

Effects of virus infection on growth of the invasive alien *Impatiens glandulifera*

Vliv virové infekce na růst invazního druhu *Impatiens glandulifera*

Johannes Kollmann¹, María José Bañuelos^{1,2} & Steen Lykke Nielsen³

¹Department of Ecology, University of Copenhagen, Rolighedsvej 21, 1958 Frederiksberg C., Denmark; email: jok@life.ku.dk; ²Department of Biology, Organisms and Systems, Ecology Unit, University of Oviedo, 33071 Oviedo, Spain; ³Department of Integrated Pest Management, Research Centre Flakkebjerg, Faculty of Agricultural Sciences, University of Aarhus, 4200 Slagelse, Denmark

Kollmann J., Bañuelos M. J. & Nielsen S. L. (2007): Effects of virus infection on growth of the invasive alien *Impatiens glandulifera*. – Preslia 79: 33–44.

The absence of fungal or viral diseases of some invasive alien plants partially explains their success. However, for several species this issue has not been studied and no account of such infections are recorded for *Impatiens glandulifera*, a problematic weed in moist and half-open habitats of central and western Europe. We record for the first time viral infections in plants from different European regions grown in a common garden experiment. The infection was systemic and could be transferred to two species of *Chenopodium* and five species of *Nicotiana*, and resulted in the development of local necrotic spots within a week. The symptoms resembled Tobacco Rattle Virus, but this was not confirmed by an ELISA-test. In *I. glandulifera* the virus led to reduced above-ground biomass. Relative stem biomass and basal diameter were also lower in diseased plants, but there was no significant differences in plant height and number of main branches. Also virus infection did not affect the following reproductive traits: time to flowering, pollen viability, fruit abortion, seed/ovule ratio, seed number per fruit and individual seed mass. This virus was not transmitted via seed. The potential effects of such viral infections on the population dynamics and biological control of this alien plant are discussed.

Key words: aboveground biomass, basal diameter, invasive alien plant, latitudinal gradient, stem biomass, therophyte, virus indicator plant

Introduction

Invasive alien plants are a focal area of current ecological research, because biological invasions are large-scale (natural) experiments, which allow us to address fundamental questions in population and community ecology using a variety of classical and modern methods (Drake et al. 1989, Lodge 1993, Vitousek et al. 1996, Daehler 2006, Richardson 2006). The innovative potential of the science of biological invasions is demonstrated by numerous studies on global and local patterns in plant invasions, invasibility of plant communities, differences between phylogenetic groups, strategies of invasive plants, mechanisms and control of biological invasions (e.g. Pyšek et al. 1995, Brock et al. 1997, Pyšek 1998, Alpert et al. 2000, Hänfling & Kollmann 2002, Mandák et al. 2004, Chytrý et al. 2005, Kollmann et al. 2007). Less information is available about the diseases of invasive plant species (but see Malmstrom et al. 2005a,b, 2006), although strong effects of fungal or viral infections on population dynamics have been demonstrated in non-invasive plants (Gilbert 2002). Diseases can be inadvertently introduced with alien plants (Guy et al. 1998, Pearson et al. 2006), although the success of some invasive plant species might actually be explained by the escape from native diseases and herbivores

(Enemy Release Hypothesis; Keane & Crawley 2002, Mitchell & Power 2003). Moreover, it has also been observed that some introduced plants indirectly increase disease incidence in nearby native species (Malmstrom et al. 2005b).

Invasive alien species are a major problem for habitat management, because of the associated economic costs and concerns about losses in biodiversity. Invasive alien plants lead to devaluation of agricultural land, interfere with forest management, increase costs for maintenance of road margins, railways and waterways, and they can cause extinction of native species. Control of invasive aliens is difficult and expensive – for specific calculations of the costs associated with invasive species see Sandlund et al. (1999) and Mack et al. (2000), but suitable management strategies are still lacking for many species and habitats (Hobbs & Humphries 1995, Luken & Thieret 1997, Sheppard et al. 2006). Natural diseases are a potential method of controlling invasive plant species (cf. Erneberg et al. 2003), but this topic is poorly studied in Europe compared with North America or Australia (Sheppard et al. 2006).

A major invasive alien plant in Europe (Pyšek & Prach 1995, Dawson & Holland 1999, Weber 2000, Peltre et al. 2002), but also in North America (Toney et al. 1998), is the east-Asian *Impatiens glandulifera* (Balsaminaceae; $2n = 18, 20$). This tall annual plant was selected for study because it is currently expanding its European range (Beerling 1993) and causes problems for ecosystem management (Wadsworth et al. 2000). However, little knowledge exists about possible herbivores (but see Schmitz 1995), and virtually nothing is known about fungal or viral diseases as stated in the reviews by Beerling & Perrins (1993), Shaw (2003) and Sheppard et al. (2006).

The present study reports the results of a common garden experiment on latitudinal variation in *I. glandulifera* from nine European regions (Kollmann & Bañuelos 2004), which accidentally became infected by a virus disease in its second year. These data are used to (1) identify the disease and to explore its host range, (2) investigate the effects of the disease on vegetative growth and reproduction of *I. glandulifera* and (3) assess differences among populations along a latitudinal gradient.

Material and methods

Study species

Impatiens glandulifera Royle is native of the Himalayan mountains from Kashmir to Garhwal; it was introduced into Europe in 1839 (Kew Gardens), became naturalized in England as early as 1855, and has experienced an exponential increase in abundance and distribution during the past 30–40 years (Beerling 1993). The species is now common in the lowlands and the lower montane belt below 800 m a.s.l. in 18 European countries within the latitudes 30–64°N; however, plants were recently found at 1550 m in the Alps (H. Buschmann, pers. comm., October 2003). Its northern distribution is controlled by the length of the growing season, but the species may spread northwards with rising global temperatures. It is a tall therophyte with no clonal growth and no long-lived seed bank. The flowers are self-fertile but protandrous; seeds are dispersed by explosive capsules, hydrochory and human transport. Large and dense stands are common on riverbanks, waste ground and in open woodlands. Crawley (1987) considered it to be one of the ‘top twenty’ British aliens. It is suppressing and endangering native species in some vegetation types (Hulme & Bremner 2006), however, once *I. glandulifera* is removed communities may recover without any consequences for species diversity (Hejda & Pyšek 2006).

Plant material

Plant material from nine European regions was used; in each region seeds were collected from 1–5 populations at least 1 km apart (in total 23 populations), and population size varied from 50–20,000 plants (Table 1). Sampling was not balanced due to limitations in local availability of seed. Habitat types included riverbanks, lakeshores, mesic forest edges, roadsides and abandoned gardens; most sites had no management or only irregular mowing. Seeds were collected from 10–25 plants per population (5–10 seeds per plant) in September–October 2001. Only ripe capsules with brown or black seeds were harvested. The seeds were dried at room temperature for 1–2 weeks and then stored at 0–5 °C for 15–16 months.

Germination and growth conditions

In mid March 2003, seeds from all populations were put between moist blotting paper in Petri dishes at 0–5 °C for a 3-weeks period of stratification; a fungicide (1% Dithane M45) was added to reduce fungal infections. At the end of this period some seeds had already started germinating in the fridge. Thus, 60 seeds of each population were laid out in transparent plastic boxes (12 × 8 × 5 cm) with blotting paper over a plastic bridge and 100 ml distilled water (plus fungicide); unusually small or empty seeds were discarded. The boxes were randomly placed and repeatedly rearranged in a germination cupboard with a temperature regime of 12 °C at night (12 h) and 22 °C with light during the day (12 h). Germination was recorded for 50 days but after 1 week only few changes were observed. Germination in all populations was high (70–95%).

In late April 2003, 12 seedlings of each population were transferred to a glasshouse and planted into plastic trays with individual wells (5 cm diameter, 6 cm depth) filled with a peat-based substrate (N, 74 g m⁻³; P, 165 g m⁻³, K, 260 g m⁻³; pH 6.0); once a week the position of the trays was randomized. After 3 weeks the plants were transferred to larger pots (12 cm diameter, 10 cm depth) with the same substrate. Average day temperature in the glasshouse was 21.9±0.6 °C (mean±SE) with 59.1±2.1% air humidity and 15.1±0.8 klux light (one measurement per minute). Nocturnal values were 16.8±0.3 °C, 67.3±1.6% humidity and 1.3±0.1 klux light.

In early June 2003, eight randomly chosen individuals from each population were placed outdoors to harden the plants before planting them into the common garden. One week later one (two) plant(s) of each population were planted randomly in five double rows (in total 140, see Table 1) with a guard plant at the end of each row (total 20 plants); the latter were excluded from the analysis. The rows were N–S oriented, with 40–50 cm distance between the plants within rows and 80–100 cm between rows. However, after about four weeks a closed canopy had developed. The experimental bed was not shaded but protected against wind by adjacent buildings. Average day temperature was 20.6±0.4 °C and 14.3±0.5 klux light; nocturnal values 17.2±0.3 °C and 1.5±0.1 klux light (one measurement per minute). The loamy soil was tilled twice before planting and was fertilized four weeks later; no herbicides were used but weeding was hardly needed because of the rapid growth of the study plants. Water was added when necessary. Few herbivores were observed, but 4–6 plants had black aphids in late June albeit without clear patterns in relation to plants with virus symptoms, regions or rows.

Table 1. – Site characteristics and sample size of the plant material of *Impatiens glandulifera* tested for potential effects of virus infection. Regions are ranked based on latitude. Sources of climatic data: ¹Eimeldingen, Mühr (2003); ²České Budějovice, K. Prach; ³Hagen, Mühr (2003); ⁴Eelde, Rudloff (1981); ⁵Durham, S.G. Willis; ⁶Umeå, C. Nilsson; all others Rudloff (1981). For further details of the seed material see Kollmann & Bañuelos (2004). LatN/LongE – latitude north and longitude east; AnnT – annual average temperature; AnnP – annual average precipitation.

Region	Location	LatN/LongE	Elevation (m)	AnnT (°C)	AnnP (mm)	Study plants [populations]	Plants with virus symptoms (%)
N Switzerland	Zurich	47°23′/08°34′	569	8.0	1137	10 [1]	30
E France ¹	Mulhouse	47°45′/07°24′	250	9.8	786	7 [1]	0
S Czech Republic ²	České Budějovice	48°58′–50°15′ / 13°00′–14°46′	356–439	7.2–7.9	600–628	25 [4]	0
W Germany ³	Hagen	51°20′/06°32′	120	9.5	903	7 [1]	14
E Germany	Halle-Leipzig	51°18′–51°28′ / 11°58′–12°20′	99–108	9.0	559	26 [5]	42
E Netherlands ⁴	Assens	53°00′/06°38′	5	9.0	767	10 [1]	70
N England ⁵	Durham	54°45′/-1°52′	50	9.4	593	10 [1]	60
E Denmark	Copenhagen	55°41′–55°47′ / 12°28′–12°36′	2–19	8.0	602	25 [5]	16
N Sweden ⁶	Umeå	63°48′–63°50′ / 20°10′–20°20′	10–37	2.0	700	20 [4]	10

Screening for virus

The study plants were monitored daily. In late June 2003, 24% of the plants developed symptoms of a virus infection as indicated by necrotic spots and wrinkled leaves (Fig. 1). The infected plants were irregularly distributed within the experimental plot with no apparent border or row effects (J. Kollmann, unpubl. data). In July and August, no further plants developed virus symptoms, but one infected (and one apparently uninfected) individual died.

In late July 2003, leaves from four plants (from different regions) showing clear disease symptoms were sampled and analysed for viral infection. As a control, leaves from a symptomless plant were included as well. The plant material was tested for presence of virus following standard procedures for first screening for unknown viruses at Faculty of Agricultural Sciences (University of Aarhus). The procedures include mechanically inoculating a group of indicator plants that are susceptible to a broad range of viruses (Hill 1984, Jayasinghe & Chuquillanqui 1989). The indicator plants included two *Chenopodium* species (*C. amaranticolor* Coste et Reynier, *C. quinoa* Willd.) and five *Nicotiana* species (*N. benthamiana* Domin., *N. clevelandi* A. Gray., *N. debneyi* Domin., *N. rustica* L., *N. tabacum* L. ‘Xanthi’ and ‘Samsun’). The leaf material was macerated in a phosphor extraction buffer (40 g PEG 6000, 4.8 g Na₂HPO₄, 0.4 g KH₂PO₄ up to 1000 ml H₂O, pH 7.7) and leaves of the indicator plants were rubbed with the extract using an abrasive silicium carbid mesh 400. The inoculated plants were grown in a glasshouse at 18 °C and supplementary light to 16 hours per day. Symptoms were recorded for 2 weeks. In addition a DAS-ELISA test for Tobacco Rattle Virus was carried out following a standard procedure (Clark & Adams 1977) using antibodies produced by Faculty of Agricultural Sciences.



Fig. 1. – Flowering *Impatiens glandulifera* plants lacking (left) and showing symptoms of virus infection (right) in early August 2003. Photo: J. Kollmann.

Measurement of vegetative traits

In mid August 2003, all plants were harvested at ground level; sampling the root system was not feasible because it proved impossible to separate the fragile roots from the loamy soil. At this time all plants were flowering and fruiting and had not started to senesce. Plant height, circumference at the second basal internode and number of 1st order branches were measured. Plants were pre-dried at 20–40 °C in a glasshouse for 12 days, followed by 3 days at 70 °C. Above-ground biomass was determined separately for stems plus branches, and leaves plus flowers and fruits.

Measurement of reproductive traits

The date of first flowering of all plants until harvest in mid August 2003 was recorded. To assess virus effects on other reproductive traits only those populations with a sufficient number of plants showing virus symptoms, and at least six flowers and six fruits available for harvest were used, resulting in four populations from Germany, two from Denmark and Sweden and one from Switzerland, The Netherlands and United Kingdom, respectively (see Table 1). From each of these 11 populations one plant was randomly chosen per treatment (symptomatic/symptomless). In mid August, six flowers per plant were sampled in the male phase (1–2 days after opening) for analysis of pollen viability. Pollen from one anther per flower was transferred with a cotton brush to a glass slide where a drop of 33% cotton blue in

phenol was added. Viable pollen grains turned dark and percentage viability was determined for a random sample of 100 grains per flower. Also after natural pollination in mid August, six fruits per study plant were collected for analysis of the number of seeds per fruit and the seed/ovule ratio (small seeds < 4 mg were excluded). Seed mass was determined after drying at room temperature for 10 weeks. Furthermore, six naturally pollinated young fruits per plant were labelled and bagged to assess differences in fruit abortion.

The common garden experiment was repeated in 2004 to assess whether or not the viral disease was seed-transmitted. Equal amounts of wild seed (2001) and seed from infected plants (2003) were stored and germinated as described above. The resulting individuals were cultivated in the same plot, infection was monitored throughout the growing season, and all plants were harvested and analysed following the methods used in 2003.

Statistical analyses

The data set of the various plant traits was not balanced because the nine European regions were not evenly represented, and presence of virus symptoms differed among regions (Table 1). Moreover, *I. glandulifera* shows latitudinal variation in size and reproduction (Kollmann & Bañuelos 2004), as do other invasive alien plants (Weber & Schmid 1998, Olsson & Ågren 2002, Bastlová & Květ 2003). Therefore, individual regression analyses between latitude of origin and all traits were calculated separately for infected and uninfected plants. When one or both groups showed no significant latitudinal trend, two-way ANOVAs were calculated, considering ‘symptoms’ (fixed factor) and ‘latitude’ (random factor) as main effects. When the linear regressions were significant in both groups ($P < 0.05$), their slopes and y intercepts were compared. For comparison of slopes an ANOVA was calculated with latitude and symptom state as factors; significant interactions ‘latitude \times symptom’ indicated differences in the slopes of the two regression lines. For comparison of the intercept, t-tests were applied for each paired set of data. The frequency of viral symptoms in plants from infected vs. uninfected seeds in the 2004 experiment was investigated using chi-square contingency tables. Proportional data were arcsin-transformed and other measurements log-transformed in case of deviation from normality of the residuals and unequal variance.

Results

Evidence for virus infection

After inoculation with samples from infected *I. glandulifera* plants, all eight indicator species developed local necrotic spots on their leaves within a week. Symptoms remained local in *Chenopodium quinoa*, *C. amaranticolor* and *Nicotiana debneyi*, but became systemic in *Nicotiana tabacum* ‘Xanthi’ and ‘Samsun’, *N. rustica*, *N. clevelandi* and *N. benthamiana* with necrotic lesions that increased to large necrotic areas resulting in leaf death. No such effects were observed in plants treated with leaf extracts from symptomless *I. glandulifera* plants. The development of the symptoms in the indicator plants resembled those associated with Tobacco Rattle Virus (TRV), which is known to have a broad host spectrum and fast development of symptoms. However, the ELISA test for TRV was negative.

Effect of virus on vegetative traits

Frequency of virus symptoms in *I. glandulifera* was different among the nine European regions albeit with no clear geographic or climatic pattern (Table 1). Symptoms were frequent in Dutch and English plants, intermediate in East German and Swiss plants, and low in Danish, West German and Swedish plants, while Czech and French plants were not infected at all.

Total above-ground biomass, relative stem biomass and basal diameter were significantly lower in infected plants (ANOVA; $F > 6.0$, $P < 0.02$; Table 2), whereas no effect of the virus symptoms on plant height and number of 1st order branches was observed ($F < 1.1$, $P > 0.29$). Latitudinal gradients in total and relative biomass, basal diameter, plant height and number of branches were observed in the symptomless plants (Pearson product-moment correlation; $R^2 = 0.19\text{--}0.51$, $P < 0.05$), whereas in the infected individuals the gradient disappeared for relative stem biomass and basal diameter ($R^2 = 0.08\text{--}0.09$, $P > 0.05$). Therefore, the analyses were re-done including latitude. Comparison of the respective linear regressions against latitude revealed significant effects of the virus only on total biomass, indicated by a significant difference in the intercepts with the y axis (Fig. 2; t-test; $T = -2.5$, $P < 0.05$).

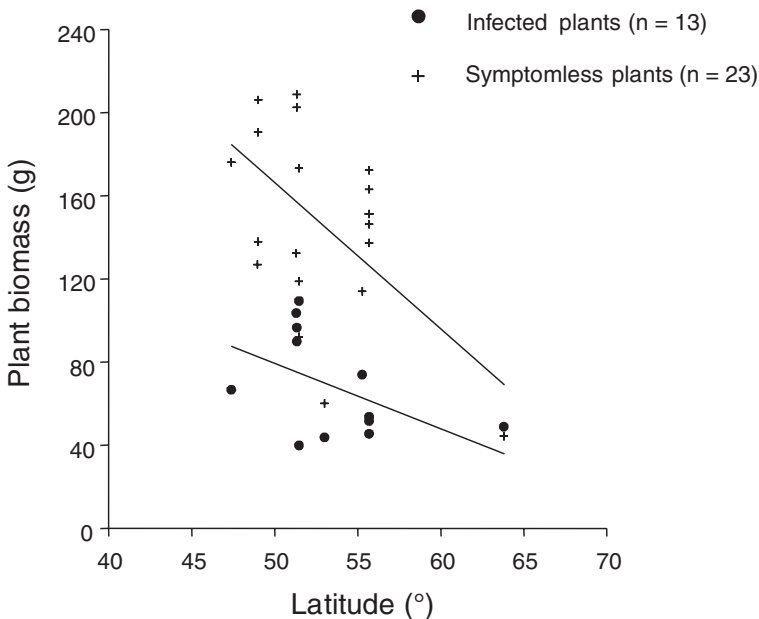


Fig. 2. – Differences in total above-ground biomass of *Impatiens glandulifera* lacking and showing virus symptoms from nine European regions. The details of the two linear regressions with latitude are in Table 3; the regression lines differed in y intercept (t-test; $T = -2.5$, $P < 0.05$) but not in slope (ANOVA; $F = 1.9$, $P = 0.14$).

Table 2. – Effects of the virus on vegetative and reproductive traits in *Impatiens glandulifera* (means \pm SE; number plants studied in brackets), including statistical results of one-way ANOVAs (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P > 0.05$).

Plant traits	Plant status		F
	Symptomatic	Symptomless	
Vegetative traits			
Total above-ground biomass (g)	66.7 \pm 6.9 (33)	145.3 \pm 6.2 (106)	28.6***
Relative stem biomass (%)	63.8 \pm 1.0 (33)	67.8 \pm 0.5 (106)	6.0*
Plant height (cm)	164.8 \pm 4.7 (33)	176.4 \pm 2.8 (106)	1.0 ^{ns}
Basal diameter (cm)	2.5 \pm 0.1 (33)	3.2 \pm 0.1 (106)	14.9**
Number of 1st order branches	20.6 \pm 0.9 (33)	22.1 \pm 0.5 (106)	1.1 ^{ns}
Reproductive traits			
Time to flowering (days)	74.5 \pm 0.3 (33)	69.5 \pm 0.1 (103)	2.9 ^{ns}
Pollen viability (%)	86.3 \pm 3.4 (66)	96.0 \pm 1.2 (66)	0.1 ^{ns}
Fruit abortion (%)	57.6 \pm 9.6 (11)	43.9 \pm 6.5 (11)	0.001 ^{ns}
Seed/ovule ratio (%)	43.4 \pm 5.7 (66)	47.8 \pm 5.4 (66)	0.7 ^{ns}
Number seeds per fruit	5.6 \pm 0.7 (66)	6.5 \pm 0.7 (66)	1.1 ^{ns}
Seed mass (mg)	8.1 \pm 0.7 (66)	7.7 \pm 0.5 (66)	0.2 ^{ns}

Table 3. – Latitudinal gradients in eight vegetative and reproductive traits of infected and symptomless plants of *Impatiens glandulifera* (+/–, positive or negative correlation with latitude; significant results in bold). Pollen viability, seed/ovule ratio and seeds per fruit showed no significant relation to latitude. When both regressions were significant, regression line slope and y intercept of infected and symptomless plants were compared.

Plant traits	R ²	df	F	P
Total above-ground biomass				
Infected	0.32	1, 11	5.3	0.04 (–)
Symptomless	0.50	1, 21	21.1	<0.001 (–)
Relative stem biomass				
Infected	0.08	1, 11	1.0	0.34
Symptomless	0.19	1, 21	5.1	0.03 (+)
Plant height				
Infected	0.29	1, 11	4.6	0.05 (–)
Symptomless	0.35	1, 21	11.4	<0.01 (–)
Basal diameter				
Infected	0.09	1, 11	1.1	0.32
Symptomless	0.34	1, 21	10.9	<0.01 (–)
Number of 1st order branches				
Infected	0.59	1, 11	16.4	<0.01 (–)
Symptomless	0.51	1, 21	22.3	<0.01 (–)
Time to flowering				
Infected	0.59	1, 11	15.8	<0.01 (–)
Symptomless	0.57	1, 21	27.9	<0.01 (–)
Fruit abortion				
Infected	0.37	1, 9	5.5	0.04 (+)
Symptomless	0.06	1, 9	0.6	0.45
Seed mass				
Infected	0.05	1, 9	0.4	0.52
Symptomless	0.42	1, 9	6.8	0.02 (+)

Effects of virus on reproductive traits

There were no significant differences between infected and symptomless plants for the six reproductive traits listed in Table 2 (ANOVA; $F < 3.0$, $P > 0.05$). Of the reproductive traits only 'time to flowering' correlated with latitude for both symptomless and infected plants, with earlier flowering in plants from northern regions (Table 3). In the infected plants there was also a greater tendency of abortion in those from the southern regions, and average seed mass of symptomless plants was higher in northern plants. There were no latitudinal gradients in pollen viability, seed/ovule ratio and the number of seeds per fruit.

In the 2004 experiment, a higher proportion of plants developed virus symptoms (48% of 90 plants), but there was no significant difference in virus infection of plants grown from seed from infected vs. symptomless mothers (chi-square contingency table; $\chi^2 = 2.2$, $P = 0.14$).

Discussion

Virus symptoms in invasive alien plants are rarely studied (but see Davis & Guy 2001, Malmstrom et al. 2005a,b, 2006) and this is the first report of a viral infection in the invasive annual *Impatiens glandulifera*. The virus significantly reduced above-ground biomass of the plants. This was mainly due to a reduction in stem biomass, indicated by a smaller basal diameter, and higher relative mass of leaves and reproductive structures in infected plants. Reduction in plant growth resulting in lower above-ground biomass of virus infected plants is a common phenomenon, caused by less effective functioning of chloroplasts in infected leaves (Hull 2002). Most often it results in stunted individuals, but not in our experiments. There were no significant differences in other vegetative traits and in all reproductive traits. Latitudinal variation in plant traits are recorded for the invasive species *Solidago altissima* and *S. gigantea* (Weber & Schmid 1998), and *Lythrum salicaria* (Olsson & Ågren 2002, Bastlová & Květ 2003). However, none of these studies considered the effect of viral infection, which in our case reduced the latitudinal gradient in five of eight traits of *I. glandulifera* as measured by explained variation in the linear regressions. This is probably due to the additional variation introduced by the virus infection. Pollen viability, seed/ovule ratio and seed number per fruit showed no latitudinal variation, maybe because these traits are more determined by internal conditions of the plant and thus less subject to environmental selection along the European latitudinal gradient.

Impatiens glandulifera plants from the nine European regions differed in the frequency of virus symptoms, which is not associated with either latitude or a longitude of origin. It might be that the Czech and French populations have developed some form of resistance to the virus as part of rapid evolutionary change, which is characteristic of invasive alien species (Lee 2002). Future experiments and field observations in these countries are needed to test our common garden results. There might also be more subtle differences among plants in severity of the symptoms, but the degree of infection was not quantified.

It is interesting that no viral or fungal infection of European populations of *I. glandulifera* has been reported and it is unlikely that they have been overlooked in the numerous studies on this plant (Beerling & Perrins 1993, Pyšek & Prach 1995, Schmitz 1995, Dawson & Holland 1999, Collingham et al. 2000, Chittka & Schürkens 2001, Willis & Hulme 2002, Hulme & Bremner 2006). This apparent rarity of virus infection could support the Enemy Release Hypothesis, but comparable studies are still lacking for the

natural range of the species in the Himalayan Mountains. For example, Mitchell & Power (2003) showed that on average 84% fewer fungi and 24% fewer virus species infected naturalized European plants in the United States compared with in their native ranges, and species released from pathogens are more harmful invaders in both natural and agricultural ecosystems. Since it seems improbable that the virus infection was unique to the common garden situation, it is likely that similar diseases will be found in naturalized populations in Europe, and they could rapidly spread, especially along rivers, the preferred habitat of the species (Pyšek & Prach 1995). As the disease reduces total above-ground biomass it might affect population dynamics and thus could contribute to a natural control of the plant (cf. Sakai et al. 2001). Lower biomass may diminish the competitive ability of this annual species. High competitive ability is a key factor in the success of *I. glandulifera* in its typical habitat in European floodplains and along lakeshores (Beerling & Perrins 1993). On these moist and relatively nutrient-rich soils other tall herbs (*Epilobium hirsutum* L., *Phalaris arundinacea* L., *Urtica dioica* L.) may outcompete infected *I. glandulifera*, and smaller thin-stemmed plants might more easily be damaged by wind or animals. No changes in six reproductive traits of infected plants were observed, but fecundity (albeit not measured) might have been reduced, since in annual species total biomass and seed production often are positively correlated (e.g. Primack 1979, Thompson et al. 1991). Although natural dispersal of the virus can be advantageous in terms of management of this invasive alien, the pathogen is less suitable for using in biological control because of its rather broad host spectrum. However, we suggest that more attention is paid to the diseases of *I. glandulifera* in field surveys and future experiments, especially in central Europe, in an attempt to find suitable biocontrol agents and observe their effects on the population dynamics of the species.

Acknowledgements

We are grateful to Christer Nilsson, Dani Prati, Dick Pegtel, Ewald Weber, Gabi Jakobs, Harald Auge, Karel Prach and Steve Willis for supplying local seed material. Anne Jind, Birthe Dalsø Schmidt, Elisabeth Johansen, Elze Astrup and Mads Nielsen helped with the setting up, maintenance and harvesting of the experiment. We are grateful to the Editor Petr Pyšek and three anonymous referees for critical comments and helpful suggestions to the manuscript. Tony Dixon kindly improved our English. The study was supported by grant 21-03-0204 of the Danish Research Agency to JK; MJB received a Spanish post-doctoral fellowship while in Denmark (EX2002-0028, Ministerio de Educación, Cultura y Deporte).

Souhrn

Přestože absence houbových nebo virových onemocnění v druhotném areálu může v některých případech vysvětlit úspěšnou invazi zavlečeného druhu, pro řadu druhů nejsou v tomto ohledu k dispozici žádné informace; jedním z nich je *Impatiens glandulifera*, invadující na vlhkých a polostinných stanovištích ve střední a západní Evropě. V této studii je poprvé popsána virová infekce, pozorovaná u rostlin z 9 oblastí Evropy, pěstovaných na experimentální zahradě. Infekce byla systémová a přenosná na 2 druhy rodů *Chenopodium* a 5 druhů rodu *Nicotiana*, u nichž během týdne vyvolala nekrotické skvrny na listech. Symptomy připomínala virus nekrotické kadeřavosti tabáku, test ELISA byl však negativní. Zasažené rostliny *I. glandulifera* vytvořily méně nadzemní biomasy, alokovaly relativně méně biomasy do lodyhy a měly menší průměr bazální části lodyhy. Výška rostliny, počet hlavních větví a reprodukční charakteristiky (doba kvetení, životnost pylu, počet abortovaných plodů, poměr mezi počtem plodů a vajíček, počet semen v plodu a váha semene) nebyly přítomností viru ovlivněny. Přenos viru semeny infikovaných rostlin pozorován nebyl. V závěru práce je diskutován dopad virových infekcí na populační dynamiku a možné využití v biologické kontrole invazních druhů.

References

- Alpert P., Bone E. & Holzapfel C. (2000): Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. – *Persp. Plant Ecol. Evol. Syst.* 3: 52–66.
- Bastlová D. & Květ J. (2003): Phenotypic variability in native populations of *Lythrum salicaria* L. across geographical gradient: between- and within-population differences. – In: Child L. E., Brock J. H., Brundu G., Prach K., Pyšek P., Wade P. M. & Williamson M. (eds.), *Plant invasions: Ecological threats and management solutions*, p. 237–246, Backhuys Publ., Leiden.
- Beerling D. J. (1993): The impact of temperature on the northern distribution-limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. – *J. Biogeogr.* 20: 45–53.
- Beerling D. J. & Perrins J. M. (1993): *Impatiens glandulifera* Royle (*Impatiens roylei* Walp.). – *J. Ecol.* 81: 367–382.
- Brock J. H., Wade M., Pyšek P. & Green D. (1997): *Plant invasions: Studies from North America and Europe*. – Backhuys Publishers, Leiden.
- Chitka L. & Schürkens S. (2001): Successful invasion of a floral market: an exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. – *Nature* 411: 653.
- Chytrý M., Pyšek P., Tichý L., Knollová I. & Danihelka J. (2005): Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. – *Preslia* 77: 339–354.
- Clark M. F. & Adams N. A. (1977): Characteristics of the microplate method of enzyme-linked immunosorbent assay for detection of plant viruses. – *J. Gen. Virol.* 34: 475–483.
- Collingham Y. C., Wadsworth R. A., Huntley B. & Hulme P. E. (2000): Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. – *J. Appl. Ecol.* 37: 13–27.
- Crawley M. J. (1987): What makes a community invulnerable? – In: Gray A. J., Crawley M. J. & Edwards P. J. (eds.), *Colonization, succession and stability*, p. 429–453, Blackwell Sci. Publ., Oxford.
- Daehler C. C. (2006): Invasibility of tropical islands by introduced plants: partitioning the influence of isolation and propagule pressure. – *Preslia* 78: 389–404.
- Davis L. T. & Guy P. L. (2001): Introduced plant viruses and the invasion of a native grass flora. – *Biol. Invas.* 3: 89–95.
- Dawson F. H. & Holland D. (1999): The distribution in bankside habitats of three alien invasive plants in the UK in relation to the development of control strategies. – *Hydrobiologia* 415: 193–201.
- Drake J. A., Mooney H. A., di Castri F., Groves R. H., Kruger F. J., Rejmánek M. & Williamson M. (1989): Biological invasions. A global perspective. – J. Wiley & Sons, Chichester.
- Erneberg M., Strandberg B. & Dahl Jensen B. (2003): Susceptibility of a plant invader to a pathogenic fungus: an experimental study of *Heracleum mantegazzianum* (Giant Hogweed) and *Sclerotinia sclerotiorum*. – In: Child L. E., Brock J. H., Brundu G., Prach K., Pyšek P., Wade P. M. & Williamson M. (eds.), *Plant invasions: Ecological threats and management solutions*, p. 355–372, Backhuys Publ., Leiden.
- Gilbert G. S. (2002): Evolutionary ecology of plant diseases in natural ecosystems. – *Annu. Rev. Phytopathol.* 40: 13–43.
- Guy P. L., Webster D. E., Davis L. & Forster R. L. S. (1998): Pests of non-indigenous organisms: hidden costs of introduction. – *Trends Ecol. Evol.* 13: 111.
- Hänfling B. & Kollmann J. (2002): An evolutionary perspective of biological invasions. – *Trends Ecol. Evol.* 17: 545–546.
- Hejda M. & Pyšek P. (2006): What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? – *Biol. Conserv.* 132: 143–152.
- Hill S. A. (1984): *Methods in plant virology*. – Blackwell Sci. Publ., Oxford.
- Hobbs R. J. & Humphries S. E. (1995): An integrated approach to the ecology and management of plant invasions. – *Conserv. Biol.* 9: 761–770.
- Hull R. (2002): *Mathews' plant virology*. – Academic Press, London.
- Hulme P. E. & Bremner E. T. (2006): Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. – *J. Appl. Ecol.* 43: 43–50.
- Jayasinghe U. & Chuquillanqui C. (1989): Use of indicator plants for detection of potato viruses. – CIP Research Guide 21, International Potato Center, Lima.
- Keane R. M. & Crawley M. J. (2002): Exotic plant invasions and the enemy release hypothesis. – *Trends Ecol. Evol.* 17: 164–170.
- Kollmann J. & Bañuelos M. J. (2004): Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). – *Diversity Distrib.* 10: 377–385.
- Kollmann J., Frederiksen L., Vestergaard P. & Bruun, H. H. (2007): Limiting factors for emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biol. Invas.* 9: 31–42.
- Lee C. E. (2002): Evolutionary genetics of invasive species. – *Trends Ecol. Evol.* 17: 386–391.
- Lodge D. M. (1993): Biological invasions – lessons for ecology. – *Trends Ecol. Evol.* 8: 133–37.
- Luken J. O. & Thieret J. W. (1997): *Assessment and management of plant invasions*. – Springer-Verlag, New York.

- Mack R. N., Simberloff D., Lonsdale W. M., Evans H., Clout M. & Bazzaz F. A. (2000): Biotic invasions: causes, epidemiology, global consequences, and control. – *Ecol. Appl.* 10: 689–710.
- Malmstrom C. M., Hughes C. C., Newton L. A. & Stoner C. J. (2005a): Virus infection in remnant native bunchgrasses from invaded California grasslands. – *New Phytol.* 168: 217–230.
- Malmstrom C. M., McCullough A. J., Johnson H. A., Newton L. A. & Borer E. T. (2005b): Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. – *Oecologia* 145: 153–164.
- Malmstrom C. M., Stoner C. J., Brandenburg S. & Newton L. A. (2006): Virus infection and grazing exert counteracting influences on survivorship of native bunchgrass seedlings competing with invasive exotics. – *J. Ecol.* 94: 264–275.
- Mandák B., Pyšek P. & Bímová K. (2004): History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: a hybrid spreading faster than its parents. – *Preslia* 76: 15–64.
- Mitchell C. E. & Power A. G. (2003): Release of invasive plants from fungal and viral pathogens. – *Nature* 421: 625–627.
- Mühr B. (2003): Klimadiagramme weltweit. – URL: [http://www.klimadiagramme.de/all.html]
- Olsson K. & Ågren J. (2002): Latitudinal population differentiation in phenology, life history and flower morphology in the perennial herb *Lythrum salicaria*. – *J. Evol. Biol.* 15: 983–996.
- Pearson M. N., Clover G. R. G., Guy P. L., Fletcher J. D. & Beever R. E. (2006): A review of the plant virus, viroid and mollicute records for New Zealand. – *Australas. Plant Path.* 35: 217–252.
- Peltre M. C., Muller S., Ollivier M., Dutarte A., Barbe J., Hauri J. & Tremolieres M. (2002): Aquatic plant proliferations in France: biological and ecological features of the main species and favourable environments. I. Synthesis of a bibliographic survey. – *Bull. Fr. Peche Piscic.* 365–366: 237–258.
- Primack R. B. (1979): Reproductive effort in annual and perennial species of *Plantago* (*Plantaginaceae*). – *Am. Nat.* 114: 51–62.
- Pyšek P. (1998): Is there a taxonomic pattern to plant invasions? – *Oikos* 82: 282–294.
- Pyšek P. & Prach K. (1995): Invasion dynamics of *Impatiens glandulifera* – a century of spreading reconstructed. – *Biol. Conserv.* 74: 41–48.
- Pyšek P., Prach K., Rejmánek M. & Wade M. (1995): Plant invasions: General aspects and special problems. – SPB Academic Publ., Amsterdam.
- Richardson D. M. (2006): *Pinus*: a model group for unlocking the secrets of alien plant invasions? – *Preslia* 78: 375–388.
- Rudloff W. (1981): World-climates: with tables of climatic data and practical suggestions. – Wissenschaftliche Verlagsgesellschaft, Stuttgart.
- Sakai A. K., Allendorf F. W., Holt J. S., Lodge D. M., Molofsky J., With K. A., Baughman S., Cabin R. J., Cohen J. E., Ellstrand N. C., McCauley D. E., O'Neil P., Parker I. M., Thompson J. N. & Weller S. G. (2001): The population biology of invasive species. – *Annu. Rev. Ecol. Syst.* 32: 305–332.
- Sandlund O. T., Schei P. J. & Viken Å. (1999): Invasive species and biodiversity management. – Kluwer Publ., Dordrecht.
- Schmitz G. (1995): Neophyten und Fauna: Ein Vergleich neophytischer und indigener *Impatiens*-Arten. – In: Böcker R., Gebhardt H., Konold W. & Schmidt-Fischer S. (eds.), *Gebietsfremde Pflanzenarten*, p. 195–204, Ecomed, Landsberg.
- Shaw R. H. (2003): Biological control of invasive weeds in the UK: opportunities and challenges. – In: Child L. E., Brock J. H., Brundu G., Prach K., Pyšek P., Wade P. M. & Williamson M. (eds.), *Plant invasions: Ecological threats and management solutions*, p. 337–354, Backhuys Publ., Leiden.
- Sheppard A. W., Shaw R. H. & Sforza R. (2006): Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations and other barriers to adoption. – *Weed Res.* 46: 93–117.
- Thompson B. K., Weiner J. & Warwick S. I. (1991): Size-dependent reproductive output in agricultural weeds. – *Can. J. Bot.* 69: 442–446.
- Toney J. C., Rice P. M. & Forcella F. (1998): Exotic plant records in the northwest United States 1950–1996: an ecological assessment. – *Northwest Sci.* 72: 198–213.
- Vitousek P. M., D'Antonio C. M., Loope L. L. & Westbrooks R. (1996): Biological invasions as global environmental change. – *Am. Sci.* 84: 468–487.
- Wadsworth R. A., Collingham Y. C., Willis S. G., Huntley B. & Hulme P. E. (2000): Simulating the spread and management of alien riparian weeds: are they out of control? – *J. Appl. Ecol.* 37: 28–38.
- Weber E. (2000): Switzerland and the invasive plant species issue. – *Bot. Helv.* 110: 11–24.
- Weber E. & Schmid B. (1998): Latitudinal population differentiation in two species of *Solidago* (*Asteraceae*) introduced into Europe. – *Am. J. Bot.* 85: 1110–1121.
- Willis S. G. & Hulme P. E. (2002): Does temperature limit the invasion of *Impatiens glandulifera* and *Heracleum mantegazzianum*: in the UK? – *Funct. Ecol.* 16: 530–539.

Received 16 August 2006

Revision received 4 December 2006

Accepted 5 December 2006