HISTORY OF THE SPREAD AND HABITAT PREFERENCES OF *ATRIPLEX SAGITTATA* (CHENOPODIACEAE) IN THE CZECH REPUBLIC

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Abstract

In the Czech Republic, an alien species *Atriplex sagittata* has been spreading rapidly recently. The paper analyses the rate of its spread and pattern of habitat preferences in the course of more than 150 years. The ancient distribution is inferred from archaeological records and compared with recent situation. The oldest record from the study area comes from the Bronze Age. The first recent report is dated 1810. *A. sagittata* is known from 64.6 % of the map squares of the European phytogeographical grid. An exponential regression fits the increase in the cumulative number of localities. The curve obtained can be divided into four parts corresponding to periods in which the number of localities increased abruptly. The most remarkable increase follows the Second World War, and can be explained by species autoecology and creation of suitable habitats. The species is closely confined to ruderal sites and habitats facilitating transport. It prefers warm and moderately warm climatic regions. The main determinants of success of *Atriplex sagittata* in Central Europe are probably a combination of (a) special adaptation mechanisms, such as heterocarpy and salt-tolerance which favour the species survival in disturbed habitats, and (b) increasing frequency of suitable habitats, related to frequent disturbances of the landscape and human-related transport activities. These habitats are similar, in terms of temporal and spatial variability, to those in which the species occurs in the native distribution area (i.e. salt steppe and riparian habitats).

Introduction

The *Chenopodiaceae* is known as a family containing many extremely specialized species, adapted to dry (deserts and semideserts) and saline (temperate salt marshes and sea shore) situations, often occupying habitats disturbed by human activities and/ or stressed (McArthur and Sanderson 1984). The occurrence in extreme ecological situations is made possible by a number of adaptive modifications such as the presence of different photosynthetic pathways, seed dormancy mechanisms, heterocarpy, xeromorphy, and leaf area reduction. The distribution of *Chenopodiaceae* is largely conditioned by another very important factor, their ability to grow in saline habitats (see e.g. Osmond *et al.* 1980; Flowers *et al.* 1986; Breckle 1995). The species of *Atriplex* are often facultative halophytes (Kelley *et al.* 1982). It is generally suggested that majority of halophytes are restricted to salt habitats because of their limited ability to compete with other species in other habitats (Kelley *et al.* 1982). *Atriplex* is a very heteromorphic genus, including various life forms.

Globally, the *Chenopodiaceae* is amongst the most invasive plant families. Possible

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clues to the success of the family could be high reproductive rate, long viability of seeds, salt tolerance, heterocarpy, and C4 photosynthetic pathway (Pyšek 1998).

Within the *Chenopodiaceae*, it seems useful to distinguish between two main ways of translocations, between-continents and within-continent. The former way is determined by the fact that semi-arid regions in Australia, Central Asia and North America dominated by endemic species have been used for sheep grazing. Consequently, in the last 100 years species were introduced, particularly into Europe, by to the wool trade. For example Probst (1949) reported 15 Australasian species of *Atriplex* in the "Wolladventiv" flora of Europe and a few South American and Central Asian species have found their way into Europe in the same way (Aellen 1960; Aellen and Akeroyd 1993). These species are usually classified as neophytes (i.e. introduced after 1500 A. D., see e.g. Holub and Jirásek 1967 and Pyšek 1995a for terminology); the Australian species *A. semilunaris* Aellen is an example in the Czech Republic. Relatively large number of *Atriplex* species, now in Central Europe, were involved in the within-continent movements. They are not native to this region and their introduction happened during the ancient colonization of Europe. These species are archeophytes, i.e. introduced before 1500: *A. oblongifolia*, *A. patula*, *A. rosea*, *A. sagittata* or *A. tatarica.* Others in the genus are, from the geographical point of view, native to the region; from their natural habitats, i.e. small-scale salt marshes, expanded into other habitats; *A. prostrata* subsp. *latifolia* is an example. These species probably occurred in warmer regions of the Czech Republic and now have expanded and increased their distribution due to the human activities creating suitable habitats beyond the limits of their native distribution. Hence, in case of this group of *Atriplex* species, the native distribution is sometimes rather obscure and very difficult to identify.

The present paper aims at describing the invasion history of an alien species *Atriplex sagittata* in the Czech Republic, demonstrating changes in habitat preferences in the course of the invasion process and characterizing the main community types in which it occurs. This alien species was chosen for the study because of the following reasons: (i) it is remarkably successful in the present landscape, (ii) it produces three different types of fruit which makes it very special not only among its congeners but among heterocarpic species in general, and this fact (iii) makes it possible to infer on the role of heterocarpy in the process of invasion.

Study species

Description and ecological characteristics

Atriplex sagittata Borkh. (syn. *A. acuminata* W. et K., *A. hortensis* L. subsp. *nitens* (Schkuhr) Pons, *A. nitens* Schkuhr, see Kirschner 1984 for notes on nomenclature) belongs to the section *Dichosperma* Dumort. of the *Chenopodiaceae*. This section contains three annual species each possessing three types of dimorphic achenes (Iljin 1936; Aellen 1960). The species of this section bear on the same plant female flowers subtended in bracts and ebracteolate flowers with perianth. The latter flowers are very similar to the perfect flowers of *Chenopodium* and most other chenopods (Stutz *et al.* 1990, 1993). Phylogenetically, these species seem to be an intermediate evolutionary link between types with perianth flowers and "true" *Atriplex* lacking perianth and having female flowers subtended in bracts extremely variable in shape and size (Osmond *et al.* 1980).

A more primitive species of this section is a Central Asiatic species *A. aucheri* which inhabits salt steppes, deserts and semideserts. Aellen (1960) considered *A. sagittata* a cultivated species which evolved from *A. aucheri* and then escaped from cultivation.

A. sagittata is an annual herb reaching the height of 1–2 m. The species is monoecious with non-Krantz anatomy, 2n = 18. Leaves are usually over 10 cm long, often irregularly and coarsely dentate. In the Czech Republic, flowering starts in July and seeds mature from the middle of October. Flowers in terminal or axillary spicate inflorescences are dimorphic and produce three types of fruits (Kirschner and Tomšovic 1990; Kopecký and Lhotská 1990): The first type (further termed A) originates from female or bisexual flowers and contains small, dormant, black lens-shaped seeds with glossy, smooth testa and 5-lobed perianth. The second type (B) is produced by female flowers and contains medium-size dormant seeds of similar appearance as the previous type; the seed is covered by extended bracteoles. Finally, the third type (C) is produced by female flowers, contains rather big, brown non-dormant seeds, that are covered by extended bracteoles (Mandák 1998).

The species of *Atriplex* have been often studied for salt tolerance (Black 1958; Moore *et al.* 1972; Osmond *et al.* 1980; Kelley *et al.* 1982; Schirmer and Breckle 1982; Freitas and Breckle 1993, 1994; Breckle 1995). Of the two principal groups reducing the salt concentration in the plant body, i.e. salt excluders and salt absorbers (Schirmer and Breckle 1982), all the species of genus may be classified as salt excluders. This happens through bladder hairs located on the leaf surface (Freitas and Breckle 1993, 1994; Breckle 1995). *A. sagittata* is common along roads, in habitats rich in salt (KCl and NaCl) due to the winter treatment of roads.

Distribution and dispersal

At present, *A. sagittata* is widely distributed from western Europe through central and southeastern Europe to Central Asia, Asia Minor and western Siberia; it is classified as an Irano-Turanian floristic element (Meusel *et al.* 1965; Hultén and Fries 1986). The westernmost localities are in western Germany on the border with Netherlands and in south-eastern France.

Jalas and Suominen (1987) published a map of the European distribution where they made an attempt to distinguish between native and adventive occurrence. However, what they consider as native distribution probably corresponds to the territory the species inhabited before 1492 (i.e. the discovery of America). In this area, the species should be considered as an archaeophyte. The western part of the European distribution is probably of a more recent origin and the species can be viewed as a neophyte there. The problem is, however, that the boundary between the archaeophytic and neophytic distribution follows perfectly the border between the former eastern block and the rest of Europe. Hence this border reflects rather different concepts of understanding the native vs. adventive status than the real situation. There is no doubt that the occurrence of *A. sagittata* in some areas is of very recent character but the map of Jalas and Suominens (1987) is over-generalized.

The native distribution area of the species covers Central Asia, Asia Minor and eastern Europe from where the species has spread across southeastern and eastern Europe to western Europe (see Meusel *et al.* 1956; Aellen 1960). A remarkable spread was recorded after The Second World War, especially on ruins and ruderal places of German cities (Gebhardt 1954; Schreier 1955; Fröde 1956; Korneck 1956; Ullman 1977; Brandes 1982).

Materials and methods

Present distribution and history of spread

The data on the distribution of *A. sagittata* in the the Czech Republic were taken from the following sources: (a) major Czech herbaria – BRNU, HR, MJ, MP, PB, PL, PR, PRC, ZMT, (b) floristic literature, (c) unpublished floristic data obtained from personal communication, (d) our own data from recent years. The information about habitat, altitude, and number of inhabitants was recorded for each locality. The distribution was mapped using a grid of approximately 12×11 km which is commonly used in phytogeographical mapping (Schönfelder and Bresinsky 1990). The probability of being occupied (i.e. the proportion of occupied squares) was calculated separately for squares in warm, moderate and cold regions. Classification of climatic districts was taken from Quitt (1971). The distinction between warm and cooler regions was the –5°C January isotherm.

Previous papers (Pyšek 1991; Pyšek and Prach 1993, 1995) demonstrated how floristic data, systematically gathered over an area for a long time, may be used to reconstruct the pattern of invasion of a species on a large geographical scale. There are, however, some limitations to the floristics data which should be emphasised. A sufficient intensity of floristic research within an area is necessary for a successful retrospective analysis of species spread. This is possible because of the strong, long-term floristic tradition in the Czech Republic. If systematic recording of the flora is carried out, one can assume that the more common a species is, the more often it is recorded. The species itself should be currently (1) worthy of note, i.e. rare enough or otherwise interesting from the point of view of ecology, spreading dynamics etc., (2) conspicuous in order not to be overlooked and (3) taxonomically unproblematic, i.e. easily recognisable by amateur botanists who are the main producers of floristic data (Pyšek 1991). These points may be considered reasonably fulfilled by *Atriplex sagittata.*

The spread of the species on an historical time scale was expressed by constructing a plot of the cumulative number of localities reported or squares occupied (i.e. the number reported/occupied up to the given year) against time (Trewick and Wade 1986; Pyšek 1991). An exponential regression model best fitted the data. The rate of invasion was expressed as the value of the slope *b* of the linear regression of the log-transformed cumulative number of localities on time: Log (CUMULATIVE NUMBER OF LOCALITIES) = a + b × YEAR. (see Pyšek 1991; Pyšek and Prach 1993, 1995 for details).

The curve describing the increase in the cumulative number of localities (or “invasion curve”) was divided into particular sections. The division was made in a year in which the dynamics of the invasion curve changes. Regressions were fitted to the particular sections and the best fit was found for the log-linear model in each part of the curve. Four distinct periods were found (Fig. 2), and analysed separately.

Although the calculations of the rate of spread were performed on log-transformed data, the figures of invasion curves are shown in the real scale (i.e. untransformed) throughout the paper as it provides a more realistic picture of the dynamics of spread.

Analysis of communities with Atriplex sagittata

In total, 97 phytosociological relevés of communities in which *A. sagittata* occurred were made. All vegetation types were sampled (i.e. including those with low representation of *A. sagittata*) to cover the variation of plant communities in which the species grows in the Czech Republic.

Canonical correspondence analysis (ter Braak 1987) with all species present in a relevé was used to treat the data. Habitat type was used as a nominal environmental variable with the following categories distinguished: dumps, arable land, dung heaps, road margins. Successional stage was coded as follows: 1 – initial, 2 – intermediate, 3 – later successional stages. These characteristics were recorded for each relevé in the field.

Results

The history of spread

Archaeobotanical records prove that the species has been present at the territory of the Czech Republic for about 4,000 years. The oldest report comes from the Bronze Age (Khün 1981a), and up to 15th century, there were at least 33 localities located in 18 mapping squares (i.e. 2.7 % of the total number of squares located at the territory of the Czech Republic were occupied then). The earliest floristic record is from 1810; a herbarium specimen collected in Prague by J. and C. Presl for the first Czech Flora (Presl and Presl 1819). Up to 1900, the distribution of the species was scattered and the localities known were concentrated mostly in warmer regions and close to big cities (Fig. 1b). At that time, the distribution very closely reflects that inferred from archaeobotanical data (compare Figs. 1a with 1b).

At present, *A. sagittata* is significantly over-represented in mapping squares located in warm and moderate climatic regions compared to those located in cold regions; it is rather rare in the latter (Table 1). The total number of localities reported up to

Table 1. The effect of climate on the present distribution of *Atriplex sagittata* in the Czech Republic. Difference between the observed number of squares occupied by the species and expected value derived from the total number of squares located in particular climatic regions was tested by using the χ^2 goodness-of-fit test.

Climatic region	Observed frequency	Expected frequency	Contributions to χ^2
Warm	126	129	0.07
Moderate	264	394	42.89
Cold	48	155	73.86
Total	438	678	116.82
Significance level P = 0.0001 (df 2)			

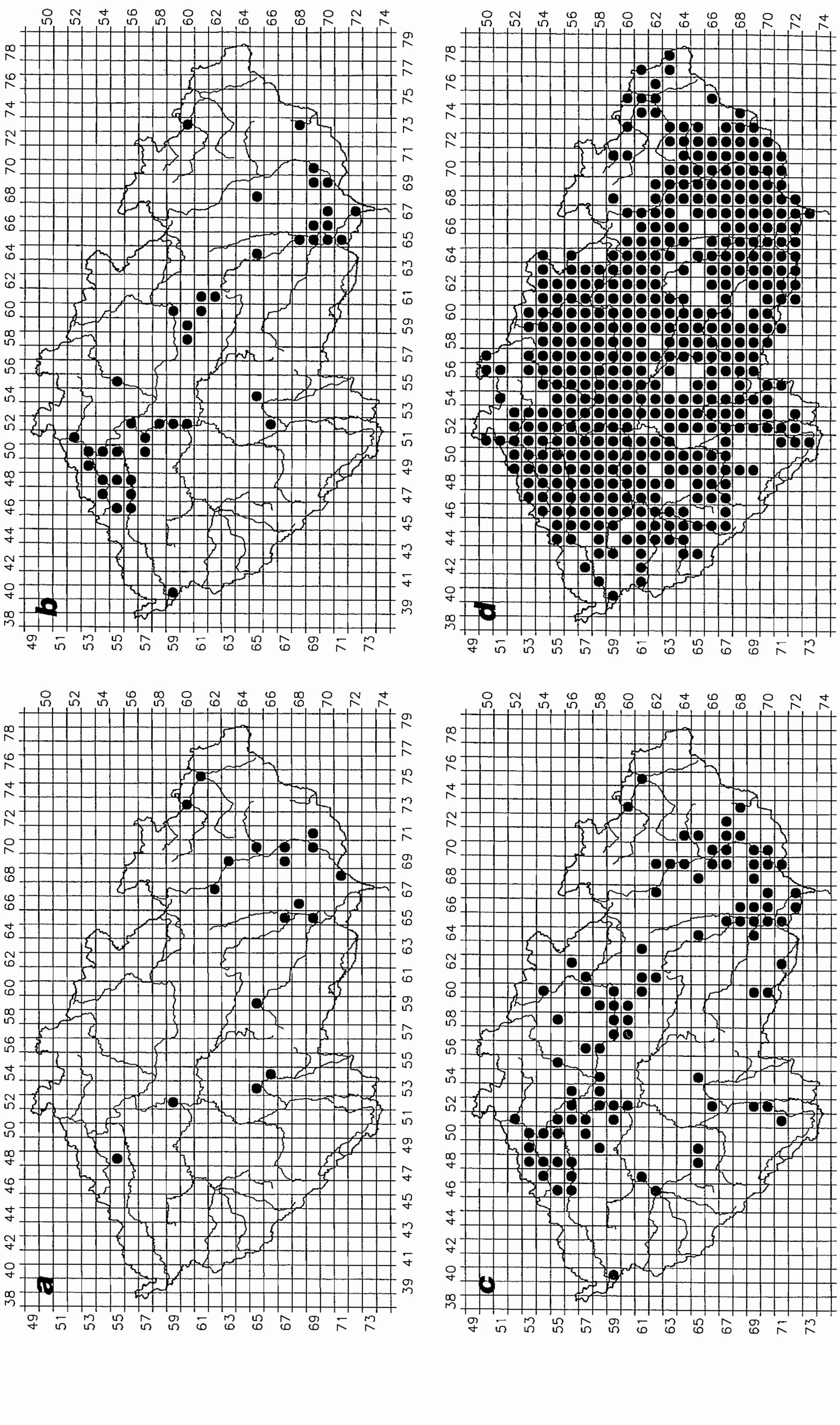

Fig. 1. Distribution of *Atriplex sagittata* in the Czech Republic based on (a) archaeobotanical data (Khün 1981a, 1981b, 1994, Opravil 1965, 1969, 1972a, 1972b, 1976a, 1976b, 1979, 1980a, 1980b, 1980c, 1981, 1985a, 1985b, 1987, 1990a, 1990b, 1990c, 1993a, 1993b, 1994, 1996, Šikulová and Opravil 1974), and floristic records: (b) up to 1900, (c) up to 1950 and (d) up to 1996.

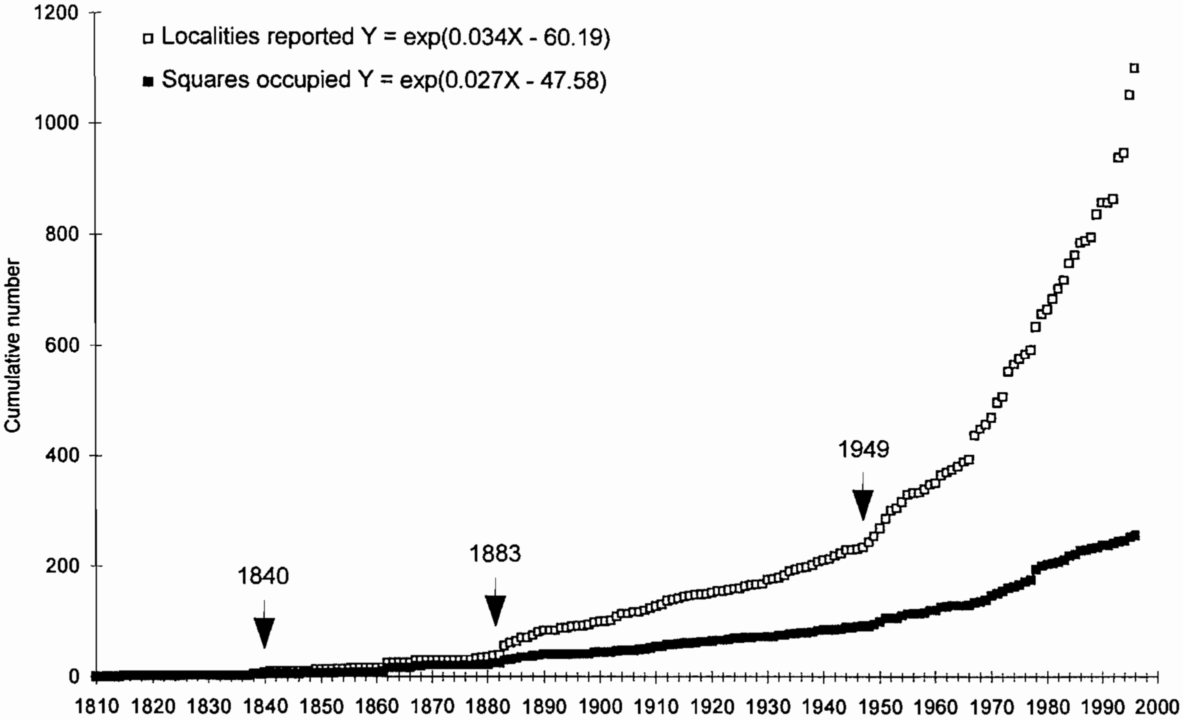

Fig. 2. Cumulative number of localities reported and squares occupied plotted against time. Arrows are used to divide the invasion curve into several parts corresponding to particular periods of invasion (see text for explanation).

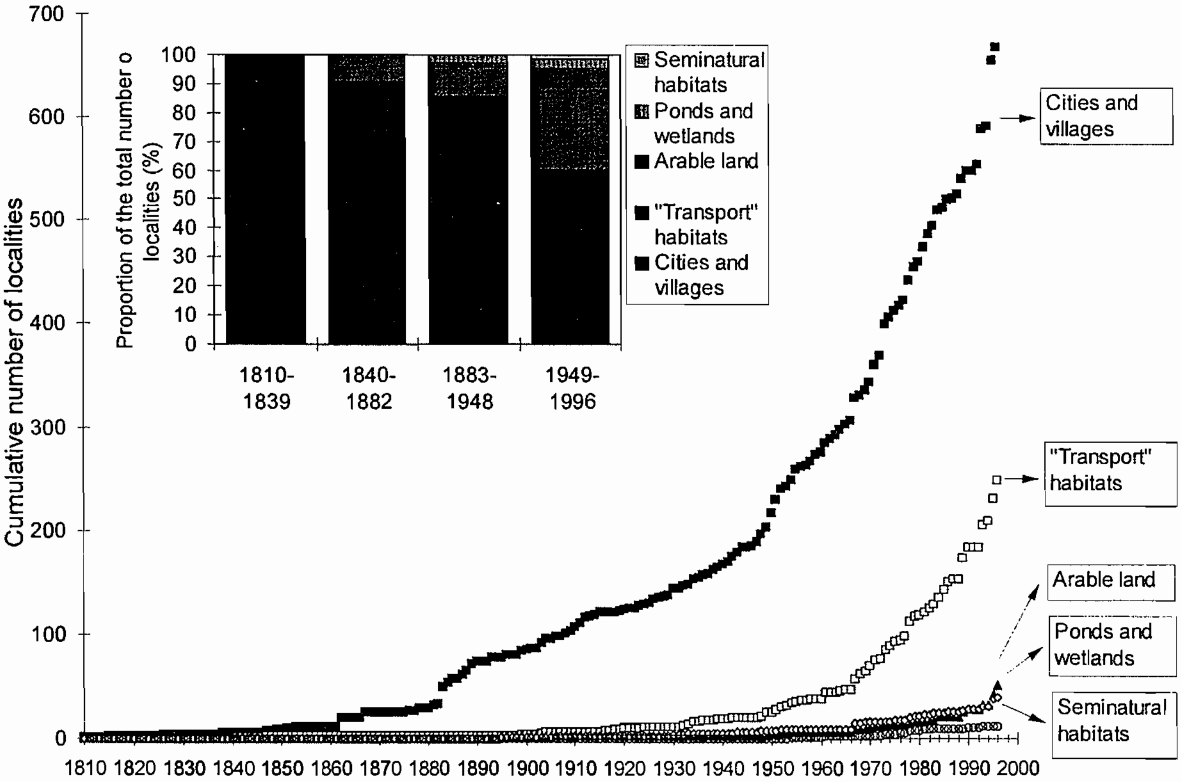

Fig. 3. Cumulative number of localities reported for particular habitats plotted against time. Changes in proportion of particular habitats expressed for particular periods of invasion (see text for details on estimation) are shown in the upper left part of the diagram.

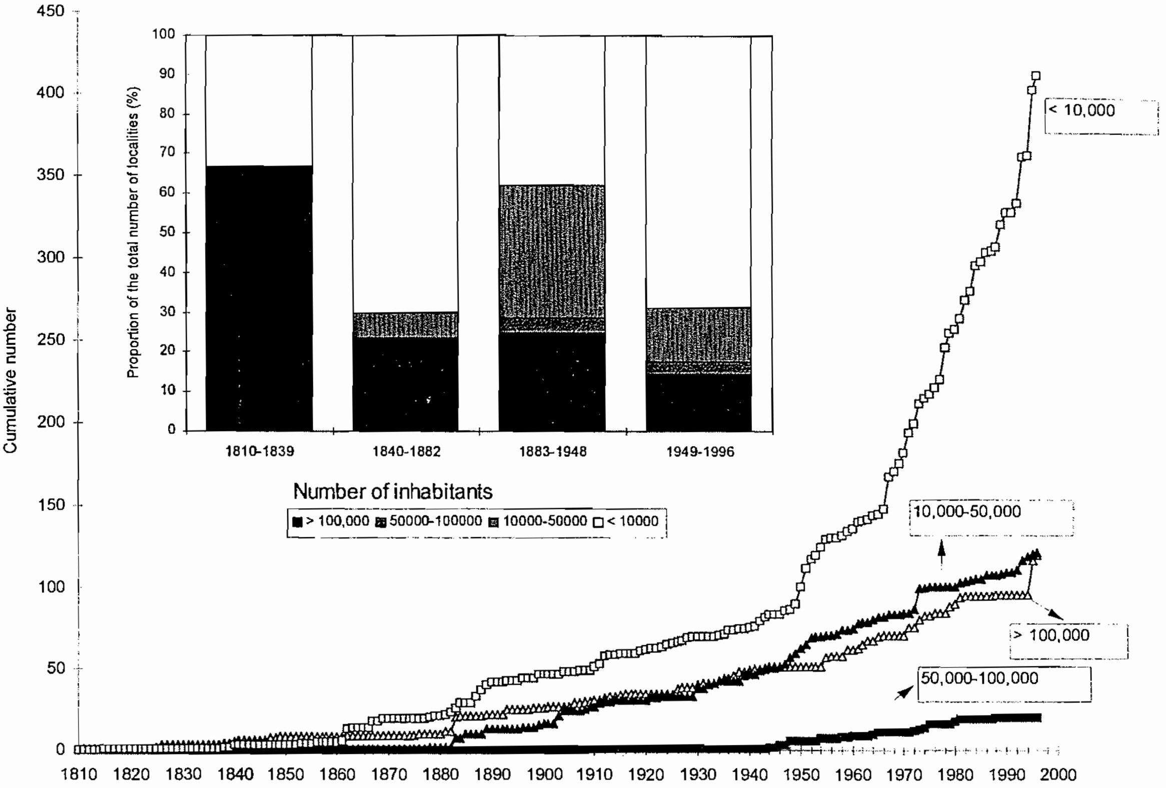

Fig. 4. Increase in the cumulative number of localities reported from cities and villages. Contribution of settlements of different size to the total number of localities is shown for particular periods of invasion (see text for details on estimation) in the upper left part of the diagram.

now is 1101 and 438 mapping squares are occupied, i.e. 64.6 % of the total number located in the area studied (Fig. 1d).

The cumulative number of localities reported and squares occupied has been increasing exponentially over time (Fig. 2). Four rather distinct phases of spread can be recognized. A remarkable increase in the number of localities occurred after 1840, 1883 and 1949 (Fig. 2). Assuming that different habitat types may play different parts in various period of the spreading process, the four phases were analysed separately (Fig. 3).

The spread was fastest (*b* = 0.013) in cities and villages; until the 1940s, the occurrence in habitat types other than these two was rather negligible. After the Second World War, the number of localities reported from the vicinity of roads, railways, paths etc. (or "transport habitats") began to increase rapidly. A remarkable increase in other habitat types, i.e. arable land, ponds and wetlands happened as late as the latest decades. The species is almost absent from semi-natural habitats (meadows, forests and their margins, scrub margins) where only 11 localities were recorded (Fig. 3).

The spread in cities and villages was analysed with respect to the number of inhabitants. In 1839, 66.6 % of localities (out of 6) were reported from cities with more than 100,000 inhabitants; the proportional contribution of these big cities to the total number of localities gradually decreased over time (Fig. 4). At present, the species is present in settlements of any population size; the highest number of localities is from cities and villages up to 10,000 inhabitants (Fig. 4).

The "transport habitats" have gradually become more important; this probably reflects their dispersal role in the spreading of the species from cities and villages into

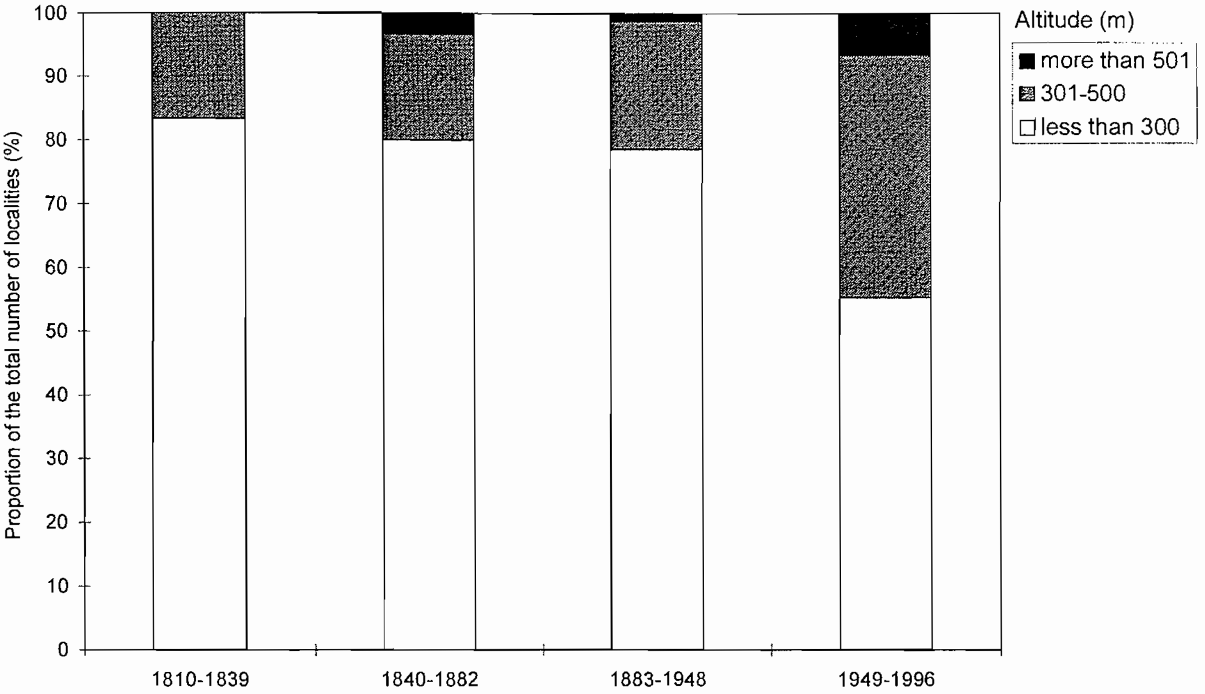

Fig. 5. Distribution of localities with respect to altitude. Proportional contribution of localities found in particular altitudinal ranges is shown for particular periods of invasion.

the open landscape (b = 0.013) (Fig. 3). Analysing separately particular "transport habitats", the localities along roads contributed most to the total number of "transport" localities (i.e. 46 %) and the rate of spread was faster in this habitat (b = 0.011) compared to railways (b = 0.008, 16 % of localities), path margins (b = 0.007, 20 % of localities) and water courses (b = 0.009, 15 % of localities).

A consistent pattern was found when the spread of the species was related to the altitude (Fig. 5). Up to 1948, 78.7 % of localities reported were located in lower altitudes (below 300 m a. s. l.), and the invasion into higher altitudes started after that. From 1949, there were more than 40 % of localities reported from altitudes above 300 m a. s. l. and the proportion of those occurring above 500 m a. s. l. reached 6.6 %, compared to 1.2 % up to 1948 (Fig. 5). The altitudinal maximum recorded at the territory of the Czech Republic is 763 m a. s .l. (herbarium specimen from the Šumava Mts).

In a similar vein, the probability of a square being occupied was highest, over the whole period of spread, in warm regions (Fig. 6). A remarkable increase in moderate regions was observed about a century later and its timing corresponds to the post-war changes in the landscape. In the cold climatic regions, only 30.9 % of the total number of squares are occupied (Table 1).

Analysis of communities with Atriplex sagittata

Fig. 7 displays the CCA ordination of relevés. The first axis (λ = 0.18) is seen to separate the stands with respect to the successional status (r = 0.75) with initial stages located in the right part of the diagram. The first axis accounted for 36.2 % variance in the data set and the Monte Carlo test for this axis was highly significant ($P < 0.01$). The

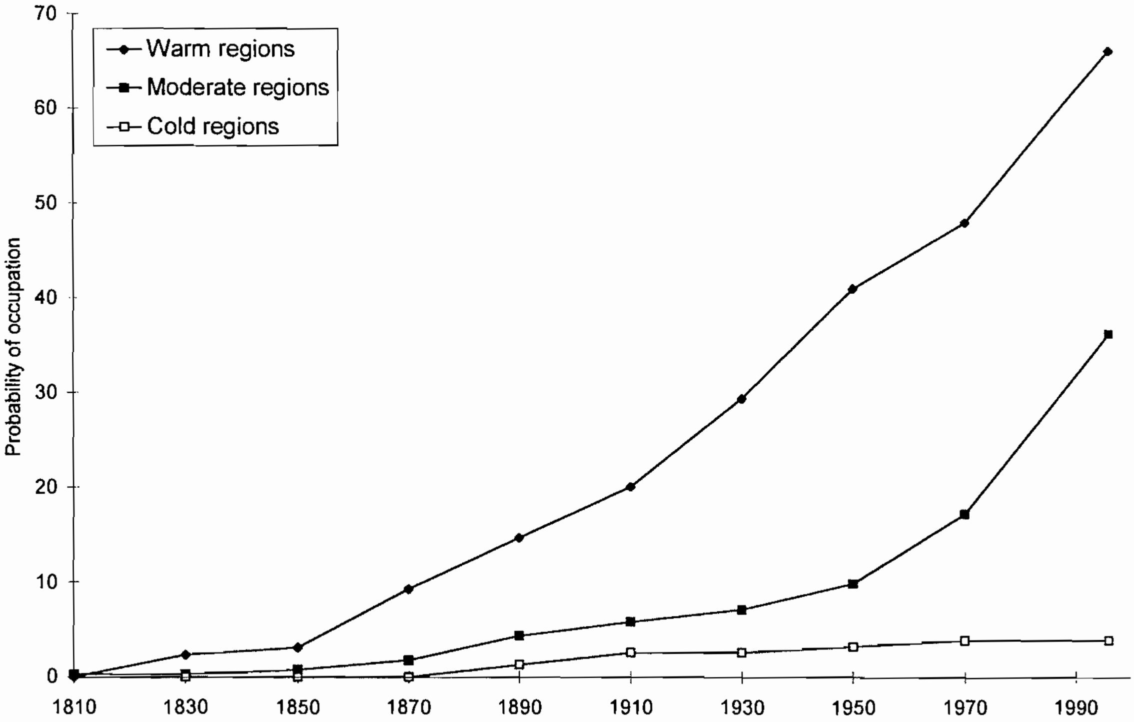

Fig. 6. Probability of being occupied (expressed as a proportion of occupied squares) shown for squares located in warm, moderate and cold climatic regions. Classification of climatic district was taken from Quitt (1971).

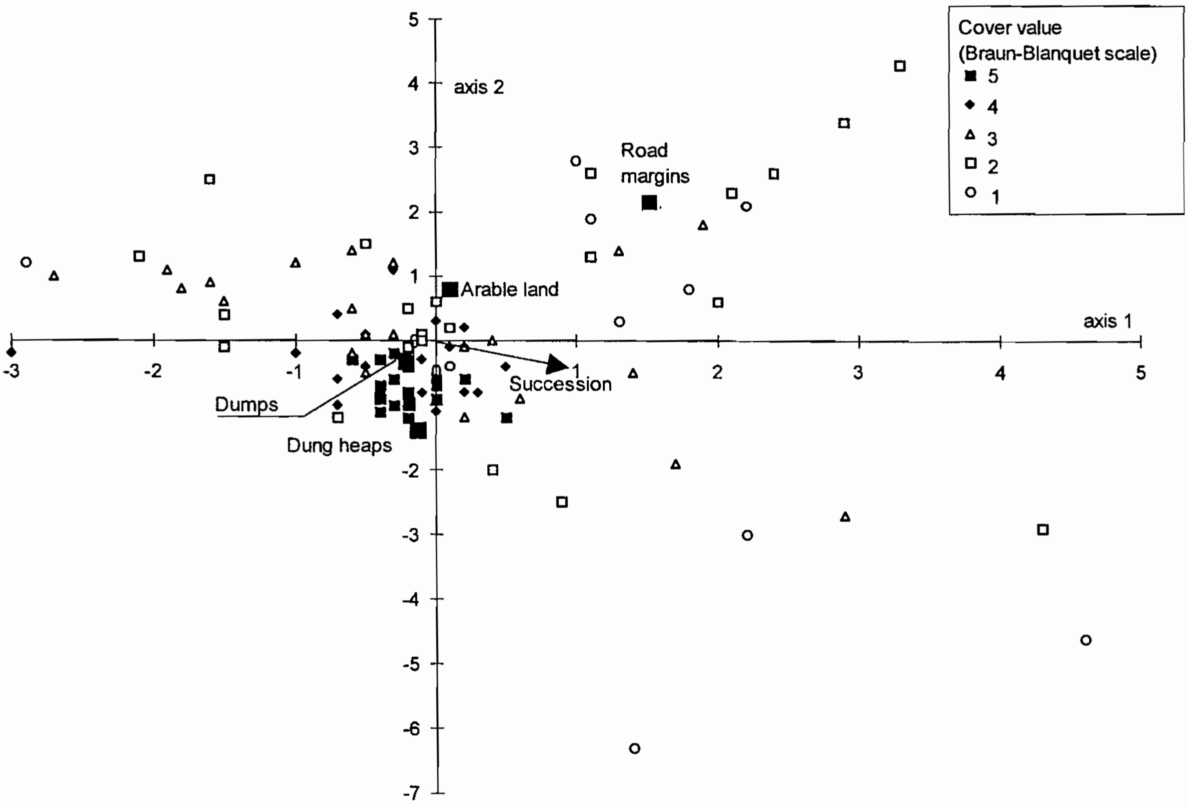

Fig. 7. Correspondence analysis ordination diagram of the relevés of plant communities with *Atriplex sagittata* in the area of the Czech Republic. The performance of *Atriplex sagittata* in particular stands is expressed by using different symbols according to the cover/abundance value the species reached in the respective relevés. Centroids for nominal variables (habitats) are hatched.

second axis ($\lambda = 0.15$) was best correlated with roads ($r = 0.47$). *A. sagitatta* reaches higher dominance (degrees 4 and 5 of the Braun-Blanquet scale) in the post-initial successional stages, and has its optimum on dumps and dung heaps (Fig. 7). The occurrence in the other habitats and communities is more accidental or represents remnants from previous successional stages.

Twenty-three species were present in more than 20 % of the total number of relevés (i.e. in 97 relevés): *Achillea millefolium* agg., *Amaranthus retroflexus*, *Artemisia vulgaris*, *Atriplex oblongifolia*, *A. patula*, *Ballota nigra* subsp. *nigra*, *Carduus acanthoides*, *Chenopodium album*, *Cirsium arvense*, *Convolvulus arvensis*, *Echinochloa crus-galli*, *Elymus repens*, *Galium aparine*, *Lactuca serriola*, *Lolium perenne*, *Plantago major* subsp. *major*, *Polygonum aviculare* agg., *Sisymbrium loeselii*, *Sonchus oleraceus*, *Stellaria media*, *Taraxacum* sect. *Ruderalia*, *Tripleurospermum inodorum*, *Urtica dioica*.

In total, 236 species were recorded in the complete data set, indicating a high variation in species composition of communities with *A. sagittata*. Even in those stands where *A. sagittata* dominated (value 4–5 in the Braun-Blanquet scale), that are usually treated as a single association *Atriplicetum nitentis* Knapp 1945 (1948), there were still 145 species recorded.

Discussion

History of spread

Studying the spread of an alien species which arrived in the area long ago before herbaria and floristic records were available is extremely difficult. Fortunately, much archaeobotanical research have been done in the Czech Republic (see caption to Fig. 1a). These data make it possible to outline the approximate distribution of some archaeophytes, i.e. those possessing fruits easily recognizable in archaeological excavations. For *A. sagittata*, the picture of the distribution before the 15th century obtained by this method corresponds very closely to the distribution at the end of the last century. Despite some limitations imposed by using floristic records to analyse the spread of an alien species in the last two centuries (see e.g. Pyšek 1991), the rapid spread of *A. sagittata* in the Czech landscape is evident. It may be argued the spread expressed by using the cumulative number of reported localities is partly an artefact of increasing floristic activity. However, a simple comparison of the present occurrence of this very common species with the situation 50 years ago, when it was considered very rare, and up to 1962, when it was missing from relatively large regions (Skalický *et al.* 1962; Kopecký and Lhotská 1990) shows without doubt its remarkable spread.

As in many other invading species (Pyšek *et al.*, this volume), ruderal habitats played the most important role in the spread of *A. sagittata*. These habitats are usually characterized by (1) a high level of disturbance, (2) low moisture, (3) high concentration of nitrogen and other nutrients, (4) high habitat heterogeneity, and (5) specific climatic conditions (many of them lie in big cities in the so-called "heat islands" – Gilbert 1989; Wittig 1991). The rapid spread in these habitats and capability to persist in a site for relatively long time (> 3 years) is probably due to the adaptive mechanism of the species, i.e. (1) heterocarpy and (2) salt-tolerance, and other features determining its successional position (e.g. annual life cycle, vigorous growth, high production of biomass, high fecundity).

A remarkable biological feature of the species, heterocarpy, is one of the typical attributes of plants in arid and semiarid regions (Mandák 1997). The species which produce two or more fruit types represent groups where divergent strategies usually found in different taxa are combined by one individual. In such groups, there is a tendency for fruit functions to diverge, each type specializing on some aspect of environmental variation to which it is predisposed while being buffered by the other seed type (Venable *et al.* 1987, 1995). Variation in dispersal and dormancy strategies of diaspores have been suggested to represent an adaptive response to desert conditions (Venable and Lawlor 1980). Species with special mechanisms such as heterocarpy are at an advantage under high levels of disturbance and unpredictable occurrence of suitable habitats, and their chance of survival is increased. A high level of disturbance is typical of habitats harbouring *A. sagittata*. In spite of this, the species can persist in a site for more than three years (B. Mandák and P. Pyšek, personal observation). The success of *A. sagittata* in Central Europe can be thus explained as an adaptation to such habitats that are similar, in terms of temporal and spatial variability, to those in which it occurs in the native distribution area (i.e. salt steppe and riparian habitats).

In *A. sagittata*, the particular fruit types differ in their ecological functions (Mandák and Pyšek, in preparation). The A type is undispersed, deeply dormant, with low germinability, forming a Type IV seed bank (Thompson and Grime 1979). The B type is easily dispersed, dormant, with germinability intermediate between the A and C types. It forms a Type IV seed bank. The fruit type C is easily dispersed, non-dormant and with Type II seed bank. In general, A-type fruits represent behaviour which favours later germination and restricted dispersal with less survival risk, in contrast to the C type which favours earlier germination and more efficient dispersal with associated survival risk. The intermediate ecological position of the B type helps create an ecological continuum between the two contrasting strategies.

The role of salt tolerance in the species spread probably increased in the last three decades. The winter treatment of roads by salt (mainly NaCl and KCl) favours species with physiological predisposition to growth in such habitats, consequently keeping them free from competition of native plants the majority of which are not salt tolerant. This phenomenon is well documented by the massive spread of the halophytic grass *Puccinelia distans* (B. Mandák and P. Pyšek, personal observation), which is common along roads exposed to winter salt treatment and does not occur in other habitats. Human activities thus created a very specialized niche which may be used for the spread and persistence of species with specific ecology in modern countryside which was relatively poor in salt affected habitats in the past. Salinity-tolerance with an increase of human-induced transport activity have been probably important determinants of the fast spread of the study species.

Heterocarpy and salt tolerance are ecological properties which, along with others (such as annual life cycle, vigorous growth, high production of biomass, high fecundity fruits) determine the species early successional position (Harper 1977). Most of the habitats occupied by *A. sagittata* are in human settlements and the occurence of the species is therefore associated with building activities, creating specific "urban" niches broadly characterized by mechanical perturbation of soil. The establishment of *A. sagittata* in these habitats is enabled by creating open space and reduced competition from other species (Kowarik 1995).

The preference for bigger cities in the early stages of expansion was due to their warmer climate in comparison to surrounding countryside (Wittig 1991; Pyšek 1995b) *A. sagittata* is a thermophilous and heliophilous species (indicator value for temperature = 7 on 9 degree scale, that for light = 9 on 9 degree scale – Ellenberg *et al.* 1991) and the presence of habitats meeting these demands played a significant role in the process of naturalization in the present-day countryside.

In general, two factors or their combination could have caused the invasion of *A. sagittata*, i.e. (1) genetic adaptation, or (2) increasing number of suitable habitats. A high level of genetic plasticity is commonly mentioned as one of the properties of colonizing species (see Baker and Stebbins 1965; Bazzaz 1986). A plant which occurred in a region for a long period has had time to select genetically successful types which are better predisposed to local conditions. On the other hand, the increase of building activity in the second half of the 20th century was remarkable and the rapid spread could have been only a response to this fact and to increased dispersal possibilities. A North American invasive species *Conyza canadensis* is an example of another alien with similar history and determinants of spread.

The main determinants of success of *Atriplex sagittata* in Central Europe are probably a combination of (a) special adaptation mechanisms and (b) increasing frequency of suitable habitats which are similar, in terms of temporal and spatial variability, to those in which the species occurs in its native distribution area (i.e. salt steppe and riparian habitats).

Communities with Atriplex sagittata

A. sagittata is an early successional species (Pyšek and Pyšek 1991). However, it can persist in a site for more than three years (B. Mandák and P. Pyšek, personal observation) and occassionally appears even later in succession as a “successional relic” from preceding stages.

Communities dominated by *A. sagittata* are usually species-poor due to the close canopy, strong competition for water, nutrients, and shading. This community type is common on dumps and dung heaps where *A. sagitata* has its ecological optimum. Pyšek (1977) described two different successional pathways following the stands dominated by *A. sagittata,* depending on the nutrient status of the site: (1) On soils with moderate contents of nutrients, *A. sagittata* populations are followed by the community of tall perennial forbs *Tanacetum vulgare* and *Artemisia vulgaris*; later on a mixture of ruderal grasslands and woodlands is formed. (2) On sites very rich in nutrients, the sequence proceeds from *A. sagittata* community to those dominated by *Ballota nigra* and *Chenopodium bonus-henricus*, later on followed by the stands dominated by *Agropyron repens* and *Aegopodium podagraria*, and the communities with *Sambucus nigra.*

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References

Aellen, P. 1960. *Atriplex*. In: Hegi, G. (eds.), Illustrierte Flora von Mitteleuropa. 3/2: 664–693. München.

Aellen, P. and Akeroyd, J.R. 1993. *Atriplex*. In: Tutin, T.G. *et al.* (eds.), Flora Europaea. Vol. 1. pp. 115–117. Cambridge University Press, Cambridge.

Baker, H.G. and Stebbins, G.L. (eds.) 1965. The genetics of colonizing species. Academic Press, London.

Bazzaz, F.A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. In: Mooney, H.A. and Drake, J.A. (eds.), Ecology of biological invasions of North America and Hawaii. pp. 96–110. Springer Verlag, New York.

Black, R.F. 1958. Effect of sodium chloride on leaf succulence and area of *Atriplex hastata* L. Austr. J. Bot. 6: 306–321.

Brandes, D. 1982. Das *Atriplicetum nitentis* Knapp 1945 in Mitteleuropa - insbesondere in Südost-Niedersachsen. Documents Phytosociol. 6: 131–153.

Breckle, S.-W. 1995. How do halophytes overcome salinity? In: Khan, M.A. and Ungar, I.A. (eds.), Biology of salt tolerant plants. pp. 199–213. Dept. of Botany, University of Karachi, Pakistan.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot. 18: 1–248.

Flowers, T.J., Hajibagheri, M.A. and Clipson, N.J.W. 1986. Halophytes. Quart. Rev. Biol. 61: 313–337.

Freitas, H. and Breckle, S.-W. 1993. Accumulation of nitrate in bladder hairs of *Atriplex* species. Plant Physiol. Biochem. 31: 887–892.

Freitas, H. and Breckle, S.-W. 1994. Importance of bladder hairs for seedling of some *Atriplex* species. Mésogée 53: 47–54.

Fröde, E. 1956. Zur Frage der Versteppung im Braunschweiger Raum. Braunschw. Heimat 42: 65–69.

Gebhardt, E. 1954. Notizen über die Trümmerflora in Franken. Hess. Flor. Briefe 3(34): 3.

Gilbert, O. 1989. Ecology of urban habitats. Chapman and Hall, London.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, New York and San Francisco.

Holub, J. and Jirásek, V. 1967. Zur Vereinheitlichung der Terminologie in der Phytogeographie. Folia Geobot. et Phytotax. 2: 69–113.

Hultén, E. and Fries, M. 1986. Atlas of North European vascular plants North of the Topics of Cancer. Vol. 1. Koeltz Scientific Books, Königstein.

Iljin, M.M. 1936. *Atriplex*. In: Komarov, V.L. and Šiškin, B.K. (eds.), Flora URSS. Vol. 6. pp. 77–116. Academiae Scientarium URSS, Moskva and Leningrad.

Jalas, J. and Suominen, J. 1987. Atlas Florae Europaeae. Distribution of vascular plants in Europe. II. map 516. Cambridge University Press, Cambridge.

Kelley, D.B., Goodin, J.R. and Miller, D.R. 1982. Biology of *Atriplex*. In: Sen, D.N. and Rajpurohit, K.S. (eds.), Tasks for vegetation science. Contributions to the ecology of halophytes. Vol. 2. pp. 79–107. Dr. W. Junk Publishers, The Hague.

Khün, F. 1981a. Crops and weeds in Šlapanice near Brno from early Bronze Age to now. Zeitschrift f. Archäol. 15: 191–198.

Khün, F. 1981b. Rozbory nálezů polních plodin. Přehled Výzkumů (Archeol. Ústav ČSAV Brno) 1979: 75–79.

Khün, F. 1994. Pěstované rostliny v Brně v době hradištní a ve středověku. Sborník Prací Filos. Fak. Brněn. Univ., Brno, E39: 83–91.

Kirschner, J. 1984. *Atriplex sagittata* Borkhausen. A nomenclature note. Preslia 56: 159–160.

Kirschner, J. and Tomšovic, P. 1990. *Atriplex*. In: Hejný, S. and Slavík, B. (eds.), Flora of the Czech Republic. Vol. 2. pp. 266–280. Academia, Praha.

Kopecký, K. and Lhotská, M. 1990. K šíření druhu *Atriplex sagittata*. Preslia 62: 337–349.

Korneck, D. 1956. Beiträge zur Ruderal- und Adventivflora von Mainz und Umgebung. Hess. Flor. Briefe 5(60): 1–6.

Kowarik, I. 1995. On the role of alien species in urban floras and vegetation. In: Pyšek, P., Prach, K., Rejmánek, M. and Wade, M. (eds.), Plant invasions – general aspects and special problems. pp. 85–103. SPB Academic Publishing, Amsterdam, The Netherlands.

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

Mandák, B. 1998. Reproductive ecology of *Atriplex sagittata*. PhD Thesis, Czech Agricultural University Praha.

McArthur, E.D. and Sanderson, S.C. 1984. Distribution, systematics, and evolution of *Chenopodiaceae*: an overview. In: Tiedmann, A.R., McArthur, E.D., Stutz, H.C., Stevens, R. and Johnson, K.L. (eds.), Proceedings - symposium on the biology of *Atriplex* and related chenopods. Provo, UT. General Technical Report INT-172.

Meusel, H., Jäger, E. and Weinert, E. 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Gustav Fischer Verlag, Jena.

Moore, R.T., Breckle, S.-W and Caldwell, M.M. 1972. Mineral ion composition and osmotic relations of *Atriplex confertifolia* and *Eurotia lanata*. Oecologia 11: 67–78.

Opravil, E. 1965. Rostlinné nálezy z archeologického výzkumu středověké Opavy prováděného v roce 1962. Čas. Slez. Muz., ser. A, Opava, 14: 77–83.

Opravil, E. 1969. Synantropní rostliny dvou středověkých objektů ze SZ Čech. Preslia 41: 248–257.

Opravil, E. 1972a. Rostliny z velkomoravského hradiště v Mikulčicích. Stud. Archeol. Úst. Čs. Akad. Věd, Brno, 1/2: 6–31.

Opravil, E. 1972b. Synantropní rostliny ze středověku Sezimova Ústí (jižní Čechy). Preslia 44: 37–45.

Opravil, E. 1976a. Archeobotanické nálezy z městského jádra Uherského Brodu. Stud. Archeol. Úst. Čs. Akad. Věd, Brno, Praha, 3/4: 1–60.

Opravil, E. 1976b. Z nejmladší historie luhu řeky Moravy u Kvasic (okres Kroměříž). Zpr. Vlastiv. Úst. Olomouc, 181: 5–11.

Opravil, E. 1979. Rostlinné zbytky z Mohelnice 1. et 2. – Čas. Slez. Muz., ser. A, Opava, 28: 1–13 [1.] et 97–109 [2.].

Opravil, E. 1980a. Rostlinné nálezy ze středověku Starého Města (okres Uherské Hradiště). Přehl. Výzk. Archeol. Úst. ČSAV Brno 1977: 103–105.

Opravil, E. 1980b. Rostlinné zbytky z pravěkého sídliště a zaniklé středověké vsi. In: Unger, J. *et al.*, Pohořelice-Klášterka, 8/2: 96–101, Stud. Archeol. Úst. Čs. Akad. Věd Brno, Praha.

Opravil, E. 1980c. Z historie synantropní vegetace 1–6. Živa 28 (66): 4–5, 53–55, 88–90, 130–161, 167–168, 206–207.

Opravil, E. 1981. Rostlinné zbytky z archeologické výzkumu v Jihlavě. Přehl. Výzk. Archeol. Úst. ČSAV Brno 1979: 62–65.

Opravil, E. 1985a. Rostliny z mladší doby hradištní z Olomouce. Přehl. Výzk. Archeol. Úst. ČSAV Brno 1983: 51–54.

Opravil, E. 1985b. Výsledky archeobotanických analýz z historického jádra města Uherské Hradiště. Přehl. Výzk. Archeol. Úst. ČSAV Brno 1983: 74–82.

Opravil, E. 1987. Rostlinné zbytky z historického jádra Prahy. Archeol. Prag., Praha, 7(1986): 237–271.

Opravil, E. 1990a. Die Vegetation in der jüngeren Burgwallzeit in Přerov. Čas. Slez. Muz., ser. A, Opava, 39: 1–32.

Opravil, E. 1990b. Postmedievální archeobotanické nálezy z Olomouce. Stud. Postmediaev. Archeol., Praha, 1: 231–248.

Opravil, E. 1990c. Archeobotanické nálezy z Kolářské ulice v Opavě. Archeol. Hist., Brno, 15/90: 491–509.

Opravil, E. 1993a. Archeobotanické nálezy z Hrnčířské ulice v Opavě (hotel Orient – dostavba). Čas. Slez. Muz., Opava, A42: 193–214.

Opravil, E. 1993b. Rostliny ze středověku Uherského Brodu – Soukenická ulice a Lidový dům. Přehl. Výzk. Archeol. Úst. ČSAV Brno 1989: 135–143.

Opravil, E. 1994. Příspěvek k poznání rostlinných makrozbytků ze staré Prahy. Archeol. Rozhledy, Praha, 46: 105–114.

Opravil, E. 1996. Archeobotanické nálezy z historického jádra Opavy z výzkumné sezony 1993–1994. Čas. Slez. Muz., Opava, A45: 1–15.

Osmond, C.B., Björkman, O. and Anderson, D.J. 1980. Physiological processes in plant ecology – towards a synthesis with *Atriplex*. Springer Verlag, Berlin, Heidelberg and New York.

Presl, J.S. and Presl, C.B. 1819. Flora Čechica. Kwětena-Česká. Pragae.

Probst, R. 1949. Wolladventivflora Mitteleuropas. Vogt. Schild., Solothurn.

Pyšek, A. 1977. Sukzession der Ruderalpflanzendesellschaften von Gross-Plzeň. Preslia 49: 161–179.

Pyšek, P. 1991. *Heracleum mantegazzianum* in the Czech Republic: dynamics of spreading from the historical perspective. Folia Geobot. et Phytotax. 26: 439–454.

Pyšek, P. 1995a. On the terminology used in plant invasion studies. In: Pyšek, P., Prach, K., Rejmánek, M. and Wade, M. (eds.), Plant invasion – General aspects and special problems. pp. 71–81. SPB Academic Publishing, Amsterdam, The Netherlands.

Pyšek, P. 1995b. Approaches to studying spontaneous settlement flora and vegetation in central Europe: a review. In: Sukopp, H., Numata, M. and Huber, A. (eds.), Urban ecology as the basis of urban planning. pp. 23–39, SPB Academic Publishing, Amsterdam.

Pyšek, P. 1998. Is there a taxonomic pattern to plant invasions? Oikos 82: 282–294.

Pyšek, P. and Prach, K. 1993. Plant invasion and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeogr. 20: 413–420.

Pyšek, P. and Prach, K. 1995. Invasion dynamics of *Impatiens glandulifera* – a century of spreading reconstructed. Biol. Conserv. 74: 41–48.

Pyšek, P. and Pyšek, A. 1991. Succession in urban habitats: an analysis of phytosociological data. Preslia 63: 125–128

Pyšek, P., Prach, K. and Mandák, B. 1998. Invasion of alien plants into habitats of Central European landscape: an historical pattern. (this volume)

Quitt, E. 1971. Klimatische Gebiete der Tschechoslowakei. Stud. Geogr. 16: 1–73.

Schirmer, U. and Breckle, S.-W. 1982. The role of bladders for removal in some *Chenopodiaceae* (mainly *Atriplex* species). In: Sen, D.N. and Rajpurohit, K.S. (eds.), Tasks for vegetation science. Contributions to the ecology of halophytes. Vol. 2. pp. 215–231. Dr. W. Junk Publishers, The Hague.

Schönfelder, P. and Bresinsky, A. 1990. Verbreitungsatlas der Farn- und Blütenpflanzen Bayerns. Eugen Ulmer, Stuttgart.

Schreier, K. 1955. Die Vegetation auf Trümmer-Schuttzerstörten Stadtteile in Darmstadt und ihre Entwicklung in pflanzensoziologischer Betrachtung. Schriftenr. Naturschutzstelle Darmstadt, 3 (1).

Skalický, V. 1962. Příspěvek ke květeně Rychnovska. Acta Mus. Reginaehradec. et Pardub., ser. A, 47: 63–81.

Stutz, H.C., Chu, G-L. and Sanderson, S.C. 1990. Evolutionary studies of *Atriplex*: Phylogenetic relationships of *Atriplex pleiantha*. Amer. J. Bot. 77: 364-369.

Stutz, H.C., Chu, G-L. and Sanderson, S.C. 1993. Resurrection of the genus *Endolepis* and clarification of *Atriplex phyllostegia* (*Chenopodiaceae*). Amer. J. Bot. 80: 592-597.

Šikulová, V. and Opravil, E. 1974. Nález zvířecích kostí a rostlinných zbytků ve Vávrovicích. Přehl. Výzk. Archeol. Úst. ČSAV Brno 1973: 122–124.

ter Braak, C.J.F. (1987): CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 2.1). Agricultural Mathematics Group, Wageningen.

Thompson, K. and Grime, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol. 67: 893–921.

Trewick, S. and Wade, P.M. 1986. The distribution and dispersal of two alien species of *Impatiens*, waterway weeds in the British Isles. – Proceedings EWRS/AAB Symposium on Aquatic Weeds 1986: 351–356.

Ullman, I. 1977. Die Vegetation des südlichen Maindreiecks. Hoppea, Denkschr. Regensb. Bot. Ges. 36: 5–190.

Venable, D.L. and Lawlor, L. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46: 272–282.

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

Venable, D.L., Dyreson, E. and Morales, E. 1995. Population dynamics consequences and evolution of seed traits of *Heterosperma pinnatum* (*Asteraceae*). Amer. J. Bot. 82: 410–420.

Wittig, R. 1991. Ökologie der Großstadtflora. Gustav Fischer Verlag, Stuttgart.