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The importance of phenotypic differentiation and plasticity in the range expansion of the annual *Atriplex tatarica* (Amaranthaceae)

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ABSTRACT

The ability of a species to adapt to sub-optimal conditions at the margin of its distribution range and to cope with environmental stress is considered to be important for its successful geographic expansion. To ascertain the roles of phenotypic differentiation and plasticity in the expansion of the annual *Atriplex tatarica*, we compared plants from populations found in Marginal and Central areas of the species' range. We grew these plants under marginal climatic conditions in pots with different types of substrate. We assessed the population genetic structure at five putatively neutral allozyme loci to evaluate whether there was any evidence of reduced genetic diversity in Marginal populations compared to Central ones. We used the Q_{ST} vs. F_{ST} approach (while F_{ST} gives a standardised measure of the genetic differentiation among populations for a genetic locus, Q_{ST} measures the amount of genetic variance among populations relative to the total genetic variance) to ascertain the roles of adaptive vs. non-adaptive processes on phenotypic differentiation. Plants native to the Marginal area of the species' range flowered earlier and had a lower shoot mass and a higher reproductive allocation than plants native to the Central part of the species' range. The Marginal populations of *Atriplex tatarica* showed lower genetic diversity at allozyme loci and higher phenotypic differentiation than the Central populations. We recorded similar plastic responses to substrates in plants native to both regions. Our results indicate that Marginal populations of expanding *A. tatarica* maintain the ability to adapt locally and to elicit a plastic response to environmental stress, despite loss of genetic diversity.

Introduction

For the process of chorological plant species expansion, also in the context of global climatic changes and worldwide dispersal of alien plants, two evolutionary strategies have been widely discussed as important: local adaptation and adaptive phenotypic plasticity (Baker, 1965; Etterson, 2004; Griffith and Watson, 2005; Parker et al., 2003). Both are effective ways of ensuring the long-term survival of a species in a heterogeneous environment, but they seem to play slightly different roles in the expansion process. The ability of a species to adapt to the local environment often plays an important role at large geographical scales, e.g., along climatic gradients (Joshi et al., 2001; Santamaría et al., 2003). Conversely, adaptive phenotypic plasticity seems to operate at smaller scales within a region or locality, although there is scant evidence for the existence of general-purpose genotypes growing optimally at very distant sites (Parker et al., 2003; Santamaría et al., 2003). Local adaptation is supposed to evolve when divergent selection occurs in different habitats, when gene flow is low relative to the strength of the selection and when plasticity is unable to be selected for (Kawecki and Ebert, 2004). The probability that plasticity is selected over specialised genotypes increases if there is gene flow among populations (Sultan and Spencer, 2002) or if there are any constraints such as genetic correlations or costs of plasticity (Gomulkiewicz and Kirkpatrick, 1992; Via and Lande, 1985).

The dynamics of species range shifts are likely to be largely determined by population responses at range margins (Hampe and Petit, 2005). Compared to populations from the centre of a species' range, the Marginal populations in an expanding range are often more fragmented, are at lower densities and are more sensitive to demographic changes. Several specific mechanisms influence selection of local adaption and phenotypic plasticity under conditions at the border of a species' range. First, asymmetric gene flow may hinder the ability of Marginal populations to adapt locally. The

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more abundant Central populations may be a source of a high number of immigrants that enrich Marginal populations by contributing new alleles representative of Central populations (Kawecki, 2008). Second, inbreeding may affect the adaptive response of populations to stress; it may decrease the plasticity of inbred populations (Armbruster and Reed, 2005; Pluess and Stöcklin, 2004). In this context, regional differences in plasticity can be expected because of higher inbreeding in isolated small populations at the margins of a species' range. Finally, there is a longstanding unresolved debate as to whether the loss of genetic diversity that is commonly observed in Marginal populations influences their evolutionary potential to adapt to extreme conditions (Hoffmann and Blows, 1994).

In this study, we attempted to ascertain the importance of phenotypic differentiation and plasticity in the range expansion of the recently expanding annual species *Atriplex tatarica* L. In Central Europe, *Atriplex tatarica* has expanded in the last few decades in some regions where it was previously recorded to marginally occur (Jarzyna et al., 2010; Zündorf et al., 2006). We grew plants from two climatically different regions (one with large and non-fragmented populations connected to a continuous distribution range – further denoted as the "Central region" – and the other with very small and highly fragmented populations outside of the continuous distribution range – further denoted as the "Marginal region") at a place situated in the Marginal region. We designed the manipulative experiment to quantify phenotypic plasticity in order to compare the amount of plasticity between Marginal and Central populations and to determine genetic diversity using allozyme analysis to assess possible genetic erosion in small Marginal populations in comparison to large Central ones. We manipulated the quality of the substrate, an important ecological determinant of the distribution of this ruderal species (Kochánková and Mandák, 2008). We applied the Q_{ST} vs. F_{ST} approach to ascertain the roles of adaptive vs. non-adaptive processes on phenotypic differentiation.

Specifically, we addressed the following questions: (a) To what extent do Marginal and Central populations differ genetically? (b) Do plants from the Marginal region differ in the means of some fitness-related traits or in the degree of phenotypic plasticity from plants of the Central region? (c) Is there any between-region difference in the extent of phenotypic population differentiation? (d) Could possible phenotypic differences be explained by adaptive or non-adaptive processes?

Materials and methods

Study species

Atriplex tatarica L. (Amaranthaceae) is a heterocarpic annual of disturbed habitats that is tolerant to a wide range of nutrients in the soil. It occurs in habitats rich in nutrients, such as dunghills, as well as in relatively nutrient-poor sites along road verges (Kochánková and Mandák, 2008). It is a species that is known to make a relatively large reproductive effort, allocating 32.7% to 43.8% of its total net resources to reproduction (Holmanová, 2002).

The species is native to middle and western Central Asia, Asia Minor, North Africa and Eastern Europe (Kochánková and Mandák, 2008). *Atriplex tatarica* is highly salt tolerant (Mandák, 2003) and therefore spreads effectively along roads treated with salt during the winter. *Atriplex tatarica* produces two morphologically distinct seed types that differ in dormancy-breaking requirements and nitrate and salinity tolerance (Kochánková and Mandák, 2009; Mandák, 2003).

Part of the north-western border of the species' continuous European distribution runs through the Czech Republic (Kochánková and Mandák, 2008). The two following areas that differ in the abundance of the species can be distinguished: (1) South Moravia (hereafter, the Central region), where the species is abundant and which probably represents part of the native continuous area of distribution from south-eastern Europe through the Pannonian lowland, and (2) the western part of Bohemia (hereafter the Marginal region), where the species occurs only rarely at several rather isolated localities (see Kochánková and Mandák, 2008, and Mandák et al., 2005, for details and a distribution map).

Plant material and population sampling

At the end of October 2006, twelve populations of *A. tatarica* were randomly chosen from the two regions: six populations from the Marginal region and six populations from the Central region (Table 1). The regions differ in yearly mean temperature (Mann–Whitney test; $U = 0$, $P = 0.002$), length of the growing season ($U = 0$, $P = 0.002$) and altitude ($U = 0.5$, $P = 0.002$); no evidence of any difference in yearly mean precipitation was found ($U = 9$, $P = 0.18$). The climate of the Marginal region at a higher altitude is thus characterised by a lower yearly mean temperature and a shorter growing season than the climate of the Central region.

Fruits were collected from five individuals per population along a transect with individuals spaced 5 m apart and stored in paper bags at room temperature until sowing. The identity of the maternal plant was maintained. *Atriplex tatarica* has a mixed mating system (Kochánková and Mandák, 2008). The offspring of a single maternal plant would therefore be both half-sib throughout outcrossing and full-sib through selfing.

Before sowing, the seeds were sorted according to their type, and only non-dormant seeds were used in the experiment. Non-dormant seeds were chosen to exclude variation in germination time (Mandák, 2003). Mandák et al. (2006) showed that non-dormant fruits [called "type C" in Mandák et al., 2006] generate more heterozygous populations than dormant fruits (type B)

Table 1

Characteristics of *Atriplex tatarica* populations (Pop) sampled in the Central (C) and the Marginal (M) regions. Localisations, locality altitudes, yearly mean temperature, length of the growing season and yearly mean precipitation from 1961–2000 are given (climatic data from Tolasz, 2007).

Pop	Latitude (WGS 84)	Longitude (WGS 84)	Altitude	Yearly mean temperature (°C)	Length of growing season[a] (days)	Yearly mean precipitation (mm)
C1	48°52′13″N	16°19′13″E	230	9.5	245	525
C2	48°51′28″N	16°34′36″E	190	9.5	235	475
C3	48°50′10″N	16°09′56″E	210	9.5	245	475
C4	48°52′12″N	16°50′40″E	160	9.5	245	525
C5	48°54′23″N	16°57′25″E	240	9.5	235	525
C6	48°51′37″N	16°03′27″E	250	9.5	235	475
M1	50°17′29″N	13°25′56″E	250	8.5	225	425
M2	50°15′22″N	13°23′40″E	290	8.5	225	475
M3	50°16′16″N	13°21′49″E	285	8.5	225	475
M4	50°16′46″N	13°24′39″E	260	8.5	225	475
M5	50°24′07″N	13°25′16″E	280	8.5	225	425
M6	50°15′04″N	14°01′37″E	290	8.5	225	525

[a] Average number of days with an average temperature ≥ 5 °C.