



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.

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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

of *I. noli-tangere* is reported from the United Kingdom (Hatcher, 2003). Population differentiation may thus be found in other traits. For more details on individual species see Perglová et al. (2009).

Seed collection

Czech localities chosen were those that host all three *Impatiens* species present in the Czech Republic and cover the climatic range. Seeds of *I. glandulifera*, *I. parviflora* and *I. noli-tangere* were collected from five sites in the Czech Republic: Černětice near Volyně (coded as VOL; 49°8'30"N, 13°53'50"E), Čelina (CEL; N 49°43'50", E 14°20'30"), Potštejn (POT; N 50°4'15", E 16°19'25"), Velký Osek (POL; N 50°07', E 15°10') and Paskov (PAS; N 49°44', E 18°18'). The species grew in mixed stands or very close at CEL, POT and VOL sites. At CEL *I. parviflora* and *I. noli-tangere* occurred in mixed forest in a narrow valley along a brook, and *I. glandulifera* grew in less shaded spots such as clearings. At POT all the species grew in a mixed deciduous forest along a river. At VOL *I. parviflora* and *I. noli-tangere* occurred in a mixed deciduous forest in a broad valley along a river and a mill-race; *I. glandulifera* occurred mostly at the forest edges close to meadows. At the POL and PAS sites, *I. noli-tangere* and *I. parviflora* were collected from mix stands in forests, and *I. glandulifera* at more distant river banks. At POL *I. parviflora* and *I. noli-tangere* grew in a mixed alluvial forest and *I. glandulifera* at a river bank about 1.5 km distant. At PAS *I. parviflora* and *I. noli-tangere* occurred in a mixed forest at a mild slope and *I. glandulifera* at a river bank about 0.7 km distant. Seeds for testing frost resistance were collected in July and August 2007. The collection was repeated in 2008 to obtain additional seeds for testing the frost resistance of seedlings of *I. noli-tangere* mainly from VOL and POT, and for determining germination dynamics in the laboratory and seedling emergence in the garden.

Seeds of *I. capensis* were collected in September 2008 from three localities in central Germany (Frankfurt am Main region): along the banks of a brook in open farmland near the village of Großseelheim (stated as GRV; N 50°48'37", E 8°52'52"), in wet pasture between the villages of Großseelheim and Schröck (GRP; N 50°48'6", E 8°50'15"), in wet meadow margins and spruce forest near the village of Hassemulle (HAS; N 50°12'8", E 8°21'20").

For each species, a mixed sample of seed from at least 50 individuals randomly chosen from the whole site was collected. As seed mass may influence seedling performance (Schmitt and Ehrhard, 1990), part of the seed collected in 2008 was used to obtain the measure of the seed mass. Due to the low mass of individual seeds, the mass of 25 seeds was recorded. Six measurements were carried out for each species and site, except *I. noli-tangere* from POL and *I. capensis* from GRV and GRP, where the mass data were not obtained for technical reasons.

Temperature variables

Temperature in the field was measured using IBTN sensors (Thermochron Generic F5ROHS DS1921G-F5#) at the localities in the Czech Republic between mid-March and the end of April 2009. The sensors were placed on the surface of the soil and covered with a thin layer of litter. Two sensors were placed at each site, with one sensor placed in sites with occurrence of *I. parviflora* and *I. noli-tangere*, and the second in sites with *I. glandulifera*. The sensors were placed at the sites in mid-March and picked up in early May. Data from 13th March till 30th April were thus available. Temperature was recorded every 2 h. Average temperatures were calculated as arithmetic means of the values of both sensors and minimum temperatures as average of minimums recorded by the two sensors at each locality. The variables were referred to as average or mini-

mum field temperature in the second half of March and average or minimum field temperature in April.

Another set of temperature variables were derived from long-term (40 years) meteorological data for the regions in which the individual sites were situated (Tolasz et al., 2007). Positions of the individual sites were assigned with ca 10 km accuracy in the map, in which the temperature gradients are mapped using zones by 1°C; if a site was at the border of the zones, the average value was used. The variables are referred to as average temperature in regions in March or April, and average date of the last frost in the region. The average date of the last frost was transformed into the length of the period since the beginning of the year (in days) for the analyses. For temperature variables of the sites of Czech *Impatiens* species see Table 1.

Germination in the laboratory

Seeds, dry-stored for 2 months, were placed in plastic Petri dishes filled with heat-sterilized river sand in autumn 2008. Seeds were kept at 5°C and moistened weekly by adding tap water. These conditions were found to break dormancy of *Impatiens* seeds, which germinate under these conditions after one to six months depending on the species (Perglová et al., 2009). There were six replicates of 30 seeds for each species and site. The number of newly germinating seeds (showing radicle longer than 1 mm) was determined twice a week until no new germinating seed were recorded over a period of three weeks. Time when 50% of the viable seeds germinated in each dish (T_{g50}) was used for testing germination dynamics of individual species from each locality.

Seedling emergence in an experimental garden

Dry-stored seeds were sown into 10 cm × 10 cm × 8.5 cm pots containing garden soil in the Experimental Garden of the Institute of Botany, Průhonice (N 49°59', E 14°34'), in October 2008. After sowing the seeds were covered with a thin layer of soil. Ten replicates were used for each species and site for each of the three invasive species and 15 for the native species; each pot contained 30 seeds. The number of seedlings was monitored once a week after the emergence of the first seedling until no new seedlings emerged over a period of two weeks. Time when 50% of the seedlings in each pot emerged (T_{e50}) was used in the analyses.

Frost damage in laboratory

The seeds were stratified on wet sand at 5°C till germination. The germinating seeds were planted into plastic trays with individual 39 ml wells filled with garden soil mixed with Merpan 1000 to prevent fungal infection of the seedlings. The seedlings were cultivated in a climatic chamber (Vötsch 1014) under a 16/8 h light/darkness regime, mean humidity of 70% during the light and 80% during the dark period, radiation of 360 W m⁻² s⁻¹, temperature simulating the gradual changing daily temperature recorded in the field in spring: from a minimum temperature of 5°C (2 am to 5 am) to a maximum of 19°C (13 pm to 15 pm). Seedlings with the first pair of stem leaves were exposed to conditions simulating morning frost: the morning temperature decreased from 7°C to -9°C over a period of 4 h, and then remained at -9°C for 1 h, before increasing to 8°C over a period of 2 h. This regime is the result of previous pilot experiments designed to cause 40–80% of the seedlings to die.

After this the seedlings were cultivated in a climatic chamber under the same conditions as experienced before the exposure to frost. After one week, state of each seedling (living or dead) was recorded.

Table 1
Temperature variables and abbreviations of the sites from which the seeds of *Impatiens* species were collected in the Czech Republic. Climatic variables are based on temperature measurements at the sites studied or on long-term meteorological data (Tolasz et al., 2007; see text for details), with the values used in analyses in brackets.

| Site | Temperature measurements in study sites | | | | Long-term regional averages | | |
|------------------|---|-----------------------|--------------------------------------|-----------------------|-----------------------------|---------------------------|--|
| | Average in second half of March (°C) | Average in April (°C) | Minimum in second half of March (°C) | Minimum in April (°C) | Temperature in March (°C) | Temperature in April (°C) | Date of the last frost (days from the beginning of the year) |
| Volyně (VOL) | 3.74 | 9.39 | 0.36 | 3.40 | 2–3 (2.5) | 6–8 (7) | 20.4–10.5 (125) |
| Čelina (CEL) | 4.03 | 9.54 | 0.84 | 3.91 | 3–4 (3.5) | 7–9 (8) | 30.4–10.5 (120) |
| Velký Osek (POL) | 5.29 | 13.00 | 2.00 | 5.00 | 4–5 (4.5) | 9–10 (9.5) | 20.4–30.4 (115) |
| Potštejn (POT) | 3.62 | 10.45 | 0.61 | 3.25 | 2–3 (2.5) | 7–8 (7.5) | 20.4–10.5 (125) |
| Paskov (PAS) | 3.35 | 11.04 | –0.50 | 2.00 | 3–4 (3.5) | 8–9 (8.5) | 20.4–30.4 (115) |

Statistical analysis

Data on germination dynamics in laboratory and seedling emergence in the garden were at first analysed using ANOVA with a nested design to investigate the effect of species, locality (nested within species) and seed mass for all the species; only dishes and pots in which germinating seeds or seedlings occurred were included into the analyses. Then species \times locality interactions were analysed for the species occurring in the Czech Republic. Effect of temperature variables at the source sites and in the regions were analysed in the next step.

If there was a species \times locality interaction, separate analyses were performed for each species. If the effect of locality persisted in a species, effects of temperature variables on the species performance were investigated. This analysis was used to determine the minimal adequate model in which all the explanatory variables were significant ($P < 0.05$). This was achieved by a stepwise process of effect addition into the model with seed mass used as covariable. First, effects of individual temperature variables were investigated separately (using seed mass as covariable). Second, the variable with the highest F value was included in the model and effect of other variables was tested by adding them individually into the model. Third, the variable with the highest F value and a significant effect was then included into the model and the process was repeated. It was not possible to use the simplification method because of the lack of degrees of freedom. Data on the frost resistance of seedlings were analysed by a similar process but using generalized linear models with binomial errors and logit link functions. The model was tested using chi-square. All calculations were made using statistical software S-Plus 2000 (Mathsoft, 2000).

Results

Germination dynamics in laboratory

There were significant differences in germination dynamics (the time when 50% of the viable seeds germinated – Tg_{50}) between species and localities, and significant species \times locality interaction for the species occurring in the Czech Republic (Table 2). The effect of locality was significant in *I. parviflora* and *I. noli-tangere* ($F = 10.01$ and 5.22 , $P < 0.001$ and $P = 0.005$, respectively). Effects of temperature variables were thus investigated in these species. Tg_{50} of *I. parviflora* significantly depended on average field temperature in the second half of March ($F = 4.23$, $P = 0.049$). Tg_{50} of *I. noli-tangere* depended on average March temperature in the region ($F = 8.64$, $P = 0.010$). Germination of seed of both these species from localities with higher temperatures was delayed (Fig. 1).

Seedling emergence in an experimental garden

There were significant differences between species in time when 50% of the seedlings emerged (Te_{50}) with effect of

locality close to significance (Table 2). Due to non-significant species \times locality interactions for the species occurring in the Czech Republic, effects of temperature variables were investigated for all the species together. Te_{50} was dependent on the minimum field temperature in April ($F = 7.35$, $P = 0.007$). Seedlings from localities with higher minimum temperatures emerged later (Fig. 2).

Frost resistance of seedlings in the laboratory

Seedling survival was significantly influenced by species and locality, with effect of seed mass close to significance (Table 2). *Impatiens noli-tangere* was the most frost-resistant (72% seedling survival averaged across all localities), followed by *I. capensis* (60%)

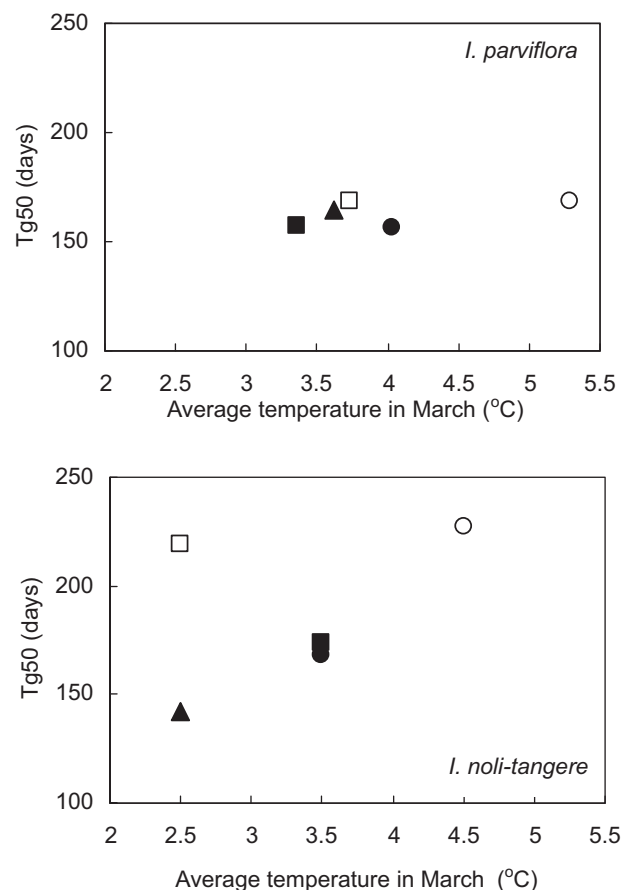


Fig. 1. Relationships between the time when 50% of the seeds germinated (Tg_{50}) and average field temperature in the second half of March for *Impatiens parviflora* ($F = 4.23$, $P = 0.049$), and average temperature in the region in March for *I. noli-tangere* ($F = 8.64$, $P = 0.010$); localities: (▲) Potštejn; (■) Paskov; (●) Čelina; (○) Velký Osek; (□) Volyně.

Table 2

Effect of locality from which a species was collected on germination dynamics (the time when 50% of the viable seeds germinated; T_{g50}) and seedling emergence (time when 50% of the seedlings emerged; T_{e50}) tested using ANOVA, and frost resistance (survival of individual seedlings one week after frost treatment) tested in the four *Impatiens* species using generalized linear models. Significant effects are shown in bold, those close to significance in italics (Bonferroni correction used).

| | Germination dynamics | | | Seedling emergence | | | Frost resistance | | |
|----------------------------------|----------------------|----------|------------------|--------------------|----------|------------------|------------------|-----------------------|------------------|
| | d.f. | <i>F</i> | <i>P</i> | d.f. | <i>F</i> | <i>P</i> | d.f. | <i>R</i> ² | <i>P</i> (Chi) |
| All species | | | | | | | | | |
| Species | 3 | 658.00 | <0.001 | 3 | 30.42 | <0.001 | 3 | 0.0477 | <0.001 |
| Seed mass | 1 | 0.26 | 0.613 | 1 | 1.66 | 0.200 | 1 | 0.0023 | 0.043 |
| Locality (nested within species) | 10 | 6.37 | <0.001 | 14 | 2.06 | 0.031 | 10 | 0.0604 | <0.001 |
| Residuals | 70 | | | 155 | | | 1268 | | |
| Czech species | | | | | | | | | |
| Species | 2 | 920.41 | <0.001 | 2 | 41.03 | <0.001 | 2 | 0.0463 | <0.001 |
| Seed mass | 1 | 0.20 | 0.659 | 1 | 1.56 | 0.214 | 1 | 0.0025 | 0.043 |
| Locality | 4 | 4.64 | 0.002 | 4 | 2.50 | 0.045 | 4 | 0.0169 | <0.001 |
| Species × locality | 6 | 6.72 | <0.001 | 6 | 1.55 | 0.191 | 6 | 0.0480 | <0.001 |
| Residuals | 65 | | | 116 | | | 1179 | | |

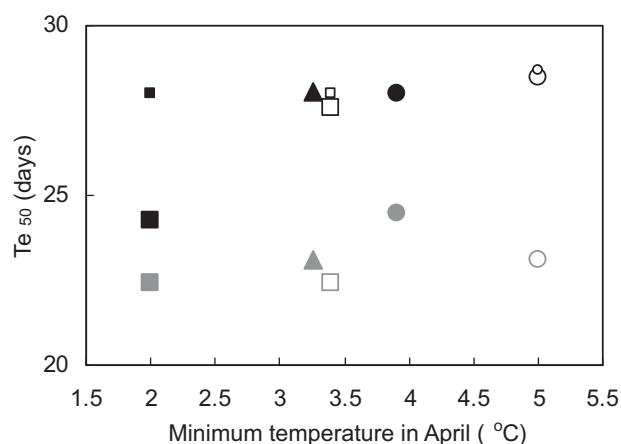


Fig. 2. Relationship between time when 50% of the seedlings emerged (T_{e50}) and minimum field temperature in April for *Impatiens glandulifera* (grey symbols), *I. parviflora* (small black symbols) and *I. noli-tangere* (big black symbols) ($F=7.35$, $P=0.007$); localities: (▲) Potštejn; (■) Paskov; (●) Čelina; (○) Velký Osek; (□) Volyně. Note that in *I. parviflora* and *I. noli-tangere* from Potštejn and Čelina T_{e50} were the same so the symbols overlap.

and *I. glandulifera* (57%) with *I. parviflora* the least resistant (40%) (Fig. 3). There was a significant species × locality interaction for the species present in the Czech Republic (Table 2). The effect of locality was significant in all of them with $R^2=0.069$, 0.040 and 0.097, and $P<0.001$ for *I. glandulifera*, *I. parviflora* and *I. noli-tangere*, respectively.

Frost resistance in *I. glandulifera* was dependent on the average temperature in the region in March and time of seedling emergence

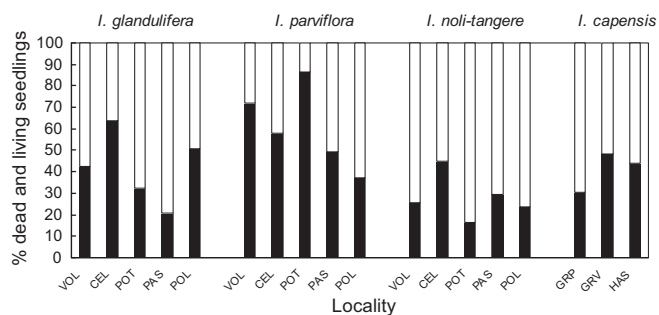


Fig. 3. Percentage of seedlings of four *Impatiens* species from five localities in the Czech Republic (*I. glandulifera*, *I. parviflora*, and *I. noli-tangere*) and three localities in Germany (*I. capensis*) that died (black part of the column) and survived (white part) the exposure to frost. See Table 2 for the significance of results.

in the garden ($R^2=0.042$ and 0.015, respectively, with $P<0.001$). Seedlings from localities with lower temperature and those germinating earlier in the garden were more resistant to frost (Fig. 4a and b). In *I. parviflora* frost resistance was dependent on the average temperature in the region in April ($R^2=0.062$, $P<0.001$). Seedlings from localities in regions with higher April temperature were more resistant (Fig. 4c). Frost resistance of the native *I. noli-tangere* was not affected by any of the temperature variables investigated.

Discussion

Overall performance of the species studied

There were significant differences in the performance of the four *Impatiens* species tested. Germination and seedling emergence was in accordance with the previously reported results (Perglová et al., 2009). The invasive species were more sensitive to frost than native *I. noli-tangere*. Considerable frost sensitivity of early-emerging *I. glandulifera* seedlings may impose considerable risk of death due to late frosts. This risk may be serious because of the simultaneous seed germination in this species (Beerling and Perrins, 1993; Perglová et al., 2009), which makes it impossible for it to compensate for any loss of seedlings. In the highly frost sensitive *I. parviflora* the risk of damage by early frost may be at least partly avoided by later seedling emergence. Late frost may thus reduce competitive strength of *I. glandulifera* and so favour the two later-emerging species, especially *I. noli-tangere*, which is very frost-resistant. Different responses to late frosts in the spring might contribute to coexistence of the three species in the field. Frost resistance of *I. capensis* was within the range of that of the three species occurring in the Czech Republic. Despite of this species originating from sites with milder climate than in the Czech Republic (Müller, 1982), this indicates that in terms of frost sensitivity there seem to be no barriers to this species spreading further east from the west of Europe, where it is currently invasive. The limited invaded range of this species may be therefore attributed to other factors (for more details see Perglová et al., 2009).

Variability within species

There were significant differences between plants from seeds from different sites of all the species studied. In native *I. noli-tangere* differentiation was found in all traits studied. This supports observations of Hatcher (2003) who found differences between populations at a similar scale in the United Kingdom. Plants from seeds from different sites of the invasive species differed only in some traits. In *I. parviflora* they differed in seed germination

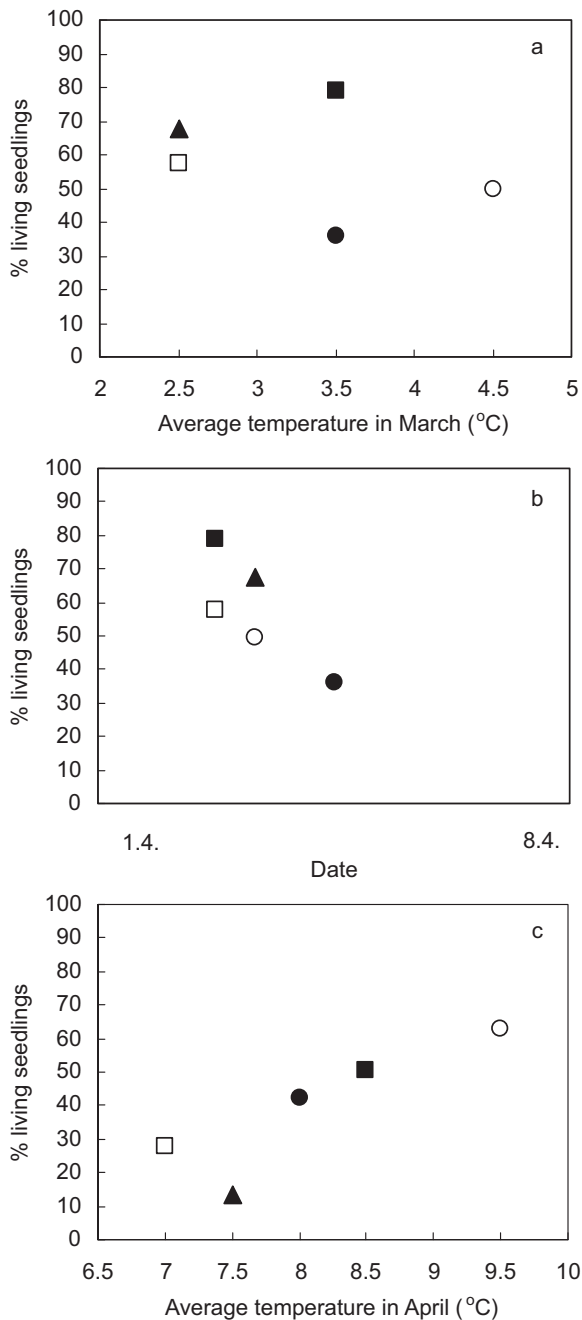


Fig. 4. Relationship between the percentage of seedlings that survived the exposure to frost and (a) average temperature in the region in March for *Impatiens glandulifera* ($P < 0.001$), (b) time when 50% of the seedling emerged in common garden (T_{e50}) for *I. glandulifera* ($P < 0.001$), and (c) average temperature in the region in April for *I. parviflora* ($P < 0.01$). Localities: (▲) Potštejn; (■) Paskov; (●) Čelina; (○) Velký Osek; (□) Volyně.

dynamics and frost resistance. This differentiation is not in accordance with the low local variation found in Europe (Coombe, 1956). On the other hand, colonization of various less disturbed Central-European habitats by *I. parviflora* suggests that this species is in the secondary phase of invasion in which adaptations may develop (Wade, 1997; Dietz and Edwards, 2006).

In *I. glandulifera* significant differentiation was found only in frost resistance of the seedlings and differentiation was not found in potentially invasive *I. capensis*. The absence of differentiation in germination and dynamics of seedling emergence is surprising

because considerable differentiation was found in another life history trait, i.e. flowering phenology. In *I. glandulifera* it changes along latitudinal gradient in the invaded area (Kollmann and Bañuelos, 2004). In *I. capensis* differentiation in flowering phenology was found at a scale similar to that in this study (Simpson et al., 1985) together with differentiation in response to other environmental factors (Dudley and Schmitt, 1995; Donohue et al., 2001; Heschel et al., 2002). It is possible that both species are variable in only some traits or that differentiation has been in process. The low differentiation in *I. capensis* may also be due to the limited number and proximity of localities from which seed was collected. The maximum distance between the sites is 70 km, and two of the three are assumed to have originated from an identical source, i.e. Botanical Garden of University of Marburg, from which the species probably spreads along a brook (Ute Becker, pers. com).

Relationship to the environment in sites from which seeds were collected

The differences found among populations of *I. noli-tangere*, *I. parviflora* and *I. glandulifera* were often correlated with climatic conditions at the sites from which they were collected (after removing the effect of seed mass which was demonstrated to influence seedling size (Schmitt and Ehrhard, 1990) and may thus affect seedling performance). Temperature variables measured directly at the localities sometimes explained the differences better than variables derived from long-term meteorological data for the regions. This indicates the important role of local conditions, such as relief and vegetation cover, as factors modifying local climate.

The differentiation of populations along gradients in climatic conditions at the source localities is, as previously suggested, likely to be a result of selection (Leon et al., 2006). Like seed from high altitudes (Gimenez-Benavides et al., 2007; Leger and Rice, 2007; Li and Feng, 2009) that of *I. parviflora* and *I. noli-tangere* species collected from populations growing at localities with lower spring temperature germinated earlier. Early germination may enable plants to effectively use the growing season, which is shorter at sites located in colder regions. Seeds from warmer localities germinated later in the laboratory, indicating deeper dormancy and need for longer stratification (Okagami and Kawai, 1982). As seedlings emerged later in the garden, the stratified seeds from localities in warmer regions may also have higher threshold for germination following stratification (Fenner and Thompson, 2005), probably in order to prevent from early seedling emergence in warm regions.

Differences between the populations may reflect frost sensitivity of the species studied. In the highly frost-sensitive *I. parviflora* differentiation explained by local conditions was found both in germination and frost resistance of individual populations. In the moderately sensitive *I. glandulifera* differentiation was only in frost resistance. Like those in germination, the differences in frost resistance between populations may be due to different threshold for induction of the freezing tolerance (Fowler, 2008). In highly resistant *I. noli-tangere* differentiation was only in germination.

Variability interpretation

The differences found among the populations of *I. noli-tangere*, *I. parviflora* and *I. glandulifera* were often dependent on climatic conditions at the sites from which the seed was collected. Similarly as in other studies (Kollmann and Bañuelos, 2004; Montague et al., 2008; Weber and Schmidt, 1998; Dlugosch and Parker, 2008; Allan and Pannell, 2009), it may be interpreted as evolutionary adaptation to climate heterogeneity. As most previous authors we used plants grown from seed collected in the field without previous

cultivation under common garden conditions and testing genetic differences (but see Dlugosch and Parker, 2008). Thus, it is not clear whether the differences are due to genetic or epigenetic factors (Roach and Wulff, 1987) or combination of both (Bossdorf et al., 2008). Epigenetic modifications have recently been considered an additional layer of heritable phenotypic variation that is, unlike genetic variation, environmentally labile and reversible (Richards et al., 2010). Epigenetic variation due to DNA methylation may be involved in population differentiation in ecologically important traits (Herrera and Bazaga, 2010). The epigenetic modifications have been shown to modify plant traits including life history independently of genetic variation (Bossdorf et al., 2010). They thus may play a role in differentiation of the *Impatiens* populations. There are also some studies documenting environmental maternal effects particularly for early traits including dormancy and germination (Roach and Wulff, 1987; Luzuriaga et al., 2006). Frost resistance may be also due to maternal effect because materials stored in the seed may influence the early juvenile phenotype (Roach and Wulff, 1987). On the other hand, Monty et al. (2009) did not detect any environmental maternal effects in differentiation of the populations of alien invasive plants along altitudinal gradient.

In our study, local adaptations were indicated both in native and invasive species studied, therefore they are unlikely to provide the invasive *Impatiens* species with an advantage against the native congener, at least in terms of the traits investigated. One avenue of future research within this species complex would be to identify the sources of observed differences to obtain better insights into mechanisms generating possible adaptive differentiation (Schmitt and Dudley, 1996).

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