the data on dispersal by wind and water.

Standard statistical methods were used in other analyses (Sokal & Rohlf 1981).

Results

POTENTIAL FOR FRUIT DISPERSAL

Survival analysis (comparing multiple samples; data from Kopecký & Lhotská 1990) showed highly significant differences in the floating ability of fruit types ($\chi^2 = 761.8$, d.f. = 2, $P < 10^{-5}$). Each fruit type was significantly different from both the others ($Z = -15.2$, d.f. = 1, $P < 10^{-5}$). Fruits without bracts (type A) sank immediately (personal observation; Kopecký & Lhotská (1990) did not record until after 1 hour), type B started to sink after 8 h and almost all the fruits had sunk within 48 h, whereas type C started to sink after 2 hours and all the fruits had sunk within 24 h (Fig. 1).

Terminal velocity differed between fruit types (Kruskal–Wallis ANOVA, $\chi^2 = 17.946$, d.f. = 2, $P < 0.001$). Potential for dispersal by both wind and water was $B > C > A$ (terminal velocities 111.74 ± 7.20 , 123.21 ± 5.65 and 164.28 ± 7.20 cm s⁻¹, respectively). Analysis of pooled data showed a close correlation between terminal velocity of fruits and their various morphological characters (Table 1). Stepwise multiple regression, which was used because predictors were intercorrelated, indicated that the ratio of dispersal unit area to fruit weight explained most variation (89.8%, $F_{5,24} = 42.231$, $P < 10^{-5}$).

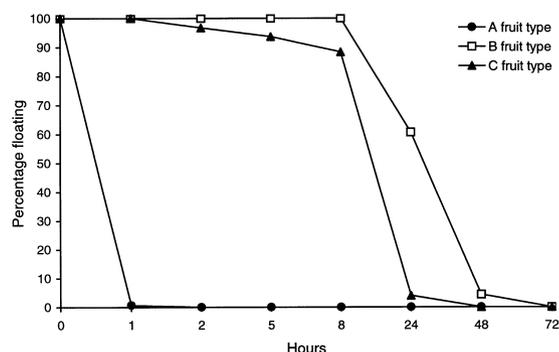


Fig. 1 Buoyancy patterns for particular fruit types of *Atriplex sagittata*, based on data from Kopecký & Lhotská (1990).

Table 1 Relationship between terminal velocity and morphological characteristics of *Atriplex sagittata* fruits. The value of the Spearman correlation coefficient is shown. Pooled data were analysed ($n = 30$). See Methods for information on calculation of bracteole area. Dispersal unit refers to fruit plus bracteoles

Morphological characteristic	Spearman R	P level
Dispersal unit weight	-0.50	0.005
Bracteole area	-0.53	0.003
Bracteole weight per fruit weight	-0.74	0.00001
Bracteole area per fruit weight	-0.82	0.00001
Bracteole area per dispersal unit weight	-0.84	0.00001

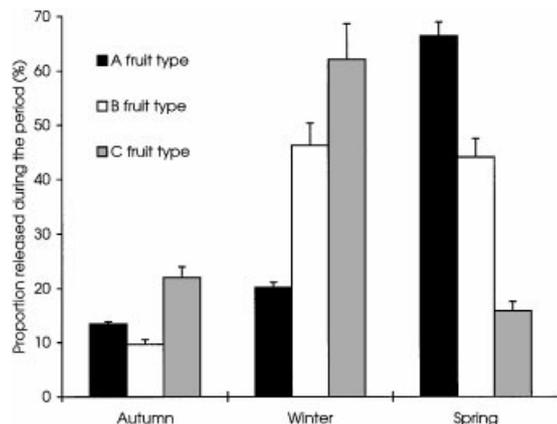


Fig. 2 Seasonal release of fruits from mother plants of *Atriplex sagittata* as a proportion of the total number of fruits. Standard deviations are shown, $n = 10$. Autumn: 23 September to 20 December; Winter: 21 December to 20 March; Spring: 21 March to the end of release.

FRUIT RELEASE FROM THE MOTHER PLANT

The pattern of fruit release from the mother plant differed between fruit types. Few fruits were released in the autumn. Type A was dispersed mainly in spring and type C in winter, whereas type B fruit were released in both these season (Fig. 2). The pattern of fruit release over time differed conspicuously between particular types (Fig. 3, $\chi^2 = 8440.2$, d.f. = 4, $P < 10^{-6}$).

In all fruit types, release from mother plant was strongly affected by weather. Survival analysis (proportional hazard (Cox) regression), testing the effect of climatic factors, was highly significant for all types ($\chi^2 = 13124.3$, 11391.1 and 24782.6 for A, B and C, respectively; d.f. = 6, $P < 0.0001$ in all cases). At least one measure of each aspect (temperature, wind and rainfall) had a significant effect for each fruit type, but the effect of particular factors differed between types. Only bracteate fruit types B and C were released more at greater maximum wind velocity and only type C with decreased maximum precipitation. Both the sum of precipitation and range of temperatures showed negative correlation with release of all types (Table 2).

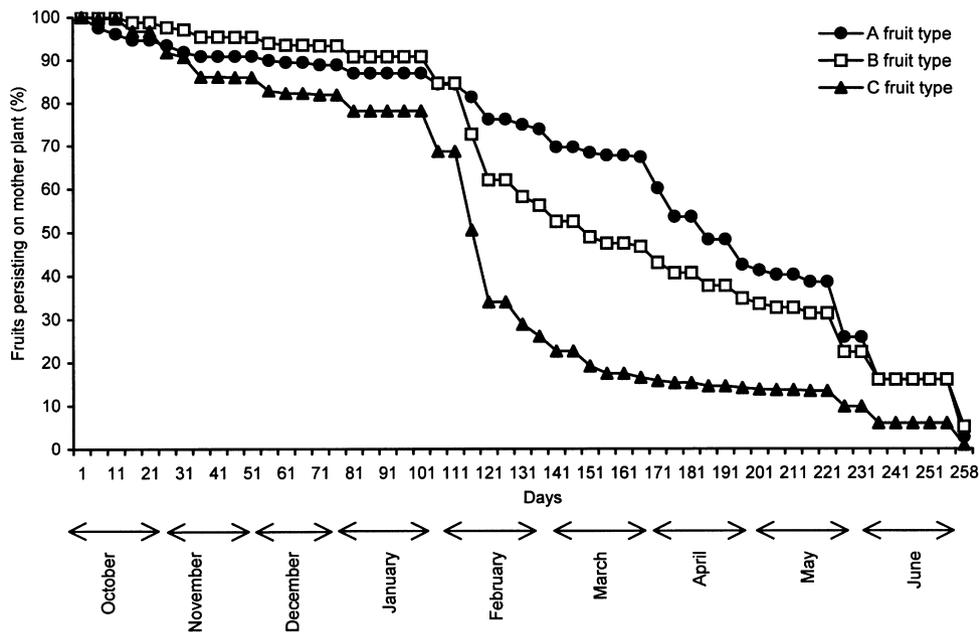


Fig. 3 Pattern of fruit release from the mother plant for particular fruit types of *Atriplex sagittata*. Days from the beginning of the experiment are displayed on x-axis.

Table 2 Effect of climatic variables on *Atriplex sagittata* fruit release from the mother plant over time. Results of survival analysis (proportional hazard (Cox) regression) are shown. Climatic variables used for the correlations covered the period over which fruits had been released, i.e. between the collection concerned and the immediately preceding one. In the analysis, fruits persisting on the plant were taken as survivors. ****P* < 0.001; NS, non-significant

Fruit type	Climatic parameters	Beta	S.E.	<i>P</i>
A	Maximum wind velocity	-0.02	0.02	NS
	Average wind velocity	0.24	0.02	***
	Range of temperatures	-0.36	0.01	***
	Maximum precipitation	-0.01	0.01	NS
	Sum of precipitation	-0.06	0.01	***
B	Maximum wind velocity	-0.08	0.01	***
	Average wind velocity	0.36	0.01	***
	Range of temperatures	-0.37	0.01	***
	Maximum precipitation	0.01	0.01	NS
	Sum of precipitation	-0.05	0.01	***
C	Maximum wind velocity	0.21	0.01	***
	Average wind velocity	0.09	0.01	***
	Range of temperatures	-0.59	0.01	***
	Maximum precipitation	-0.05	0.01	***
	Sum of precipitation	-0.03	0.01	***

SEED BANK

The total number of fruits in the soil was highest in February falling gradually to a minimum by May and not increasing again until the beginning of September (Table 3) when new fruits began to be released. However, as the total number of fruits decreased, the ratio of dormant (A + B) : non-dormant (C) types increased from 1.5 to 6.2 in May (Table 3). All seeds of type C fruits germinated or were otherwise lost from the seed bank between February and May, whereas a

Table 3 Seasonal dynamics of the soil seed bank in *Atriplex sagittata*. Mean number of fruits in the soil (m⁻²) and the ratio of dormant fruits (types A and B) to non-dormant fruits (type C) are shown for particular months

Month	Fruit type A + B	Fruit type C	Total size of the seed bank A + B + C	Ratio A + B/C
February	37 379	24 522	61 901	1.5
March	17 903	5 190	23 093	3.4
April	15 761	2 285	18 046	6.9
May	3 856	619	4 475	6.2
June	4 523	0	4 523	-
August	4 571	0	4 571	-
September	7 142	428	7 570	16.7
October	13 761	7 809	21 570	1.8
November	17 427	8 571	25 998	2.0
December	20 094	12 904	32 998	1.6
Total	142 421	62 330	204 751	

reduced number of presumably dormant type A and B fruits remained in the seed bank throughout the summer.

Discussion

DISPERSAL ABILITY

Fruit heterocarpy in *Atriplex* is reflected in differences in dispersability, ability to germinate, depth of dormancy and/or viability of seeds, all of which can be of adaptive significance. Whilst seed dormancy enables survival in an environment which changes unpredictably over time, patterns of fruit dispersal may be an adaptation to unpredictability in space (Venable & Brown 1988). Heterocarpic fruits often show differential dispersal

(Sorenson 1978; Payne & Maun 1981; Baker & O'Dowd 1982; Venable & Levin 1985a). The possession of two dispersal strategies represents a form of bet-hedging (Venable 1985). Fruit dispersal by water is well documented for plants, e.g. *Cakile edentula* var. *lacustris* (Brassicaceae), of coastal or lake shores. This Canadian species produces a silique consisting of upper and lower segments (i.e. heteroarthrocarpy) of which the former may disperse over long distances, while the latter remains on the parent plant in the proven habitat (Payne & Maun 1981). *Atriplex sagittata* is a typical inland species, but dispersal by water aided by bracteoles is important throughout its range (Iljin 1936; Brandes 1982).

Both weight and bracteole : fruit weight ratio differ between fruit types but the high ratios (2.4 for type B vs. 3.2 for type C) in this species inhabiting disturbed sites is consistent with the tendency for values in *Atriplex* to increase from perennial species of arid shrublands to annual ruderal species (Osmond *et al.* 1980).

Unlike other heterocarpic species, where fruit dispersal ability is positively associated with the ability to germinate (Baker & O'Dowd 1982; Venable *et al.* 1995), non-dormant (type C) fruits of *A. sagittata* are dispersed less well by either wind or water than dormant type B fruits. Type A fruits which lack any structures facilitating dispersal conform to expectation and are deeply dormant. The best dispersers are fruits of the third type (B), which are found in only three *Atriplex* species of the section *Dichosperma* (Aellen 1960).

SEED RAIN

Fruits are dispersed over time as well as space (Harper 1977). In *A. sagittata*, fruit types differed strongly in their time of release from the mother plant (Fig. 3) but these patterns are affected by climatic variables. Factors such as wind velocity may determine the rate at which fruits that are ready to abscise are removed from the plant. Type C fruits show peak dispersal in winter and the majority are therefore already in the soil and able to germinate as soon as conditions become suitable in the spring. Type A fruits, however, are not dispersed until the spring and lack of stratification prevents germination until the following season.

Plants growing in highly unpredictable environments can either release fruits over a long period or concentrate dispersal into shorter periods with more favourable conditions. Heterocarpic and amphicarpic species can produce seeds adopting both strategies (Koller & Roth 1964; Wertis & Ungar 1986; Khan & Ungar 1986; Venable *et al.* 1995), with linked patterns of dispersal and germinability.

As in other heterocarpic *Atriplex* (Khan & Ungar 1986), the germination period is extended by the gradual release of fruits as well as by different levels of dispersability, germinability and dormancy. Two-thirds of type A fruits remain attached until spring, while the majority of types B and C are shed. Such patterns probably maximize the chance of survival by ensuring the presence of

appropriate fruit types in the soil when conditions for germination are favourable.

The salt tolerant species *A. triangularis* produces small, medium and large fruits. Immediate dispersal ranged from 50% of the small fruits to 85% of the large fruits being shed from the plants (Khan & Ungar 1986). This pattern, whereby those fruits that germinated best, but had the lowest capacity for survival, were shed first (large fruits in *A. triangularis*, Khan & Ungar 1986; Wertis & Ungar 1986), is similar to our results for *A. sagittata*.

SEED BANK

The large seed bank (up to 62 000 *A. sagittata* fruits m⁻²) is typical of disturbed habitats (Kropáč 1966). This is the result of high fecundity, which is typical of plants on disturbed sites (Harper 1977), and increases the chance of survival in an unpredictable environment. Without within- or between-year seed banks, whole populations would risk extinction under unfavourable conditions. Heterocarpic species can reduce further the effects of unpredictability by employing a number of contrasting strategies that are not available to a species with a single fruit type.

Atriplex sagittata, like other Chenopodiaceae, e.g. *A. triangularis* (Wertis & Ungar 1986) and *Salicornia europaea* (Philipupillai & Ungar 1984) has two types of soil seed bank strategy according to the classification of Thompson & Grime (1979). Type C fruit is absent from the soil in the summer and forms a transient (Type II) seed bank whereas types A and B form a persistent seed bank. It is however difficult to decide whether these should be classed as Type III or IV, which are not always clearly distinct (Thompson *et al.* 1997). Seed loss may be due to fruit decay, predation or fungal decomposition as well as autumn germination, but a persistent seed bank will enable survival of strong disturbances (when only non-dormant seeds are present, the entire population may be in danger of extinction), or of generally unfavourable conditions (where it is advantageous to spread the germination period over a long time).

The loose correlation between the production of particular fruits and their occurrence in the soil seed bank can be explained by the rapid depletion of type C fruits due to germination and the gradual accumulation of dormant seeds from fruit types A and B (many of which will not germinate until the following spring). As a result, although *A. sagittata* produces mainly type C fruits (Mandák & Pyšek 1999a), the soil seed bank present when germination begin in spring contains disproportionately greater numbers of dormant than non-dormant seeds.

THE EVOLUTIONARY POSITION AND ROLE OF HETEROCARPY IN THE GENUS *ATRIPLEX*

The differences in ecological behaviour of particular fruit types of *A. sagittata* (Table 4) illustrate the role of heterocarpy in the life history of this species. The atypical relationship between dispersability and germinability

Table 4 Summary of the differences in behaviour of the three fruit types (A, B and C) of *Atriplex sagittata*. Based on data from the present study and of Mandák & Pyšek (2001). Type of seed bank according to Thompson & Grime (1979)

Fruit type A	Fruit type B	Fruit type C
Remains on the parent plant until next spring	Released at any period, with maximum in winter	Released in the winter
Undispersed	Very easily dispersed	Easily dispersed
Deeply dormant	Dormant	Non-dormant
Very low germination percentage	Germination percentage intermediate between A and C	High germination percentage
Very low germinability	Intermediate germinability	High germinability
Germinability increases remarkably with increasing age	Germinability increases with increasing age	Germinability decreases with age and ceases after 2 years
Persistent seed bank	Persistent seed bank	Transient seed bank
White light stimulated germination	White light stimulated germination	White light stimulated germination
Green light unaffected germination	Green light unaffected germination	Green light weakly stimulated germination
Dark reduced germination	Dark reduced germination	Dark reduced germination
Germination stimulated by low and reduced by high nitrate concentrations	Germination stimulated by low and reduced by high nitrate concentrations	Germination stimulated by low and reduced by high nitrate concentrations
Behaviour favours later germination and restricted dispersal with less survival risk	Intermediate behaviour between A and C	Behaviour favours earlier germination and greater dispersal with attendant survival risk

(Venable & Brown 1988) is probably associated with the unique evolutionary position of this species within the genus *Atriplex*. According to the characters listed by Stutz *et al.* (1990), *A. sagittata* belongs to a group of evolutionarily primitive oraches and, together with a desert species *A. aucheri* Moq., represents an archetype of Eurasian representatives of the genus. One of the main characters distinguishing this group from the others is the presence of presumably primitive ebracteate female flowers (which produce type A fruits). Annual representatives of *Atriplex* are typically autogamous and fruits with restricted possibilities of dispersal will form very dense seedling populations and, consequently, suffer intense sib-competition. Selection pressure will therefore favour the production of fruits that are both heterocarpic and, due to the development of bracts, dispersible. Fruits differing in the presence of small or large bracteoles may thus be an evolutionary response to the high mortality resultant from high density.

The remarkable success of *A. sagittata* in the current landscape of present Central Europe (Mandák & Pyšek 1998) may be associated not only with its high biomass production, dense canopy, high fecundity and salt tolerance, but also with the species' heterocarpy. Rapid regeneration of populations after strong disturbance and their subsequent spread depends on both the availability of newly created habitats and the presence of diaspores. *A. sagittata*, although an early successional species, persists for several years after the cessation of disturbance, during which time large amounts of dormant seed are accumulated in the soil.

Since the viability of these seeds does not seem to decrease over time, at least for several years, *A. sagittata* is

capable of responding rapidly to frequent disturbances operating on various temporal and spatial scales. The persistent seed bank also enables the species to colonize sites and regions which could otherwise be difficult to reach because natural dispersal by wind- and water-dispersed bracteate fruits is augmented by soil transport (due to building activities, reclamation procedures, etc.).

The success of *A. sagittata* in Central Europe may be due to its ability to exploit habitats where the temporal and spatial variability is similar to the salt steppe and riparian habitats of its native distribution (Iljin 1936; Meusel *et al.* 1965; Mandák & Pyšek 1998). No other heterocarpic *Atriplex* species produces a non-floating type of fruit. *A. sagittata* is often associated with water in at least one part of its native range and the presence of one type of fruit that does not float ensures that some seeds will remain close to the parent even during floods, while the buoyant seeds will be well dispersed. Variation in dispersal, dormancy and longevity of *A. sagittata* seed have also allowed it to become a successful early successional species outside its native range.

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