

Germination and establishment of invasive and native *Impatiens* species in species-specific microsites

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Summary

Impatiens glandulifera (Balsaminaceae) is one of the most widely distributed invasive alien plants in Europe. In the Czech Republic, it first colonized open riverbank habitats and more recently less humid and more shaded habitats where it comes in contact with two congeners, the native *I. noli-tangere* and earlier invader *I. parviflora*; both these species are likely to be affected by competition with *I. glandulifera*. A reciprocal sowing experiment was established to explore the performance and possible microsite differentiation of the three *Impatiens* species in the field. Three triads of plots, each dominated by one *Impatiens* species, were established in surroundings of a river with a fine-grained mosaic of woody and meadow vegetation in southern Bohemia, Czech Republic. The plots were protected from the natural input of seed by cutting the vegetation 20 cm above the soil surface and covering the surface with a cloth during the period of seed release. Each plot consisted of a subplot sown with a mixture of seed of all three species collected at the same locality and a control subplot with no seed added. Sites dominated by *I. noli-tangere* and *I. parviflora* were suitable for germination of all *Impatiens* species; the *I. parviflora* sites were more suitable for the establishment and further development of *Impatiens* plants. This indicates that *I. noli-tangere* was outcompeted from sites currently dominated by *I. parviflora* and further spread of *I. glandulifera* into sites occupied by the other *Impatiens* species is likely. Experimental plots in sites dominated by *I. glandulifera* were unsuitable for growth of all species, including its own seedlings.

Key words: alien species, biomass, competition, congeners, field study, *Impatiens*, seedling

1. Introduction

Invasions by alien species represent a major threat to native biodiversity and the functioning of invaded ecosystems (Vitousek et al. 1996; Mack et al. 2000; Millennium Ecosystem Assessment 2005; Heinze 2008; Lambdon et al. 2008; Mácová 2008). Dominant invasive species often suppress resident native plants (Richardson et al. 1989; Pyšek & Pyšek 1995; Bímová et al. 2004) and their competitive advantage depends on various environmen-

tal factors (Shea & Chesson 2002; Suding et al. 2004; Vinton & Goergen 2006), as abundances of species in a community result from interspecific interactions, which can differ along environmental gradients (Tilman 1982). The invasion dynamics can thus be influenced by the features of the invaded habitat, local conditions and species composition of the invaded community. If environmental conditions are less suitable at some sites, the invading species may not have a competitive advantage there. This may lead to coexistence

with native plants, for which such sites may serve as local refugia. The response of invasive and native plants to environmental factors is usually studied by using cultivation experiments (Burns & Winn 2006; Muth & Pigliucci 2006; Funk 2008). However, field studies comparing the performance of invading species in various habitats and/or under different environmental conditions provide a more realistic basis for the prediction of invasion dynamics (Goergen & Daehler 2002; Lambrinos 2002; Gerlach & Rice 2003; Morrison & Mauck 2007).

The present paper compares the performance of three congeners, the highly invasive *Impatiens glandulifera*, the long-present invader *I. parviflora* that has a stable occurrence, and a native congener *I. noli-tangere*, at contrasting field micro-sites. *Impatiens glandulifera* is among the worst and most widely distributed invasive plants in Europe (Pyšek et al. 2009). As a very tall annual it outcompetes most other herbaceous species (Grime 1979; Beerling & Perrins 1993). The rapid growth rate of its seedlings and young plants enables it to survive in competitive environments (Koenies & Glavac 1979). This species replaces the native flora in the UK (Perrins et al. 1990, 1993; Hulme & Bremner 2005) but in the Czech Republic it has no effect on the species diversity of invaded communities, only on species composition (Hejda & Pyšek 2006). The little effect reported indicates this species can coexist with the native flora. In the Czech Republic, *I. glandulifera* initially colonized open river banks (Pyšek & Prach 1995) but in the last few decades it started to colonize less humid and more shaded habitats some distance from rivers (F. Krahulec, personal communication) where *I. noli-tangere* and *I. parviflora* occur. These species, which often form separate stands at a locality, may come into compe-

tion with *I. glandulifera* in the near future as competition between closely related species is assumed to be particularly strong (Dayan & Simberloff 2005). The performance of *I. glandulifera* at newly invaded sites might indicate whether it will out-compete the other *Impatiens* species.

To determine whether this is likely a reciprocal sowing experiment was established and the germination, establishment and early growth of the three *Impatiens* species recorded at sites dominated by the respective congeners. This study explores the probable mechanism determining the co-occurrence of the three species. Micro-site differentiation would be indicated if each species performed best at its home site and species replacement if they performed best at the sites of the other congeners.

2. Methods

2.1 Study species

The *Impatiens* (Balsaminaceae) species studied are annuals with similar life histories and reproductive characteristics, and occupy similar habitats. Seeds germinate simultaneously in the first spring following cold winter stratification (Coombe 1956; Beerling & Perrins 1993; Hatcher 2003).

Impatiens glandulifera Royle is a native of the Western Himalayas where it grows along river banks, in floodplain forests and ruderal sites at altitudes of between 1600–4300 m a.s.l. (Adamowski 2008). In the Czech Republic, the first record of cultivation is for 1846 and that of occurrence outside cultivation for 1896 (Slavík 1997). At present it is reported from 428 grid-cells of 11 × 12 km, i.e. 63% of the total number (679) in the Czech Republic (P. Pyšek et al., unpublished data). As the tallest annual plant in Europe (up to 3 m) it is a strong competitor of other species

(Grime 1979; Roy 1990; Beerling & Perrins 1993). Its massive invasion of riparian habitats is a conservation problem (Pyšek & Prach 1993, 1995).

Impatiens parviflora DC. is native to the mountains of Central Asia (1000–3000 m a.s.l.), where it grows along the banks of rivers and streams, on stony mountain slopes, in moist shady places and broad-leaved forests (Coombe 1956; Adamowski 2008). It is a widely distributed invasive species in Europe. In the Czech Republic it was first recorded in 1844 in a botanical garden in Prague, and outside cultivation around 1870 (Slavík 1997); currently it is reported from 588 grid cells (86% of the total number; P. Pyšek et al., unpublished data). This distribution was achieved by the middle of the 20th century. *Impatiens parviflora* is of a similar stature to the native *I. noli-tangere*; both species are 30–60 (130) cm tall (Coombe 1956) and occur in similar habitats, such as shaded and humid woodland, and riparian shrub and forest.

The native *Impatiens noli-tangere* L. is widely distributed from Europe to Russia and Siberia to Japan and Kamchatka (Hatcher 2003). In the Czech Republic it is reported from 630 grid cells (93%) (P. Pyšek et al., unpublished data). This species is part of the early-successional herbaceous flora of forests, and its occurrence in successional mature vegetation is maintained by soil disturbance. It grows in damp to wet, occasionally waterlogged soils and at the edges of rivers, streams and lakes.

2.2 Study site and experimental design

The experiment was carried out in the area of the Volyňka river about 3 km north of the town of Volyně, Central Bohemia (49°8'30.419"N, 13°53'57.727"E, 460 m a.s.l.) in 2006–2007. The stands with one

or more *Impatiens* species occur within an area of ca 1.0 × 0.5 km². Three experimental plots of 0.5 × 1 m² were established before seed ripening at each of the sites dominated by the three *Impatiens* species (giving a total of nine plots) in the summer of 2006. The plots with *I. noli-tangere* (stated as 'Np') were in humid shaded alder-woods. The plots with *I. parviflora* ('Pp') were situated on the bank of a brook at a relatively dry site partly shaded by oaks, alders and hornbeams. The plots with *I. glandulifera* ('Gp') were at the margin of a meadow and shaded by alder and ash trees on one side. The 'Np', 'Pp' and 'Gp' are referred to as the 'home sites' for *I. noli-tangere*, *I. parviflora* and *I. glandulifera*, respectively.

Each plot was split into two 0.5 × 0.5 m² subplots. The vegetation was cut 20 cm above the ground and the plots were protected from the natural input of seed from the surrounding populations by covering them with sheets of cloth. In autumn 2006 the cloth was removed and one part of each plot was sown with a mixture of seed collected at the same locality the previous summer; the other subplot served as a control. There were 30 germinable seeds of each species in the seed mixture sown in the treatment subplot. This was achieved by calculating the number of seeds of each species using data on germination and seedling appearance obtained in an experimental garden the previous year (I. Perglová et al., unpublished data). The number sown in each subplot was 177, 136 and 63 seeds of *I. noli-tangere*, *I. parviflora* and *I. glandulifera*, respectively.

The numbers of seedlings and adult plants of each species were recorded in late April and mid July 2007, respectively. On the latter date, the height of adult plants was measured and the plants harvested; these measurements were only of plants in Np and Pp sites because only one plant of *I. glandulifera* matured at the Gp site. The

biomass of harvested plants was determined by weighing after drying at 80 °C for 10 hours.

2.3 Data analysis

The numbers of seedlings and adult plants in the treatment subplots were related to those found in the controls; numbers in controls were subtracted from those recorded in treatment subplots. Because the cloth covering of some control subplots was damaged, the numbers of seedlings and adult plants were calculated as the average recorded in the controls of the same plot type with intact cloth coverings. In addition, the numbers of seedlings and adult plants were weighted by the germination percentage of the seed sown, which was estimated over the same period of time in an experimental garden. Relative number of seedlings and adult plants was thus calculated using formula [1] or, for plots with a damaged cover, formula [2].

$$Rn = (N_{ss} - N_{cs}) \cdot \frac{30}{N_{gs}} \quad [1]$$

where Rn = relative number of seedlings or adult plants; N_{ss} = number of plants in the sown subplot; N_{cs} = number of plants in the control subplot; 30 = seed dose; N_{gs} = number of germinable seeds;

$$Rn = N_{ss} \cdot \frac{1}{n} \cdot \sum_k \frac{N_{ssi_k} - N_{csi_k}}{N_{ssi_k}} \cdot \frac{30}{N_{gs}} \quad [2]$$

where N_{ssi} = number of plants in the sown subplot with intact control; N_{csi} = number of plants in the intact control subplot; for the other symbols see formula [1]

Numbers of seedlings and adult plants, and biomass were square-root transformed to achieve normal distributions. Effect of the species sown and the home site on the number of seedlings and adult plants,

plant height and biomass was tested using ANOVA (S-plus 2000, Mathsoft 2000). A split-plot design was used to analyze the effect of time on the number of seedlings and adult plants.

3. Results

3.1 Number of seedlings and adult plants

The highest relative numbers of *Impatiens* seedlings were recorded at *I. noli-tangere* sites (Np) (Fig. 1, Table 1). The highest numbers of adult plants were recorded at *I. parviflora* sites (Pp). The lowest numbers of both seedlings and adults were recorded at *I. glandulifera* sites (Gp).

The home site had a weak effect on the performance of individual *Impatiens* species as indicated by the marginally significant species × site interaction (Table 1). At all sites, *Impatiens glandulifera* was the best performing species, producing the highest number of seedlings and adult plants. The difference was most pronounced at the Gp sites where the numbers of seedlings and adults of the other species were very low. The performance of *I. noli-tangere* was generally the poorest; this species produced similar numbers of seedlings and adults as *I. parviflora* at its home site, but much lower numbers at Pp sites.

3.2 Height and biomass of adult plants

Plant height and biomass differed significantly among the three species (Fig. 2, Table 2). Plants of *I. glandulifera* were taller than those of *I. parviflora* and *I. noli-tangere*, and plants growing at Pp sites produced more biomass than those growing at Np sites. However, the effect of site on plant height and its interaction with species was not significant.

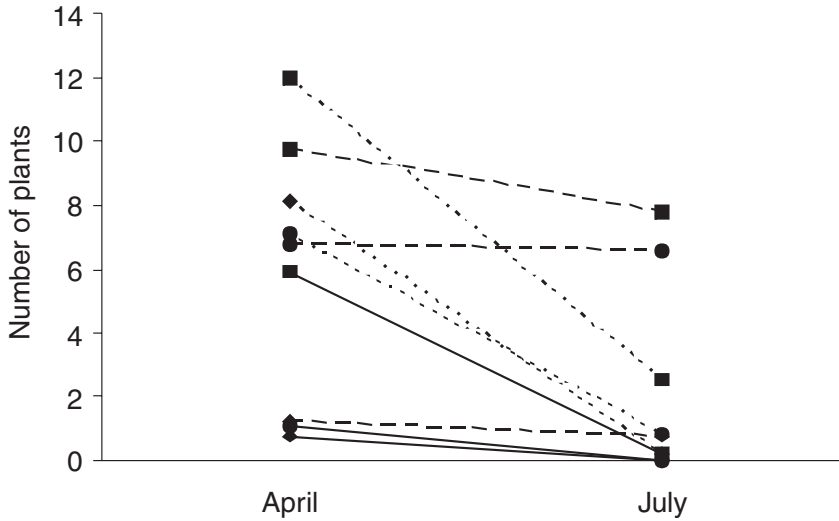


Figure 1: Relative number of seedlings (April) and adult plants (July) of the three species of *Impatiens* at individual home sites (■ *I. glandulifera*, ● *I. parviflora*, ◆ *I. noli-tangere*); complete lines – sites where *I. glandulifera* prevailed, dashed lines – sites where *I. parviflora* prevailed, dotted lines – sites where *I. noli-tangere* prevailed. See text for the calculation of relative numbers and Table 1 for the test of significance.

Table 1: Effect of the species of seed sown, home site and time on the number of plants (seedlings and adult) of the three species of *Impatiens* tested using split-plot ANOVA; significant values in bold.

Factor	df	F	P
Species	2,18	15.78	< 0.001
Site	2,18	21.58	< 0.001
Time	1,18	77.12	< 0.001
Species × Site	4,18	2.64	0.068
Species × Time	2,18	0.82	0.458
Site × Time	2,18	14.99	< 0.001
Species × Site × Time	4,18	1.87	0.159

4. Discussion

The results do not indicate a micro-site differentiation in these three congeners as none of them performed better at its home site than at the sites of other species. *Impatiens glandulifera* was the most successful species regardless of the identity of the species prevailing in experimental plots. Surprisingly, the performance of *I. glandulifera* was rather low at its home sites, which were also unsuitable for both its congeners. At these sites, seedling emer-

gence was generally low and seedling mortality high, which resulted in only one poor quality adult plant of *I. glandulifera* harvested from these plots in July. However, a dense stand of vigorous *I. glandulifera* plants occurred close to these plots, which suggests that stems persisting in the litter suppress the growth of competing seedlings of other species the following spring (Beerling & Perrins 1993). In addition, the synchronous appearance of a high number of *I. glandulifera* seedlings contributes to the elimination of competi-

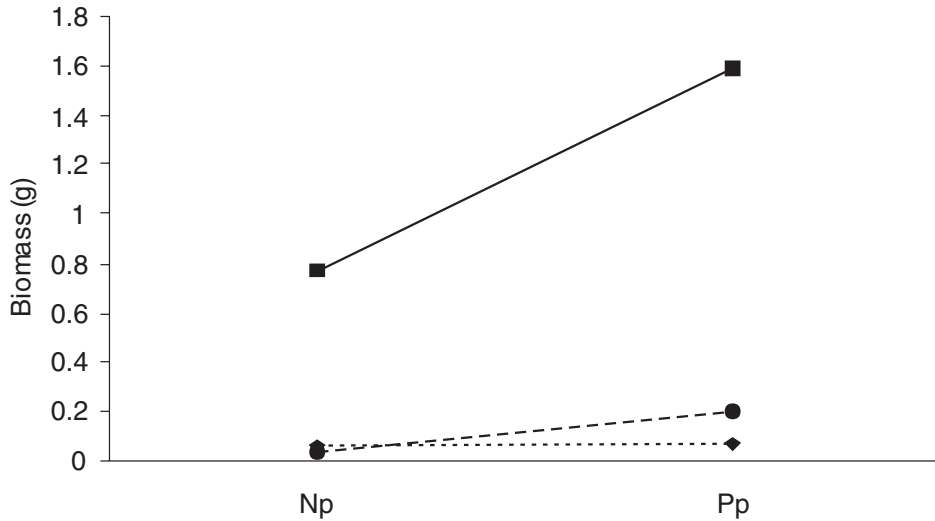


Figure 2: Biomass of adult plants of three *Impatiens* species at home sites where *I. noli-tangere* (Np) and *I. parviflora* (Pp) prevailed; ■ *I. glandulifera*, ● *I. parviflora*, ◆ *I. noli-tangere*; complete line – sites dominated by *I. glandulifera*, dashed line – sites dominated by *I. parviflora*, dotted line – sites dominated by *I. noli-tangere*. For the test of significance see Table 2.

Table 2: Effect of species of seed sown and home site on height and biomass of adult plants of *Impatiens*, tested by means of an ANOVA; significant values in bold.

Factor	df	Height		Biomass	
		F	P	F	P
Species	2,255	108.13	<0.001	57.29	<0.001
Site	1,255	0.15	0.696	6.90	0.009
Species × Site	2,255	1.09	0.338	0.47	0.625

tors (Grime 1987). It needs to be noted that adult plants were removed from the experimental plots the previous summer in order to avoid seed rain, and for technical reasons the amount of the seed sown (63 per plot, which was a dose needed to achieve 30 germinable seeds) was much lower than the naturally occurring seed density (700 seeds per plot; L. Moravcová, pers. com.). This is the reason for the high density of co-occurring species, mainly plagiotropic herbaceous species, and low density of *I. glandulifera* recorded in the plots. *Galium aparine*, which also occurred in the plots, is reported to suppress *I. glandulifera* by covering its fragile stems (Prach 1994).

Shaded and wet sites dominated by *I. noli-tangere* were suitable only for germination but not development of plants of the three *Impatiens* species. Seedling mortality in these plots was high and the performance of the adults poor. There were no signs of a clear preference of *I. noli-tangere* for these sites. As for the other species, *I. noli-tangere* had low seedling mortality and adult plants were larger at the sites dominated by *I. parviflora*. This indicates that the native *I. noli-tangere* might have been outcompeted from its sites, probably because of low seed production (Daumann 1967). If differences in fecundity are the main mechanism determining the pattern observed, it may be hypothes-

ised that in the future *I. parviflora* might be outcompeted at some of its sites by *I. glandulifera*, which is the most fecund of the three congeners. *Impatiens glandulifera* is the most water- and light-demanding of the three species and has higher indicator values for moisture and light than *I. parviflora* (Hill et al. 1999; Beerling & Perrins 1993), but the sites currently dominated by *I. parviflora* are not dry and shaded enough to prevent *I. glandulifera* colonizing them. In addition, specialized genotypes might be selected for at these sites, as reported for other species (Linhart & Grant 1996), including *I. capensis* (Dudley & Schmitt 1995).

That *I. noli-tangere* prevails at some sites might be because the seeds of alien congeners have not reached these sites, however, at localities where the invasion of *I. glandulifera* is still in progress this might only be a matter of time. On the other hand, it is unclear whether the invading species, mainly the light-demanding *I. glandulifera* (Perrins et al. 1990; Hill et al. 1999), will produce enough seeds at sites with suboptimal ecological conditions. In addition, the colonization by the invasive species of sites where native *I. noli-tangere* prevails may be delayed by the absence of a seed bank (I. Perglová et al., unpublished data). The persistence of a species at a site thus crucially depends on regular seed production, which may be endangered at sites where *I. noli-tangere* prevails because they are too shaded and wet.

Despite their generally good performance in new habitats, invasive plants may suffer from occasional but catastrophic events (Goergen & Daehler 2002). In this community, occasional high water levels may limit the invading species, especially *I. parviflora*, which does not perform well when growing in very wet soil (Coombe 1956). *Impatiens glandulifera* is considered a strong competitor due to its

size and seed production (Grime 1979; Cahill et al. 2008; Daumann 1967). However, its poor performance in less suitable habitats may promote coexistence with the other two congeners (Lambrinos 2002). In addition, a good performance of an alien species in the habitats of its congeners need not necessarily result in a successful invasion of those habitats. Despite the occurrence of a small number of individuals of the alien *Senecio madagascariensis* at the site of native congeners and a good performance of alien transplants at these sites, no evidence of the alien invasion was observed in a study dealing with growth of alien and native *Senecio* congeners at their typical sites (Radford & Cousens 2000). Based on our results it is unlikely that *I. glandulifera* will replace the other two *Impatiens* species. It is more likely that this invader will coexist with a number of resident species, as is indicated by previous studies on the impact of *I. glandulifera* on species richness and diversity of invaded communities (Hejda & Pyšek 2006; Hejda et al. 2009).

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