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Research article

Germination dynamics and seedling frost resistance of invasive and native *Impatiens* species reflect local climatic conditions

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ABSTRACT

Invasion of some alien plants is considered to be associated with inter-population differentiation and adaptations to local conditions. To obtain an insight into these processes it is convenient to compare invasive plants with their native congeners. The intra-specific differentiation during invasion was studied using four *Impatiens* (Balsaminaceae) species in Central Europe: native *Impatiens noli-tangere* and three aliens (highly invasive *Impatiens glandulifera*, less invasive *Impatiens parviflora* and potentially invasive *Impatiens capensis*). Differentiation in traits important for the establishment (germination; seedling emergence; seedling frost resistance) was measured in a laboratory and an experimental garden using seed collected from five natural populations of each species. Frost resistance of *I. capensis*, currently invasive in Western Europe, was within the scope of other congeners and it does not seem to be a barrier to spread of the species into Central Europe. Among-population differences were found within all species except *I. capensis*. In *I. noli-tangere*, *I. glandulifera* and *I. parviflora* the differences were related to the climatic characteristics in early spring at the source localities, which indicates that individuals may be adapted to local conditions. The differences found between the populations of *I. noli-tangere*, *I. glandulifera* and *I. parviflora* are likely to reflect the frost sensitivity of the species. In the highly frost-sensitive *I. parviflora* differentiation was found both in germination and frost resistance of individual populations. In *I. glandulifera* the differences among populations in frost sensitivity depended on temperature at the seed source and corresponded to the pattern of emergence of seedlings in the garden. In the native *I. noli-tangere*, the differences among populations in the time of germination depended on temperature at the seed-source locality. Since local adaptations were indicated both in native and invasive species studied, they are unlikely to provide the invasive *Impatiens* species with an advantage against the native congener, at least in terms of the traits investigated.

Introduction

Invasions by alien plants and animals continue to increase (e.g. Lambdon et al., 2008; Hulme et al., 2009) and so does their impact on invaded communities (Hejda et al., 2009; Vilà et al., 2010). Biological and ecological traits associated with the invasiveness of plant species have been studied since the beginning of invasion ecology as a subdiscipline of ecology (Pyšek et al., 2006; Richardson and Pyšek, 2008) and the importance of certain traits has been repeatedly suggested in reviews and meta-analyses (Pyšek and Richardson, 2007; van Kleunen et al., 2010). However, attempts to identify traits of successful invaders indicate that more robust explanations are likely to be found at the level of particular taxonomic groups and/or life forms rather than for vascular plants as a whole (Rejmánek and Richardson, 1996; Pyšek and Richardson, 2007). Comparisons among congeners are thus a convenient tool for identifying traits associated with invasiveness of plant species or populations. In addition, comparisons of closely related facultatively co-occurring species minimize biases associated with phylogenetic distance and habitat affinities (Caldwell et al., 1981; Burns, 2004; Pyšek and Richardson, 2007).

Many studies that explore traits associated with invasiveness highlight the importance of reproductive characteristics (Rejmánek et al., 2005; Pyšek and Richardson, 2007). Traits associated with plant reproduction and establishment, such as seed production and germination and seedling performance, are known to be different in successful and unsuccessful invaders (Rejmánek and Richardson, 1996; Moravcová et al., 2005, 2010;

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Grotkopp and Rejmánek, 2007; Morrison and Mauck, 2007), and in invaders and their native congeners (Goergen and Daehler, 2001; Kolb and Alpert, 2003; Sans et al., 2004). Those associated with generative reproduction are of crucial importance especially in annual species reproducing exclusively by seed (Crawley et al., 1996).

Many invasive plants are able to grow and reproduce in a wide range of environmental conditions. This may be due to general-purpose genotype sensu (Baker, 1965), which facilitates invasions by some of these species (Rejmánek et al., 2005; Geng et al., 2006). Phenotypic plasticity has been considered important for achieving dominance in a range of diverse habitats in many species (Sultan, 1987; Williams et al., 1995; Levin, 2000; Gerlach and Rice, 2003; Parker et al., 2003). Nevertheless, not all invasive species owe their success to general-purpose genotypes. Fast local differentiation, in terms of adaptation to local conditions, resulting in existence of locally adapted genotypes may be an alternative strategy. A common feature of plant invasions is the initial lag following introduction into a new region (Lee, 2002; Mack et al., 2000; Williamson et al., 2005; Dietz and Edwards, 2006), during which locally adapted genotypes may develop (Sakai et al., 2001). Adaptations to local conditions may occur within several years or generations (Linhart and Grant, 1996; Fischer et al., 2004). Evidence is accumulating that indicates invasive plants can adapt rapidly to new environments (Rice and Mack, 1991; Maron et al., 2004). It seems reasonable to believe that genetic differentiation through rapid evolutionary change may be important in plant invasions (Bossdorf et al., 2008).

Dietz and Edwards (2006) hypothesized that secondary phase of expansion, in which further spread is contingent upon plastic responses or genetic adaptation to new ecological circumstances, is associated among others with strategic shifts in crucial life-history traits. The timing of flowering and germination of invasive annuals is important as it determines the maximum seed production and establishment of juveniles. Large-scale latitudinal clines, interpreted as evolutionary adaptation to climate heterogeneity, has indeed been observed for different life history traits in an increasing number of introduced plant species (Weber and Schmidt, 1998; Kollmann and Bañuelos, 2004; Montague et al., 2008; Dlugosch and Parker, 2008; Allan and Pannell, 2009). Recently it has been reported that there are similar differences in plants growing at different altitudes (Leger and Rice, 2007; Leger et al., 2009; Li and Feng, 2009, but see Monty and Mahy, 2009).

Studies investigating the role of differentiation in plant invasions have been based on comparison of native and invasive populations within individual species (Bossdorf et al., 2005; Colautti et al., 2009). Such a comparison, however, does not address potential advantage of an invasive plant over the native flora. To investigate whether or not the success of an invasive species in its invaded range is due to population differentiation it seems plausible to compare differentiation within invasive species and native congeners. However, studies comparing population differentiation of invasive plant species with that of native congeners are missing.

To investigate the role of differentiation in traits associated with the establishment phase of invasion (time of germination, time of seedling emergence, and frost resistance of seedlings) we used annual species of the genus *Impatiens* (Balsaminaceae) with similar life-histories and coexisting in some habitats. We used the native *Impatiens noli-tangere*, highly invasive *Impatiens glandulifera* and less invasive *Impatiens parviflora* sampled from mixed stands or sites located very close to each other in the Czech Republic, and the potentially invasive *Impatiens capensis* in central Germany. Local differences in some traits were described in some of these species (Simpson et al., 1985; Dudley and Schmitt, 1995; Donohue et al., 2001; Heschel et al., 2002; Hatcher, 2003; Kollmann and Bañuelos, 2004). The species studied were shown to differ in stratification demands, germination and seedling emergence (Perglová et al., 2009). However, the inter-specific differences in these traits were addressed only very marginally, and frost resistance of the species has not been studied yet. Frost is an important factor in the temperate zone as it is an environmental barrier to distribution (Franklin, 1995) and limits the geographical range of many plant species, including invaders (Sakai and Wardle, 1978; Bannister and Polwart, 2001; Bruelheide, 2002). Population differences in frost resistance are reported for other invasive plants such as *Buddleja davidii* (Ebeling et al., 2008); frost hardiness was, however, not related to geographic location or climatic variables of the populations' home sites.

In order to obtain an insight into these processes, this study addresses the following questions: (i) Are there any differences in frost resistance of the species studied and could the sensitivity to frost constrain the eastward spread of *I. capensis*? (ii) Is there any variability in performance of individual populations within the native and invasive species? (iii) Is this variability related to climatic characteristics of sampling sites?

Methods

The species studied

The *Impatiens* species studied have similar life-histories and reproductive characteristics, and coexist in some habitats (Coombe, 1956; Beerling and Perrins, 1993; Kartesz and Meacham, 1999; Hatcher, 2003; Adamowski, 2008). Impatiens *noli-tangere* is native to the Czech Republic (Slavík, 1997; Pyšek et al., 2002). *Impatiens glandulifera* has been rapidly spreading in this country (Pyšek and Prach, 1995), while current spread of *I. parviflora* is less dynamic and its occurrence more stabilized. *Impatiens capensis* is invasive in Western Europe and the closest localities to the Czech Republic are in central Germany; these areas have milder climate than the Czech Republic (Müller, 1982).

Most seeds of *Impatiens* species germinate simultaneously in the early spring following cold winter stratification (Coombe, 1956; Beerling and Perrins, 1993; Hatcher, 2003), but the species differ in the stratification demands and germination rates (Perglová et al., 2009). As annuals with a limited seed bank they crucially depend on successful establishment of juveniles every year. Seeds of *I. glandulifera* need only a short period of cold-wet stratification after which most of the seed germinate. *Impatiens parviflora* requires a long period of stratification, which is followed by germination of a high percentage of seed. The native *I. noli-tangere* has the longest stratification period and the lowest germination percentage. *Impatiens capensis* requires an intermediate period of stratification and germinates well in the laboratory and the garden. The species are reported to suffer from frost damage (Coombe, 1956; Beerling and Perrins, 1993; Perrins et al., 1993; Hatcher, 2003); hence it may be one of the factors limiting their spread.

Most of the species are reported to develop locally differentiated or even adapted types. Considerable differentiation of populations in flowering phenology along a latitudinal gradient in the invaded range was recorded in *I. glandulifera* (Kollmann and Bañuelos, 2004). *Impatiens capensis* was used as a model species for testing adaptive plasticity in a study that revealed differences in its response to environmental factors such as shading and availability of water (Dudley and Schmitt, 1995; Donohue et al., 2001; Heschel et al., 2002). Simpson et al. (1985) described a differentiation in flowering phenology. Differentiation between populations