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## Seedling traits, plasticity and local differentiation as strategies of invasive species of *Impatiens* in central Europe

Hana Skálová<sup>1,\*</sup>, Vendula Havlíčková<sup>1</sup> and Petr Pyšek<sup>1,2</sup>

<sup>1</sup>Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic and <sup>2</sup>Department of Ecology, Charles University in Prague, CZ-128 44 Viničná 7, Prague, Czech Republic

\*For correspondence. E-mail [hana.skalova@ibot.cas.cz](mailto:hana.skalova@ibot.cas.cz)

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- **Background and Aims** Invasiveness of some alien plants is associated with their traits, plastic responses to environmental conditions and interpopulation differentiation. To obtain insights into the role of these processes in contributing to variation in performance, we compared congeneric species of *Impatiens* (Balsaminaceae) with different origin and invasion status that occur in central Europe.
- **Methods** Native *I. noli-tangere* and three alien species (highly invasive *I. glandulifera*, less invasive *I. parviflora* and potentially invasive *I. capensis*) were studied and their responses to simulated canopy shading and different nutrient and moisture levels were determined in terms of survival and seedling traits.
- **Key Results and Conclusions** *Impatiens glandulifera* produced high biomass in all the treatments and the control, exhibiting the 'Jack-and-master' strategy that makes it a strong competitor from germination onwards. The results suggest that plasticity and differentiation occurred in all the species tested and that along the continuum from plasticity to differentiation, the species at the plasticity end is the better invader. The most invasive species *I. glandulifera* appears to be highly plastic, whereas the other two less invasive species, *I. parviflora* and *I. capensis*, exhibited lower plasticity but rather strong population differentiation. The invasive *Impatiens* species were taller and exhibited higher plasticity and differentiation than native *I. noli-tangere*. This suggests that even within one genus, the relative importance of the phenomena contributing to invasiveness appears to be species-specific.

**Key words:** Alien species, congeners, plant traits, population differentiation, non-native plants.

### INTRODUCTION

The identification of mechanisms underlying successful invasions has been one of the important topics in plant invasion ecology (e.g. Rejmánek and Richardson, 1996; Davis *et al.*, 2000; Daehler, 2003; Seastedt and Pyšek, 2011). Species' traits (Pyšek and Richardson, 2007; Kubešová *et al.*, 2010; Moravcová *et al.*, 2010; van Kleunen *et al.*, 2010), phenotypic plasticity (Richards *et al.*, 2006; Berg and Ellers, 2010) and local differentiation (Williams *et al.*, 1995; Sakai *et al.*, 2001; Keller and Taylor, 2008; Prentis *et al.*, 2008) are documented as factors playing a role in the invasion process. 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), and this assumption is supported by studies on the role of phenotypic plasticity in plant invasions (Richards *et al.*, 2006; Funk, 2008). Thus, comparisons of closely related species are a convenient tool for identifying mechanisms linked to plant invasiveness due to minimizing biases associated with phylogenetic distance. As species from the same habitats tend to be similar to each other in terms of ecology and differ from species in other habitats (Morgan and Smith, 1979; Franks

and Farquhar, 1999), habitat- and community-related biases can be further minimized if the closely related species studied co-occur.

Studies that address species' traits favouring invasion repeatedly highlight the importance of size, growth rate, biomass allocation and survival (van Kleunen *et al.*, 2010, and references therein). Several studies also report the role of seedling traits in invasion success (Grotkopp and Rejmánek, 2007; Morrison and Mauck, 2007; Zheng *et al.*, 2009). However, most studies addressing the importance of traits associated with invasion success are limited in their scope, and ignore recommendations to measure the traits of plants growing in more than one environment (Burns, 2004; Leicht-Young *et al.*, 2007; Williams *et al.*, 2008; Berg and Ellers, 2010). It is suggested that invasive plants are highly phenotypically plastic, enabling them to grow and reproduce in a wide range of environmental conditions (Baker, 1965; Sultan, 2001; Daehler, 2003; Pigliucci, 2005; Rejmánek *et al.*, 2005), which can result in a broadening of their habitat niche in the invaded range (Richards *et al.*, 2006; Hejda *et al.*, 2009). The evolution of plasticity in response to a set of environments may be beneficial at novel sites that a species colonizes following introduction or migration in general (Agrawal, 2001; Donohue *et al.*, 2001; Yeh and Price, 2004). Plant invasions are often facilitated by disturbance (Hobbs and Huenneke, 1992; Davis *et al.*, 2000), but in later

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stages of the invasion process, some species spread into natural and semi-natural habitats where they experience increased competition from the native flora and lower levels of resources (Dietz and Edwards, 2006). This is when plasticity in physiological and morphological traits may enable invasive plants to overcome the constraints imposed by limiting resources (Funk, 2008).

Nevertheless, not all invasive species owe their success to high phenotypic plasticity (Brock and Galen, 2005; Hastwell and Panetta, 2005; Zheng et al., 2009). Locally adapted genotypes may develop during the initial lag following introduction into a new region (Sakai et al., 2001; Blackburn et al., 2011). This process can be very fast, and adaptation to novel environments can appear within  $\leq 20$  generations (Prentis et al., 2008). The role of phenotypic plasticity and genetic differentiation in plant invasions has been compared only recently (Alexander, 2010; Monty and Mahy, 2010). However, there is no study addressing their roles by comparing native and alien congeners.

To obtain insights into the role of plant traits, phenotypic plasticity and local differentiation in contributing to performance response under variable environmental factors such as light intensity, nutrients and moisture, we used four annual species of the genus *Impatiens* (Balsaminaceae) occurring in central Europe; the species have similar life histories and coexist in some habitats. The species studied included the native *I. noli-tangere* and three aliens differing in their invasion status: the highly invasive *I. glandulifera*, less invasive *I. parviflora* and potentially invasive *I. capensis*. We used growth traits of seedlings, which annual species depend on for population regeneration, to address the following questions. (1) Are there any differences in the seedling traits of the species studied? (2) Do the species differ in their plasticity in response to different levels of irradiation, nutrients and moisture? (3) What is the variability in the performance of individual populations within native and invasive species?

## MATERIALS AND 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). *Impatiens noli-tangere* is native to the Czech Republic (Slavík, 1997; Pyšek et al., 2002). The invasive species were grown in Europe and escaped from cultivation at similar times in the mid 19th century (Adamowski, 2008). *Impatiens glandulifera* is spreading rapidly in the Czech Republic (Pyšek and Prach, 1995), whereas the current spread of *I. parviflora* is slower and its occurrence more stabilized. *Impatiens capensis* is invasive in western Europe, and the closest localities to the Czech Republic are in central Germany (Skálová et al., 2011). As annuals with a limited seed bank (Perglová et al., 2009), all *Impatiens* species studied crucially depend on the successful performance of juveniles every year.

### *Seed collection*

Seeds were collected in July and August 2008. Localities in the Czech Republic were chosen that harboured all three

*Impatiens* species present in the country. Seeds of *I. glandulifera*, *I. parviflora* and *I. noli-tangere* were collected from five localities: Černětice near Volyně (coded as VOL; 49°88'3'30"N, 13°533'5'50"E), Čelina (CEL; 49°433'5'50"N, 14°200'3'30"E), Potštejn (POT; 50°44'1'15"N, 16°199'2'25"E), Velký Osek (POL; 50°07'N, 15°10'E) and Paskov (PAS; 49°44'N, 18°18'E). All three species grew in mixed stands or very close to each other in forests, along shaded brooks and river banks at VOL, CEL and POT. At POL and PAS, seeds of *I. noli-tangere* and *I. parviflora* were collected from mixed forest stands and those of *I. glandulifera* along a river bank within 1–2 km.

Seeds of *I. capensis* were collected from three localities in central Germany (the region of Frankfurt am Main) in September 2008: along the banks of a brook in open farmland near the village of Großseelheim (GRV; 50°488'3'37"N, 8°522'5'52"E), in a wet pasture between the villages of Großseelheim and Schröck (GRP; 50°488'6'6"N, 8°500'1'15"E) and in wet meadow margins and a spruce forest near the homestead village of Hassemülle (HAS; 50°122'8'8"N, 8°211'2'20"E).

For each species, a mixed sample of seed from at least 100 individuals randomly chosen from the whole site was collected. As seed mass may influence seedling performance (Schmitt and Ehrhardt, 1990), it was used as a covariate in some analyses. Because the seeds are very small their individual weight was obtained by weighing groups of 25 seeds. Six measurements were carried out for each species and site, except *I. capensis*, for which this information was not obtained for technical reasons.

### *Experiments*

Seeds, dry-stored for 2 months, were stratified on wet sand at 5 °C until germination. The germinating seeds were planted in plastic trays with individual 39 mL wells filled with pure sand. Sixteen seeds were used for each species, locality and environment. Due to very low germination, seeds of *I. noli-tangere* from only three localities (VOL, PAS and POT) were planted. The plants were cultivated in climatic chambers (Vötsch 1014) under a 16/8 h light/darkness regime, with a mean humidity of 70 % during the light and 80 % during the dark period. The temperatures used simulated the gradually changing daily temperature recorded in the field in spring from a minimum of 5 °C (0200–0500 h) to a maximum of 19 °C (1300–1500 h). Other parameters included photosynthetically active radiation (PAR) of 360  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , red radiation (R,  $\lambda = 660 \text{ nm}$ ) of 26  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and far-red radiation (FR,  $\lambda = 730 \text{ nm}$ ) of 15  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , R/FR = 1.73. The radiation was measured using a SPh 2020 photometer from Optické dílny Turnov, Czech Republic.

In the nutrient level experiment, the seedlings were supplied with Knopp nutrient solution of three concentrations (100, 50 and 10 %) under optimal moisture conditions (see below). The 50 % concentration corresponds to the nitrogen supply previously used in experiments on *I. glandulifera* (Andrews et al., 2005). Shading by the canopy was simulated by using double-layered green foil placed under the irradiation panel. It resulted in a PAR = 130  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,

$R = 4.1 \mu\text{mol.m}^{-2} \text{ s}^{-1}$ ,  $FR = 6.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ,  $R/FR = 0.65$  (for details of the foil, see Skálová and Krahulec, 1992). To assess the effect of different moisture levels, plants were supplied with 50% Knopp solution with the level in the containers maintained: (1) continuously at the soil surface, simulating flooded soil; (2) continuously at a level of 1–2 cm to provide plants with optimal conditions; or (3) to simulate drought; in this case the plants were supplied with the solution twice a week by placing the tray in a dish with the solution at a level of 1–2 cm for about 1 h. The influence of shading was studied using plants supplied with the 50% Knopp solution at the optimum (1–2 cm) moisture level. The flooding and drought treatments started when the cotyledons emerged from the testa and were horizontally oriented. Interactions among the factors were not addressed since a factorial design of the treatments was not possible due to limited space in the climatic chambers. In all the environmental conditions except drought, the plants were checked three times per week and the solution supplied to the levels indicated above. The solution was changed completely every 2 weeks. The experiment lasted for 5 weeks from the emergence of the cotyledons from the testa. Afterwards, the state of each seedling (living or dead) was recorded. For the living seedlings, stem height was measured and, when the plants were harvested, root and shoot biomass was separated. The plants were dried at 60 °C for about 6 h and then weighed. Plasticity was calculated separately for each species and each trait in each environment as an average value for a given environment/the value for the control – 1.

#### Data analysis

Data on plant survival (i.e. seedling state) were analysed using generalized linear mixed models with binomial errors and a logit link function; the model was tested using  $\chi^2$ . For the seedlings that survived until the end of the experiment (Table 1), stem height, total plant biomass and the root/shoot ratio were analysed using analysis of variance (ANOVA). Due to the absence of factorial design, separate analyses were performed for each treatment. As seed of *I. capensis* originated from localities different from that of the species occurring in the Czech Republic, i.e. *I. glandulifera*, *I. parviflora* and *I. noli-tangere*, the analyses testing the effects of species and locality were done in two steps: (1) for all species with locality nested within species; and (2) for species occurring in the Czech Republic with species  $\times$  locality interaction. For the latter analyses, seed mass was used as a covariable to eliminate a possible effect of seed mass on seedling performance. To assess the variability in individual species explained by the treatment and locality, separate analyses were done for each species using identical models for all of them. Plasticity was analysed using ANOVA in two steps, i.e. for all species and for species occurring in the Czech Republic. All calculations were run in the statistical software S-Plus 2000 (Mathsoft Inc., 2000).

TABLE 1. Survival of the four Impatiens species (average percentage of plants alive at the end of the experiment followed in parentheses by the numbers of surviving individuals from GRP, GRV and HAS localities in *I. capensis*, from PAS, POT and VOL in *I. noli-tangere* and from CEL, PAS, POL, POT and VOL in *I. glandulifera* and *I. parviflora*) kept under different conditions of simulated shading, and nutrient and moisture levels.

Species	Control	Nutrients 10%	Nutrients 100%	Flooding	Drought	Simulated canopy shade
<i>I. capensis</i>	77.1 (14, 10, 13)	93.6 (16, 14, 15)	8.3 (2, 0, 16, 100)	79.2 (16, 9, 13)	43.8 (14, 12, 1)	89.6 (14, 14, 15)
<i>I. glandulifera</i>	87.3 (15, 15, 16, 16, 11)	90.0 (15, 16, 15, 13, 15)	22.5 (16, 16, 9, 16, 16)	79.6 (16, 12, 14, 14, 9)	77.3 (14, 16, 10, 14, 10)	100.0 (16, 16, 16, 16, 16)
<i>I. noli-tangere</i>	79.2 (12, 11, 15)	93.8 (14, 16, 16, 16)	89.1 (13, 14, 16)	70.2 (11, 13, 10)	60.4 (5, 13, 11)	97.9 (16, 15, 16)
<i>I. parviflora</i>	67.5 (16, 15, 15, 16, 16)	00.0001 (16, 16, 16, 16, 16)	94.9 (16, 16, 16, 16, 16)	90.0 (16, 8, 16, 16, 16)	100.0 (16, 16, 16, 16, 16)	100.0 (16, 16, 16, 16, 16)

For the test of significance see Table 2.

TABLE 2. Effects of species, locality and treatment (simulated shading, and nutrient and moisture levels) on survival (number of seedlings alive) of the four Impatiens species recorded at the end of the experiment and tested using generalized linear models, and the effects of species, locality and treatment on stem height, total biomass and root/shoot ratio tested using ANOVA

	Plant survival			Stem height			Biomass				Root/shoot ratio				
	d.f.	R <sup>2</sup>	P (χ <sup>2</sup> )	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>
Canopy shade – all species															
Species (Spec.)	3	0.09	< <b>0.001</b>	3	502	< <b>0.001</b>	0.229	3	369	< <b>0.001</b>	0.441	3	106.74	< <b>0.001</b>	0.183
Locality (Loc.)	12	0.25	0.05	12	21.4	< <b>0.001</b>	0.039	12	7.53	< <b>0.001</b>	0.071	12	7.4	< <b>0.001</b>	0.138
Treatment (Tr.)	1	0.17	< <b>0.001</b>	1	3481	< <b>0.001</b>	0.527	1	89.3	< <b>0.001</b>	0.039	1	138.94	< <b>0.001</b>	0.148
Spec. × tr.	3	0.27	0.077	3	242	< <b>0.001</b>	0.110	3	177	< <b>0.001</b>	0.197	3	46.46	< <b>0.001</b>	0.088
Residuals	474			423				423				423			
Canopy shade – Czech species															
Seed mass	1	0	0.761	1	1614	< <b>0.001</b>	0.233	1	728.01	< <b>0.001</b>	0.409	1	130.13	< <b>0.001</b>	0.131
Species (Spec.)	2	0.09	< <b>0.001</b>	2	73.3	< <b>0.001</b>	0.021	2	21.6	< <b>0.001</b>	0.024	2	73.96	< <b>0.001</b>	0.149
Locality (Loc.)	4	0.03	0.2	4	11.5	< <b>0.001</b>	0.007	4	6.32	< <b>0.001</b>	0.014	4	8.69	< <b>0.001</b>	0.035
Treatment (Tr.)	1	0.15	< <b>0.001</b>	1	3573	< <b>0.001</b>	0.515	1	90.4	< <b>0.001</b>	0.051	1	111.66	< <b>0.001</b>	0.111
Spec. × loc.	6	0.05	0.136	5	40.8	< <b>0.001</b>	0.029	5	8.58	< <b>0.001</b>	0.024	5	3.18	<b>0.008</b>	0.016
Spec. × tr.	2	0.01	0.484	2	417	< <b>0.001</b>	0.120	2	231	< <b>0.001</b>	0.260	2	66.22	< <b>0.001</b>	0.133
Loc. × tr.	4	0.01	0.88	4	2.07	0.084	0.001	4	2.72	0.029	0.006	4	1.28	0.276	0.005
Spec. × loc. × tr.	6	0	1	6	26.4	< <b>0.001</b>	0.023	6	3.84	<b>0.001</b>	0.013	6	10.91	< <b>0.001</b>	0.066
Residuals	384			353				353				353			
Nutrient levels – all species															
Species (Spec.)	3	0.2	< <b>0.001</b>	3	79.4	< <b>0.001</b>	0.111	3	539	< <b>0.001</b>	0.550	3	170.44	< <b>0.001</b>	0.161
Locality (Loc.)	12	0.07	< <b>0.001</b>	12	11.5	< <b>0.001</b>	0.064	12	6.24	< <b>0.001</b>	0.025	12	5.63	< <b>0.001</b>	0.021
Treatment (Tr.)	2	0.26	< <b>0.001</b>	2	379	< <b>0.001</b>	0.353	2	147	< <b>0.001</b>	0.100	2	921.5	< <b>0.001</b>	0.579
Spec. × tr.	6	0.08	< <b>0.001</b>	6	60.9	< <b>0.001</b>	0.170	6	55.6	< <b>0.001</b>	0.114	6	19.48	< <b>0.001</b>	0.037
Residuals	714			526				526				526			
Nutrient levels – Czech species															
Seed mass	1	0.12	< <b>0.001</b>	1	92.6	< <b>0.001</b>	0.051	1	1212	< <b>0.001</b>	0.506	1	2.63	<b>0.106</b>	0.000
Species (Spec.)	2	0.05	< <b>0.001</b>	2	64.8	< <b>0.001</b>	0.071	2	21.5	< <b>0.001</b>	0.018	2	323.4	< <b>0.001</b>	0.183
Locality (Loc.)	4	0.01	0.124	4	4.21	<b>0.002</b>	0.009	4	8.69	< <b>0.001</b>	0.015	4	1.39	0.236	0.002
Treatment (Tr.)	2	0.15	< <b>0.001</b>	2	325	< <b>0.001</b>	0.354	2	136	< <b>0.001</b>	0.114	2	1046.73	< <b>0.001</b>	0.595
Spec. × loc.	6	0.04	< <b>0.001</b>	5	10.5	< <b>0.001</b>	0.029	5	4.33	< <b>0.001</b>	0.009	5	6.62	< <b>0.001</b>	0.009
Spec. × tr.	4	0.07	< <b>0.001</b>	4	88.5	< <b>0.001</b>	0.193	4	69.8	< <b>0.001</b>	0.117	4	35.56	< <b>0.001</b>	0.040
Loc. × tr.	8	0.02	0.301	8	4.03	< <b>0.001</b>	0.018	8	3.93	< <b>0.001</b>	0.013	8	5.07	< <b>0.001</b>	0.012
Spec. × loc. × tr.	12	0.01	0.794	12	4.4	< <b>0.001</b>	0.029	12	3.94	< <b>0.001</b>	0.020	12	8.19	< <b>0.001</b>	0.028
Residuals	580			453				453				453			
Moisture levels – all species															
Species (Spec.)	3	0.11	< <b>0.001</b>	3	207	< <b>0.001</b>	0.364	3	628	< <b>0.001</b>	0.650	3	269.39	< <b>0.001</b>	0.486
Locality (Loc.)	12	0.11	< <b>0.001</b>	12	19.8	< <b>0.001</b>	0.139	12	7.04	< <b>0.001</b>	0.029	12	7.94	< <b>0.001</b>	0.057
Treatment (Tr.)	2	0.01	<b>0.012</b>	2	48.2	< <b>0.001</b>	0.056	2	70.5	< <b>0.001</b>	0.049	2	20.76	< <b>0.001</b>	0.025
Spec. × tr.	6	0.03	<b>0.004</b>	6	16.3	< <b>0.001</b>	0.057	6	28.6	< <b>0.001</b>	0.059	6	9	< <b>0.001</b>	0.032
Residuals	733			576				576				576			
Moisture levels – Czech species															
Seed mass	1	0	0.598	1	591	< <b>0.001</b>	0.387	1	1452	< <b>0.001</b>	0.629	1	236.15	< <b>0.001</b>	0.164
Species (Spec.)	2	0.09	< <b>0.001</b>	2	12	< <b>0.001</b>	0.016	2	13.1	< <b>0.001</b>	0.011	2	258.43	< <b>0.001</b>	0.360
Locality (Loc.)	4	0.04	< <b>0.001</b>	4	14.4	< <b>0.001</b>	0.038	4	6.87	< <b>0.001</b>	0.012	4	5.99	< <b>0.001</b>	0.017
Treatment (Tr.)	2	0.01	<b>0.04</b>	2	57.5	< <b>0.001</b>	0.075	2	64.9	< <b>0.001</b>	0.056	2	17.24	< <b>0.001</b>	0.024
Spec. × loc.	6	0.04	< <b>0.001</b>	5	8.5	< <b>0.001</b>	0.028	5	3.5	<b>0.004</b>	0.008	5	2.93	<b>0.013</b>	0.010
Spec. × tr.	4	0.03	<b>0.006</b>	4	30.4	< <b>0.001</b>	0.080	4	34.5	< <b>0.001</b>	0.060	4	12.62	< <b>0.001</b>	0.035
Loc. × tr.	8	0.04	<b>0.01</b>	8	3.1	<b>0.002</b>	0.016	8	2.02	0.043	0.007	8	4.66	< <b>0.001</b>	0.026
Spec. × loc. × tr.	12	0.03	0.24	12	5.6	< <b>0.001</b>	0.044	12	1.6	0.089	0.008	12	3.37	< <b>0.001</b>	0.028
Residuals	598			483				483				483			

For all species analyses, locality was nested within species; for Czech species analyses, seed mass was used as covariable; significant values are shown in bold (using Bonferroni correction).

## RESULTS

## Species' traits

The four species studied differed significantly in terms of survival, total biomass, root/shoot ratio and stem height (Table 2).

Under control conditions (50% Knopp solution, optimal moisture, full light), *I. parviflora* survived best (97.5% of the plants were alive at the end of the experiment), followed by *I. glandulifera*, *I. noli-tangere* and *I. capensis*. Shading and low nutrients resulted in increased survival in all the species, reaching 100% in *I. glandulifera* and *I. parviflora*. High nutrient levels decreased survival in two of the invasive

species, *I. capensis* and *I. glandulifera*. Drought and flooding reduced the survival of *I. glandulifera* and *I. noli-tangere*, but not that of *I. parviflora* and *I. capensis* (Table 1).

Biomass produced by *I. glandulifera* greatly exceeded that of other species. The only exception to this trend was that *I. glandulifera* plants grown in shade had biomass comparable with that of *I. parviflora*, the second most productive species regardless of the environment (Fig. 1). Although seedlings of *I. glandulifera* produced most biomass, their stems were tallest only when grown in shade (Fig. 1). The native *I. noli-tangere* produced less biomass and was usually shorter than the two invasive species (Fig. 1). The potentially

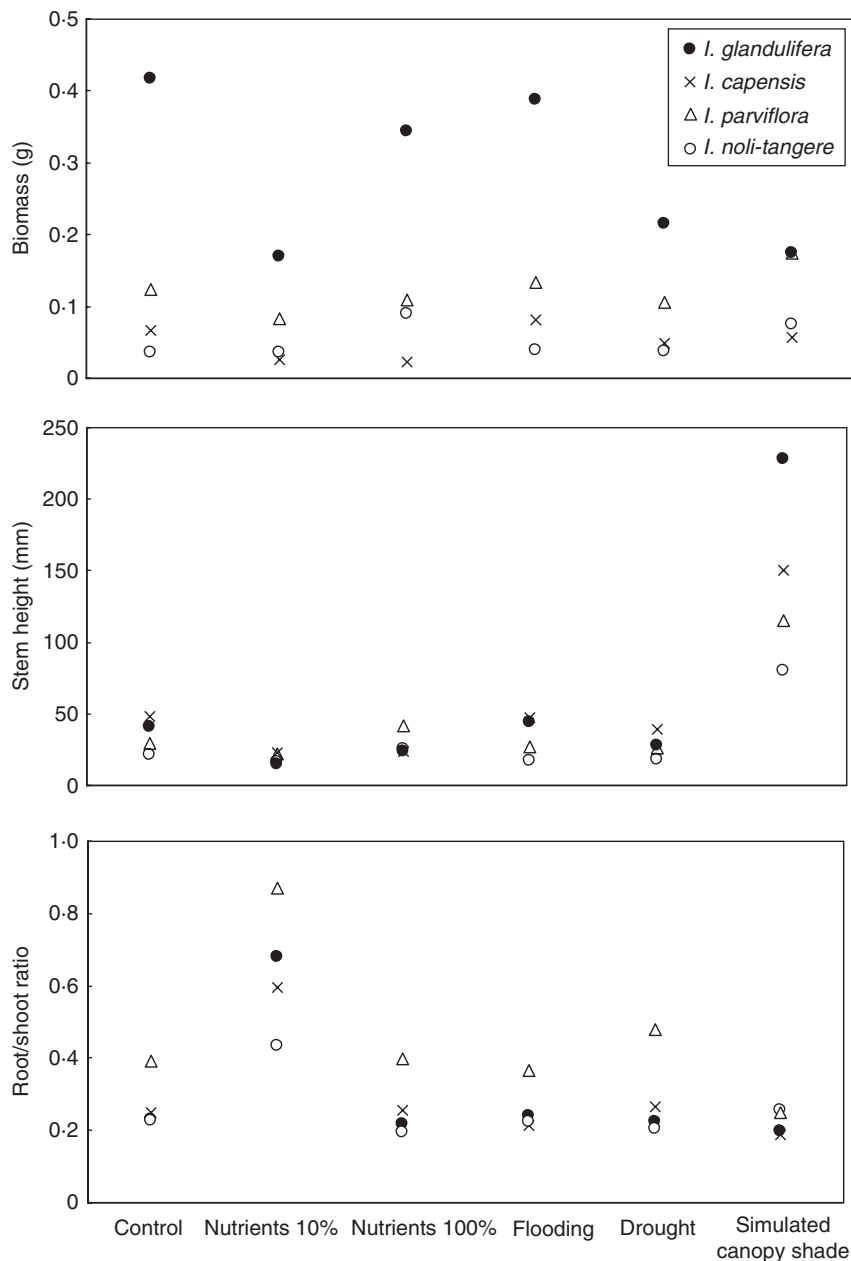


FIG. 1 Total biomass, stem height and root/shoot ratio of native and invasive *Impatiens* species recorded in the different treatments; species are indicated in the key. The points denote averages for plants from three localities for *I. noli-tangere* and *I. capensis* and five localities for *I. glandulifera* and *I. parviflora*; for the test of significance see Table 2.

invasive *I. capensis* performed similarly to *I. noli-tangere* in terms of total biomass but only under high nutrient concentration where its biomass was considerably lower (Fig. 1). Its stems were among the tallest in most of the environments (Fig. 1). *Impatiens parviflora* allocated more biomass to roots than the other species in all treatments except simulated shading (Fig. 1).

#### Species' plasticity

The response in terms of total biomass, root/shoot ratio and stem height of individual species to shading, and nutrient and

moisture levels (species  $\times$  treatment interactions, Table 2) differed. Variation in shading and nutrient levels accounted for substantially more of the variability in these traits than did moisture (Tables 2 and 3). Low levels of nutrients resulted in decreased total biomass and stem height and an increased root/shoot ratio, with plasticity being the highest in all three traits in *I. glandulifera* (Fig. 2). Simulated shading triggered intensive stem elongation, with the highest plasticity recorded in *I. glandulifera* (Fig. 2). The other environments did not result in the same response in species' traits. The total biomass of invasive species was lower in all the treatments, but that of *I. parviflora* and *I. capensis* was greater in the

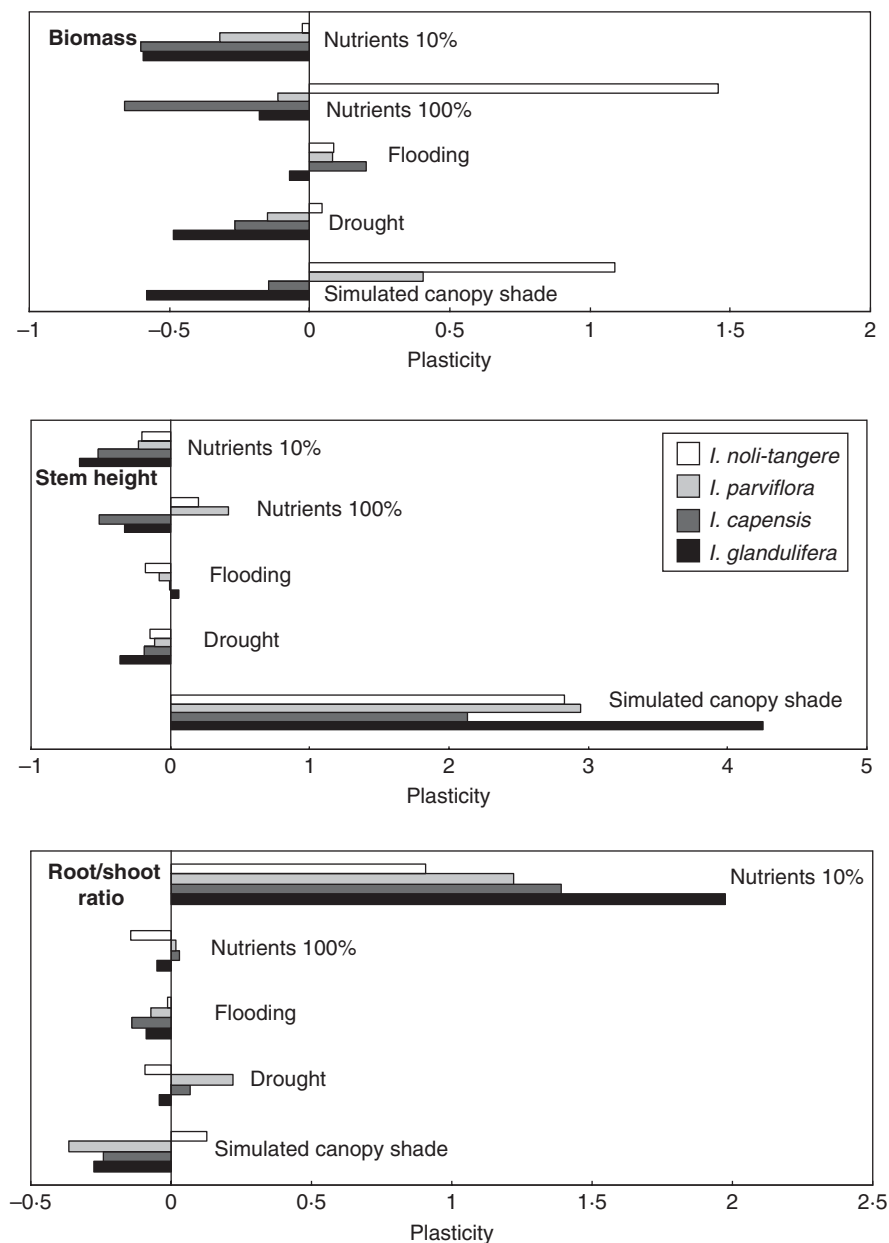


FIG. 2 Plasticity in total biomass, stem height and root/shoot ratio of native and invasive *Impatiens* species in response to individual treatments; species are indicated in the key. The plasticity of individual species was calculated as the average value recorded in a particular treatment/the value recorded for the control - 1; for the test of significance see Table 2.

TABLE 3. Effects of locality and treatment (simulated shading, and nutrient and moisture levels) on stem height, total biomass and root/shoot ratio tested using ANOVA

	Stem height				Biomass				Root/shoot ratio			
	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>
<i>I. glandulifera</i> – Control												
Locality	4	5.14	<b>0.001</b>	0.252	4	3.60	<b>0.011</b>	0.192	4	7.14	< <b>0.001</b>	0.319
<i>I. parviflora</i> – Control												
Locality	4	12.36	< <b>0.001</b>	0.414	4	17.40	< <b>0.001</b>	0.500	4	6.27	< <b>0.001</b>	0.264
<i>I. capensis</i> – Control												
Locality	2	17.34	< <b>0.001</b>	0.512	2	8.62	< <b>0.001</b>	0.343	2	8.28	<b>0.001</b>	0.334
<i>I. noli-tangere</i> – Control												
Locality	2	5.14	<b>0.011</b>	0.232	2	6.152	<b>0.005</b>	0.266	2	2.74	0.079	0.139
<i>I. glandulifera</i> – Canopy shade												
Locality	4	18.42	< <b>0.001</b>	0.033	4	2.47	0.048	0.025	4	6.35	< <b>0.001</b>	0.123
Treatment	1	1976.45	< <b>0.001</b>	0.898	1	233.60	< <b>0.001</b>	0.601	1	14.68	< <b>0.001</b>	0.071
Loc. × tr.	4	4.69	<b>0.001</b>	0.009	4	2.99	<i>0.021</i>	0.031	4	8.17	< <b>0.001</b>	0.159
<i>I. parviflora</i> – Canopy shade												
Locality	4	55.21	< <b>0.001</b>	0.117	4	40.37	< <b>0.001</b>	0.408	4	3.28	<b>0.013</b>	0.037
Treatment	1	1356.86	< <b>0.001</b>	0.720	1	75.67	< <b>0.001</b>	0.191	1	170.32	< <b>0.001</b>	0.478
Loc. × tr.	4	41.25	< <b>0.001</b>	0.088	4	4.13	<b>0.003</b>	0.042	4	7.81	< <b>0.001</b>	0.088
<i>I. capensis</i> – Canopy shade												
Locality	2	11.52	< <b>0.001</b>	0.060	2	9.19	< <b>0.001</b>	0.186	2	19.52	< <b>0.001</b>	0.287
Treatment	1	251.09	< <b>0.001</b>	0.654	1	0.90	0.346	0.009	1	25.21	< <b>0.001</b>	0.185
Loc. × tr.	2	19.96	< <b>0.001</b>	0.104	2	4.76	<b>0.012</b>	0.096	2	0.89	0.417	0.013
<i>I. noli-tangere</i> – Canopy shade												
Locality	2	70.161	< <b>0.001</b>	0.238	2	1.38	0.258	0.018	2	15.75	< <b>0.001</b>	0.256
Treatment	1	292.00	< <b>0.001</b>	0.495	1	58.39	< <b>0.001</b>	0.381	1	6.29	<b>0.014</b>	0.051
Loc. × tr.	2	39.94	< <b>0.001</b>	0.135	2	7.13	<b>0.001</b>	0.098	2	3.49	0.035	0.057
<i>I. glandulifera</i> – Nutrient levels												
Locality	4	5.87	< <b>0.001</b>	0.049	4	2.86	<i>0.026</i>	0.034	4	3.54	<b>0.009</b>	0.014
Treatment	2	151.31	< <b>0.001</b>	0.631	2	87.04	< <b>0.001</b>	0.518	2	414.41	< <b>0.001</b>	0.839
Loc. × tr.	8	2.71	<b>0.008</b>	0.045	8	2.3	<i>0.024</i>	0.055	8	1.66	0.115	0.013
<i>I. parviflora</i> – Nutrient levels												
Locality	4	5.62	< <b>0.001</b>	0.024	4	18.171	< <b>0.001</b>	0.173	4	5.40	<b>0.011</b>	0.013
Treatment	2	327.66	< <b>0.001</b>	0.698	2	35.74	< <b>0.001</b>	0.171	2	641.92	< <b>0.001</b>	0.785
Loc. × tr.	8	6.63	< <b>0.001</b>	0.057	8	8.32	< <b>0.001</b>	0.159	8	15.31	< <b>0.001</b>	0.075
<i>I. capensis</i> – Nutrient levels												
Locality	2	21.06	< <b>0.001</b>	0.151	2	11.25	< <b>0.001</b>	0.161	2	5.61	<b>0.005</b>	0.077
Treatment	2	68.98	< <b>0.001</b>	0.494	2	18.74	< <b>0.001</b>	0.131	2	47.64	< <b>0.001</b>	0.439
Loc. × tr.	3	13.16	< <b>0.001</b>	0.094	3	4.47	<b>0.006</b>	0.119	3	1.13	0.342	0.031
<i>I. noli-tangere</i> – Nutrient levels												
Locality	2	0.550	0.576	0.006	2	47.60	< <b>0.001</b>	0.225	2	0.38	0.687	0.003
Treatment	2	30.47	< <b>0.001</b>	0.309	2	71.05	< <b>0.001</b>	0.335	2	75.96	< <b>0.001</b>	0.561
Loc. × tr.	4	5.47	< <b>0.001</b>	0.111	4	18.39	< <b>0.001</b>	0.174	4	1.25	0.293	0.019
<i>I. glandulifera</i> – Moisture levels												
Locality	4	11.15	< <b>0.001</b>	0.125	4	6.02	< <b>0.001</b>	0.073	4	7.37	< <b>0.001</b>	0.127
Treatment	2	51.47	< <b>0.001</b>	0.289	2	55.35	< <b>0.001</b>	0.335	2	0.94	0.394	0.008
Loc. × tr.	8	3.02	<b>0.003</b>	0.068	8	1.33	0.229	0.032	8	1.93	0.057	0.067
<i>I. parviflora</i> – Moisture levels												
Locality	4	12.83	< <b>0.001</b>	0.120	4	16.15	< <b>0.001</b>	0.189	4	7.87	< <b>0.001</b>	0.092
Treatment	2	13.30	< <b>0.001</b>	0.062	2	9.52	< <b>0.001</b>	0.056	2	28.66	< <b>0.001</b>	0.168
Loc. × tr.	8	17.59	< <b>0.001</b>	0.329	8	6.14	< <b>0.001</b>	0.144	8	5.43	< <b>0.001</b>	0.127
<i>I. capensis</i> – Moisture levels												
Locality	2	37.00	< <b>0.001</b>	0.430	2	25.66	< <b>0.001</b>	0.336	2	7.12	<b>0.001</b>	0.107
Treatment	2	0.09	0.910	0.001	2	0.90	0.408	0.012	2	8.23	< <b>0.001</b>	0.124
Loc. × tr.	4	1.25	0.295	0.029	4	1.63	0.174	0.043	4	2.26	0.069	0.068
<i>I. noli-tangere</i> – Moisture levels												
Locality	2	0.27	0.762	0.004	2	10.62	< <b>0.001</b>	0.177	2	6.17	0.144	0.115
Treatment	2	6.79	<b>0.002</b>	0.108	2	0.56	0.573	0.009	2	0.35	0.703	0.007
Loc. × tr.	4	5.59	< <b>0.001</b>	0.178	4	2.13	0.084	0.071	4	1.34	0.262	0.050

Significant values are shown in bold and values close to significance are in italics (using Bonferroni correction).

flooding and simulated shading treatments. On the other hand, the biomass of native *I. noli-tangere* markedly increased when provided with high levels of nutrients and simulated shading, and its plasticity was greater than that of the invasive species (Fig. 2).

The highest average plasticity (0.67 averaged across all traits and environments in which plants survived to the end of the experiment) was recorded for *I. glandulifera*, followed by *I. noli-tangere* (0.50), *I. capensis* (0.47) and *I. parviflora*

TABLE 4. The results of an ANOVA of the phenotypic plasticity exhibited by the four species of *Impatiens* tested in terms of response of stem height, total biomass and root/shoot ratio of different populations to simulated shading, and different levels of nutrients and moisture

	All species			Czech species		
	d.f.	F	P	d.f.	F	P
Species	3	3.39	<b>0.007</b>	2	6.59	<b>0.002</b>
Locality	6	0.32	0.928	4	0.16	0.957
Treatment	4	57.31	<b>&lt; 0.001</b>	4	51.39	<b>&lt; 0.001</b>
Trait	2	28.52	<b>&lt; 0.001</b>	2	26.02	<b>&lt; 0.001</b>
Species × treatment	11	1.81	0.066	8	2.09	0.047
Locality × treatment	21	0.86	0.635	16	0.40	0.980
Species × trait	6	2.96	<b>0.012</b>	4	4.30	<b>0.003</b>
Locality × trait	12	0.51	0.900	8	0.30	0.966
Treatment × trait	8	52.88	<b>&lt; 0.001</b>	8	46.83	<b>&lt; 0.001</b>
Species × treatment × trait	22	1.58	0.075	16	1.92	0.031
Locality × treatment × trait	42	0.53	0.986	32	0.31	1.000
Residuals	78			78		

Significant values are shown in bold (using Bonferroni correction).

(0.45). The highest proportion of variability explained by the treatments, expressed as  $R^2$  averaged across traits and treatments, was recorded for *I. glandulifera* (0.47), followed by *I. parviflora* (0.37), *I. noli-tangere* (0.25) and *I. capensis* (0.23). However, the patterns were highly specific (Table 4); high levels of plasticity, i.e.  $\geq |0.4|$ , were recorded for all species, environments and traits (Fig. 2) and  $R^2$  over 0.3 for all species, traits and treatments, except moisture levels (Table 3).

#### Local differentiation within species

A significant effect of the locality from which the seeds were collected was found in control plants of all species and for all traits except the root/shoot ratio in *I. noli-tangere* (Table 3). Under the control conditions, the highest variability explained by locality was recorded for *I. capensis* (0.396), followed by *I. parviflora* (0.392), *I. glandulifera* (0.254) and *I. noli-tangere* (0.212). For plants under the treatments, *I. capensis* exhibited the highest variability (0.199), followed by *I. parviflora* (0.130), *I. noli-tangere* (0.116) and *I. glandulifera* (0.067) when averaging across all traits and treatments. In *I. parviflora* and *I. capensis* the locality significantly affected all the traits in all the treatments. In *I. glandulifera* there were significant or close to significant differences among localities, except for biomass in response to simulated shading. *Impatiens noli-tangere* exhibited significant differences only in four out of nine cases. However, the variability explained by locality was in general lower than that explained by the treatments. Locality explained more variability than treatment only in those treatments that had little effect (Tables 2 and 3). This was most frequently recorded in *I. capensis* and less frequently in *I. glandulifera* (Table 3).

## DISCUSSION

#### Species' traits

The highly invasive *I. glandulifera* was the most productive species in terms of biomass in all the environments, thus

exhibiting the Jack-and-master strategy (Richards *et al.*, 2006). Only under simulated shading was its biomass close to that of *I. parviflora*. However, its growth potential was not manifest in terms of achieving the tallest stem under most environments. *Impatiens glandulifera* plants were markedly taller only when grown in shaded conditions. The greater biomass and sharp increase in stem height that *I. glandulifera* exhibits in the presence of neighbouring plants suggest that it is a strong competitor of other species in plant communities (Cahill *et al.*, 2008). The impact of *I. glandulifera* on co-occurring species may be further strengthened due to the synchronous emergence of its seedlings (Beerling and Perrins, 1993). However, its success may be reduced when growing in deep shade as it produces very elongated stems that are fragile (H. Skálová, pers. obs.) and seed production may also be limited. Due to low seedling survival, the success of this species may be limited under high nutrient levels. The Jack-and-master strategy may also be relevant in invasive *I. parviflora*, the second most productive species in terms of biomass, but less different from *I. noli-tangere* and *I. capensis* than *I. glandulifera*. The relative stem height of *I. parviflora*, *I. noli-tangere* and *I. capensis* differed under individual environments, and the same was true for biomass of *I. noli-tangere* and *I. capensis*. This indicates that coexistence of *I. parviflora*, *I. noli-tangere* and *I. capensis* may be possible. As in other studies (Perglová *et al.*, 2009; Skálová *et al.*, 2011) the performance of *I. capensis* was within the range of that of the other *Impatiens* species studied. This indicates that further spread of *I. capensis* into central and Eastern Europe is possible. On the other hand, massive invasion is not probable due to the relatively poor performance of this species.

Different hierarchies in the two size traits studied (total biomass and stem height) in the control and individual environments indicate the need to investigate more traits under a range of environmental conditions (Daehler, 2003; Burns, 2004; Leicht-Young *et al.*, 2007; Williams *et al.*, 2008; Berg and Ellers, 2010).

### Plasticity and differentiation within species

All the species studied exhibited a plastic response to environmental factors, but there were considerable differences among them. *Impatiens glandulifera* was most plastic in the traits investigated and *I. parviflora* the least. The variability accounted for by the treatments was also the highest in *I. glandulifera*. The high plasticity of *I. glandulifera* is in agreement with the results of studies demonstrating that invasive plants show greater levels of plasticity than their native or non-invasive congeners (Burns and Winn, 2006; Richards et al., 2006; Funk, 2008; Davidson et al., 2011). On the other hand, *I. parviflora* and *I. capensis* may be other examples of invasive species that do not owe their success to high plasticity (Brock and Galen, 2005; Hastwell and Panetta, 2005; Zheng et al., 2009).

Differences between populations were found in all the species tested. As there were no tests of possible genetic differences between populations, it is not clear whether the differences observed are due to genetic or epigenetic factors (Roach and Wulff, 1987) or a combination of both (Bossdorf et al., 2008). The locality accounted for most of the variability in *I. capensis* and *I. parviflora*; that the variability explained by the locality for *I. glandulifera* was about a half of that of these two invasive species indicates a considerably smaller role of local differentiation in *I. glandulifera*. Differences among populations of *I. capensis* are in accordance with previously recorded genetic differences between the populations (Simpson et al., 1985; Dudley and Schmitt, 1995; Donohue et al., 2001; Heschel et al., 2002). However, these differences in *I. parviflora* are rather surprising because low local variation is reported for 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 differentiation may develop (Wade, 1997; Dietz and Edwards, 2006). It is also possible that differentiation in *I. parviflora* is manifested only in early developmental stages; considerable differentiation was recorded for time of germination and frost resistance of its seedlings (Skálová et al., 2011). To conclude, it appears that local differentiation may have contributed to the invasion success of *I. parviflora* more so than in the native *I. noli-tangere*, but it does not seem to explain the success of *I. glandulifera*. It needs to be noted, however, that our study was based on a rather limited number of localities within the greater range of specific habitats that harbour all the study species growing together. With a higher number of localities covering the whole ecological range of individual species, the differentiation may be more pronounced.

### Conclusions

Our study suggests that there are differences in seedling traits, plasticity and differentiation of the individual species studied, which may be related to their invasion success in the study area. *Impatiens glandulifera* was the largest and most plastic, but least locally differentiated, species. On the other hand, the less plastic invasive species, *I. parviflora* and *I. capensis*, were markedly differentiated. Size, plasticity and

differentiation of the native *I. noli-tangere* were low. This suggests that even within one genus, the relative importance of the phenomena contributing to invasiveness appears to be species-specific.

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