Latitudinal trends in growth and phenology of the invasive alien plant Impatiens glandulifera (Balsaminaceae)

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ABSTRACT

Geographical differentiation of populations can be interpreted as a result of adaptive processes in response to environmental gradients and biotic interactions. Such adaptations are particularly interesting in invasive alien species which have been present in an area for a relatively short time. There are few observations of latitudinal trends in alien plants, and no account exists for Impatiens glandulifera, a problematic annual weed in most countries of central and north-western Europe. Here we describe variation in growth and phenology in 26 populations of this species from nine European regions in a common garden in Denmark. Above-ground biomass (an estimate of fecundity), height and basal diameter were lower in the northern populations which were first to produce flowers. Some differences were also observed in biomass allocation to leaves, flowers and fruits, albeit without a latitudinal pattern. The latitudinal trends in growth and survival disappeared in a field experiment, probably due to suboptimal site conditions. Most variation in plant traits was explained by differences among regions with some minor effects of populations within regions. Besides latitude, no other geographical, climatic or population trait correlated with the observed differences in growth and phenology. Differences in latitude may mainly represent variation in length of the growing season. The causes and potential consequences of such latitudinal trends for population dynamics and dispersal of alien plants are discussed.

Keywords
Above-ground biomass, annual plant, biological invasions, flowering phenology, population differentiation.

INTRODUCTION

Biological invasions are a dynamic area of current ecological research, because they can be used to address fundamental questions in ecology and evolution of species diversity and distribution (Drake et al., 1989; Lodge, 1993; Sakai et al., 2001; Hännling & Kollmann, 2002; Lee, 2002). Numerous studies have focused on global and regional patterns in plant invasions, invasibility of different communities, differences between phylogenetic groups, life forms of invasive plants, and mechanisms and control of biological invasions (e.g. Pyšek & Prach, 1995; Pyšek, 1998; Alpert et al., 2000; Willis & Hulme, 2002; Woitke & Dietz, 2002). In contrast, surprisingly little information is available about regional and local adaptations of invasive plants (but see Parker et al., 2003), although such adaptations have been demonstrated in non-invasive species (Li et al., 1998; Imbert et al., 1999; Galloway & Fenster, 2000; Keller et al., 2000). Small colonizing populations often have increased rates of evolution, and that might be particularly true in invasive alien species (Eckert et al., 1996; Lee, 2002). One example is the European grass Bromus tectorum which shows local adaptations along an environmental gradient from arid steppe vegetation to subalpine forests in western North America (Rice & Mack, 1991). In the C₄ African grass, Pennisetum setaceum, on the other hand, phenotypic plasticity was more important than local adaptation to dominance across diverse habitats on Hawaii (Williams et al., 1995); similar results were reported for the invasive alien Agrostis capillaris in New Zealand (Rapson & Wilson, 1992).

Invasive alien plants are young floristic elements in the area of introduction, and regional and local differentiation might still be low compared with old inhabitants of the respective communities (e.g. Keller et al., 2000). However, such adaptations may facilitate the colonization of new habitats (Rice & Mack, 1991), and thus the spread of invasive species (Lee, 2002). For example, the Himalayan Impatiens glandulifera is more frost tolerant than European populations (Beerling & Perrins, 1993). The absence of geographical adaptations may at least partly explain the ‘lag’ phase of many biological invasions (Kowarik, 1995), and understanding such lag phases is relevant for predicting the...
effects of new invasions and for management strategies. The degree of local adaptation may depend on the matching of climatic and edaphic conditions in the native vs. the new range of the respective species, and on the history of immigration.

The east-Asian *Impatiens glandulifera* is an important invasive alien plant in Europe (Pyšek & Prach, 1995; Dawson & Holland, 1999; Weber, 2000; Pelte et al., 2002) and North America (Toney et al., 1998). This tall annual plant was selected for the study because it is currently expanding its European range (Beerling, 1993), and causes problems for ecosystem management (Wadsworth et al., 2000). As the species has been in Europe for about 150 years and covers a broad geographical range, regional adaptations may be expected, for example along latitudinal gradients. Such geographical differentiation was found in the invasive perennials *Solidago altissima* and *S. gigantea* (Weber & Schmid, 1998), but no account exists for annual invasive alien plants. Potential differentiation among regions along such gradients should be compared with variation among populations within regions, because the relative importance of regional and local adaptation has rarely been studied in invasive alien plants. Transplant experiments are appropriate tools to study regional and local adaptation and they should be done in multiple sites if they are to be relevant to management.

This study reports on a common garden experiment with 26 populations of *I. glandulifera* from nine European regions. The objectives were (1) to explore variation among regions in survival, growth and phenology; (2) to analyse the partitioning of variation among regions and among populations within regions; and (3) to correlate variation among all populations with site and population characteristics, including latitude.

**METHODS**

**Study species**

*Impatiens glandulifera* Royle (Balsaminaceae; 2n = 18, 20) is native to the Himalayan mountains from Kashmir to Garhwal (Beerling & Perrins, 1993); it was introduced to Europe in 1839 (Kew Gardens), became naturalized in England around 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 in the lower montane belt below 800 m a.s.l. in 19 European countries within the latitudes 30–64° N, and in the Alps it was recently found at 1550 m (H. Buschmann, pers. comm.). Its northern distribution seems to be controlled by length of the growing season, and the species might spread northwards with rising global temperatures (Beerling, 1993). It is a tall therophyte without clonal growth and no long-lived seed bank (Grime et al., 1988), but it is still not clear whether or not the species can have persistent seeds (K. Prach, pers. comm.). The flowers are self-fertile albeit protandrous; seeds are dispersed by explosive capsules, hydrochory and human transport. Large and dense stands are common on riverbanks, waste ground and in open moist woodlands (Demuth, 1993). Crawley (1987) considered it to be one of the ‘top twenty’ British aliens, because it is suppressing and endangering native species. It supports relatively few phytophagous insects, but is quite attractive to insect pollinators (Schmitz, 1995; Titze, 2000) which can lead to reduced pollination in native plants (Chittka & Schürkens, 2001).

### Seed populations

For the survey of regional and local adaptations, plant material from nine European regions was used (Tables 1 and 2). The latitudinal gradient covered a large part of the European range of the species from N Switzerland (47°) to N Sweden (63°), and a broad longitudinal gradient (N England, 1°, to N Sweden, 20°). In each region, seeds were collected in 1–5 populations that were at least 1 km apart; estimated population size varied from 50 to > 10,000 plants. The sampling could not be balanced due to local differences in number and size of the populations. Habitat types included riverbanks, lakeshores, mesic forest edges, roadsides and abandoned gardens; most sites had no management or only irregular mowing.

### Table 1 Site and seed characteristics of the 26 populations of *Impatiens glandulifera*. The nine regions (nearest town in parentheses) are ordered by latitude, and every region is represented by 1–5 populations. The grand mean of seed mass is based on 50 seeds per population; for the germination test 60 seeds per population were used

<table>
<thead>
<tr>
<th>Region [no. of populations]</th>
<th>Latitude N</th>
<th>Longitude E</th>
<th>Altitude (m)</th>
<th>AnnT (°C)</th>
<th>AnnP (mm)</th>
<th>Seed mass (mg)</th>
<th>Germination (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N Sweden† (Umeå) [4]</td>
<td>63°48′−63°50′</td>
<td>20°10′−20°20′</td>
<td>10−37</td>
<td>2.0</td>
<td>700</td>
<td>11.9</td>
<td>68</td>
</tr>
<tr>
<td>E Denmark (Copenhagen) [5]</td>
<td>55°41′−55°47′</td>
<td>12°28′−12°36′</td>
<td>2−19</td>
<td>8.0</td>
<td>602</td>
<td>12.1</td>
<td>83</td>
</tr>
<tr>
<td>N England‡ (Durham) [2]</td>
<td>54°43′−54°45′</td>
<td>−1°33′−1°52′</td>
<td>50−140</td>
<td>9.1−9.4</td>
<td>593−718</td>
<td>19.0</td>
<td>92</td>
</tr>
<tr>
<td>E Netherlands§ (Assens) [1]</td>
<td>53°00′</td>
<td>06°38′</td>
<td>5</td>
<td>9.0</td>
<td>767</td>
<td>10.8</td>
<td>76</td>
</tr>
<tr>
<td>E Germany (Halle-Leipzig) [5]</td>
<td>51°19′−51°28′</td>
<td>11°58′−12°20′</td>
<td>99−108</td>
<td>9.0</td>
<td>559</td>
<td>13.8</td>
<td>88</td>
</tr>
<tr>
<td>W Germany¶ (Hagen) [1]</td>
<td>51°20′</td>
<td>06°32′</td>
<td>120</td>
<td>9.5</td>
<td>903</td>
<td>13.5</td>
<td>58</td>
</tr>
<tr>
<td>S (W*) Czech Republic†† (Ceske Budejovice) [5]</td>
<td>48°58′−50°15′</td>
<td>13°00′−14°46′</td>
<td>356−439</td>
<td>7.2−7.9</td>
<td>600−628</td>
<td>15.2</td>
<td>80</td>
</tr>
<tr>
<td>E France** (Mulhouse) [2]</td>
<td>47°45′</td>
<td>7°24′−7°29′</td>
<td>250</td>
<td>9.8</td>
<td>786</td>
<td>16.5</td>
<td>58</td>
</tr>
<tr>
<td>N Switzerland (Zurich) [1]</td>
<td>47°23′</td>
<td>8°34′</td>
<td>569</td>
<td>8.0</td>
<td>1137</td>
<td>19.1</td>
<td>82</td>
</tr>
</tbody>
</table>

*One population from Karlovy Vary in W Czech Republic. Sources of the climatic data: †Umeå, C. Nilsson, pers. comm.; ‡Durham, S.G. Willis, pers. comm.; §Eelde; ¶Hagen and **Eimeldingen, Mühr (2003); ††Ceske Budejovice, K. Prach, pers. comm.; all others Rudloff (1981). AnnT, mean annual temperature; and AnnP, mean annual precipitation.
Latitudinal trends in growth and phenology of an annual invasive plant

Table 2 Site and population characteristics of the 19 populations of *Impatiens glandulifera* used to study partitioning of variation among regions and among populations within regions. Population numbers refer to Table 3

<table>
<thead>
<tr>
<th>Region</th>
<th>Population (No.)</th>
<th>Lat. N, Long. E</th>
<th>Altitude (m)</th>
<th>Habitat type</th>
<th>Population size</th>
</tr>
</thead>
<tbody>
<tr>
<td>N Sweden</td>
<td>Baggböle (1)</td>
<td>63°50′, 20°10′</td>
<td>35</td>
<td>Mesic roadside</td>
<td>c. 200</td>
</tr>
<tr>
<td></td>
<td>Tomtebo (2)</td>
<td>63°48′, 20°20′</td>
<td>37</td>
<td>Garden waste</td>
<td>c. 50</td>
</tr>
<tr>
<td></td>
<td>Röblack (3)</td>
<td>63°50′, 20°13′</td>
<td>10</td>
<td>Mesic roadside</td>
<td>&gt; 200</td>
</tr>
<tr>
<td></td>
<td>Sandbacka (4)</td>
<td>63°50′, 20°17′</td>
<td>25</td>
<td>Mesic park</td>
<td>50–75</td>
</tr>
<tr>
<td>E Germany</td>
<td>Bagvaerd So (1)</td>
<td>55°46′, 12°28′</td>
<td>18</td>
<td>Lakeshore</td>
<td>1000–5000</td>
</tr>
<tr>
<td></td>
<td>Lyngby So (2)</td>
<td>55°47′, 12°30′</td>
<td>18</td>
<td>Lakeshore</td>
<td>100–200</td>
</tr>
<tr>
<td></td>
<td>Hundeso (3)</td>
<td>55°46′, 12°33′</td>
<td>17</td>
<td>Lakeshore</td>
<td>&gt; 10,000</td>
</tr>
<tr>
<td></td>
<td>Utterslev Mose (4)</td>
<td>55°43′, 12°30′</td>
<td>19</td>
<td>Swamp margin</td>
<td>30–40</td>
</tr>
<tr>
<td></td>
<td>Christianshavn (5)</td>
<td>55°41′, 12°36′</td>
<td>2</td>
<td>Swamp margin</td>
<td>200–300</td>
</tr>
<tr>
<td>S (W) Czech Republic</td>
<td>Ceske Budovice (1)</td>
<td>49°00′, 14°27′</td>
<td>374</td>
<td>Riverbank</td>
<td>&gt; 1000*</td>
</tr>
<tr>
<td></td>
<td>Karlovy Vary (2)†</td>
<td>50°15′, 13°00′</td>
<td>356</td>
<td>Riverbank</td>
<td>&gt; 1000*</td>
</tr>
<tr>
<td></td>
<td>Ceske Budovice (3)</td>
<td>48°58′, 14°27′</td>
<td>380</td>
<td>Riverbank</td>
<td>&gt; 1000*</td>
</tr>
<tr>
<td></td>
<td>Trebon (4)</td>
<td>49°01′, 14°44′</td>
<td>439</td>
<td>Pond margin</td>
<td>&gt; 1000*</td>
</tr>
<tr>
<td></td>
<td>Trebon (5)</td>
<td>49°00′, 14°46′</td>
<td>430</td>
<td>Riverbank</td>
<td>&gt; 1000*</td>
</tr>
</tbody>
</table>

*Continuous populations along the riverbanks, †W Czech Republic.

Seeds were collected from 10 to 25 plants per population (5–10 seeds per plant) in September–October 2001. Only ripe capsules with brown or black seeds were harvested; unusually small or empty seeds were discarded. We dried the seeds at room temperature for 1–2 weeks and stored them at 0–5 °C for 5 months. Seed mass was determined for five groups of 10 seeds per population after drying at room temperature for 10 weeks. Seed mass was negatively correlated with latitude ($r^2 = 0.24$, $n = 25$, $P = 0.01$; Table 1).

Germination and growth conditions

In late March, seeds from all populations were put between moist blotting paper in Petri dishes at 0–5 °C for a 3-week 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. Sixty seeds of each population were laid out in transparent plastic boxes (12 cm × 8 cm × 5 cm) with blotting paper over a plastic bridge and 100 mL distilled water (plus fungicide). The boxes were randomly placed and daily rearranged in a germination cupboard with a temperature regime of 12 °C at night (12 h), and 22 °C with light during daytime (12 h). The experiment was terminated after 47 days as most seeds had germinated in the first week. Germination was high in all populations (58–92%) and independent of latitude ($r^2 = 0.008$, $n = 26$, $P = 0.69$; Table 1).

In mid April, 20 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 randomised. After 3 weeks we transferred the plants to larger pots (12 cm diameter, 10 cm depth) with the same substrate. Average day temperatures in the glasshouse were 21.6 ± 0.8 °C (mean ± SE) with 77.6 ± 2.1% air humidity and 10.0 ± 1.0 klux light (one record min$^{-1}$). Nocturnal values were 17.6 ± 0.4 °C, 83.4 ± 1.7% humidity and 1.7 ± 0.3 klux light.

In early June, eight randomly chosen individuals of each population were placed outdoors for hardening before planting into the common garden at the Royal Veterinary and Agricultural University (55°41′ N, 12°33′ E). One week later one plant of each population (total 130, cf. Tables 1 and 2) was planted randomly in five double rows with two guard plants on both ends of the rows (total 20 guard plants); the latter were excluded from the analysis. The rows were N–S orientated, with 40–50 cm distance between the plants within rows and 80–100 cm between rows, and after about 4 weeks a closed canopy had developed. The experimental plot was not shaded but slightly protected against wind by adjacent buildings. Mean daytime temperatures were 19.9 ± 0.4 °C and light averaged 283.9 ± 14.3 W m$^{-2}$; nocturnal values were 17.1 ± 0.3 °C and 45.3 ± 6.3 W m$^{-2}$ light (one record min$^{-1}$). The loamy soil had been tilled twice before planting, but neither fertiliser nor herbicides were applied and water only added when necessary. Little weeding was done because of rapid growth of the study plants, which prevented other species from establishing. Few herbivores were observed, except black aphids on 4–6 individuals in late June albeit without a clear pattern regarding populations or rows.

In late May, a second batch of plants from the same populations was planted with identical design in an experimental field.
at the university farm west of Copenhagen (55°40′ N, 12°19′ E).
As the plants were already 20–35 cm tall and not sufficiently robust, they were clipped just above the second node to reduce initial mortality. The loamy moraine soil was tilled before planting but otherwise no management occurred. Because this site was more exposed to wind and neither watering nor weeding was done, the growth conditions were harsher than in the common garden.

Plant measurements
In mid August, all plants were harvested in the common garden at ground level; harvest of the root system was not feasible as the species has fragile roots. At this time all plants were 4 months old, had abundant flowers and fruits and showed no signs of senescence. On fresh material we measured plant height and circumference at the second basal internode, whereas the number of flowers and fruits could not be quantified because of their ephemeral nature and continuous production. Because of the quantity of material, plants had to be predried at 20–40°C for 12 days in a greenhouse, followed by 3 days at 70°C in a drying oven. Biomass was determined separately for stems and branches vs. leaves, flowers and fruits. We also recorded the date of first flowering of all plants based on daily observations.

In the field experiment, no phenological records were done but survival was monitored. All surviving plants were harvested in late July, and above-ground biomass was determined after 3 days drying at 70°C.

Statistical analyses
We first explored regional variation in all plant traits by means of one-way ANOVAs irrespective of the latitudinal gradient. For this analysis we considered one randomly selected population per region with five plants, respectively, because the full data set of all populations was not balanced (cf. Table 1). To investigate partitioning of variation among regions and among populations within regions (five plants per population), nested ANOVAs were calculated for five populations from the Czech Republic, Denmark and Germany, respectively, and four from Sweden, considering region (fixed factor) and population (random factor) as main effects (cf. Table 2). The four regions represented the total length of the latitudinal European gradient. Population means of all 26 populations were then correlated with the most important latitude (European gradient. Population means of all 26 populations was not balanced (cf. Table 1). To investigate partitioning of variation among regions and among populations within regions (five plants per population), nested ANOVAs were calculated for five populations from the Czech Republic, Denmark and Germany, respectively, and four from Sweden, considering region (fixed factor) and population (random factor) as main effects (cf. Table 2). The four regions represented the total length of the latitudinal European gradient. Population means of all 26 populations were then correlated with the most important site and population characteristics, including latitude. In the multiple ANOVAs or regression analyses the P-values were Bonferroni corrected to avoid Type I errors. All proportional data were arcsine transformed and the other measurements log transformed in case of deviation from normality of the residuals and/or unequal variance. All statistical analyses followed Zar (1999).

RESULTS

Plant survival, growth and phenology
All transplants of Impatiens glandulifera survived in the common garden experiment, and vegetative growth, flowering and fruit production were abundant. At harvest in mid August, above-ground biomass (ANOVA; $F_{8,36} = 4.75, P < 0.001$), plant height ($F_{8,36} = 5.91, P < 0.001$), basal diameter ($F_{8,36} = 6.83, P < 0.0001$) and time till flowering ($F_{8,36} = 20.3, P < 0.001$) were significantly different among the nine European regions. No regional differences occurred in relative allocation to leaves, flowers and fruits compared with total above-ground biomass ($F_{8,36} = 2.56, P = 0.10$).

In the field experiment, 17% mortality was observed after 1 week, and about 50% of the plants were dead after 2 weeks. At harvest in late July, 34% of the plants had survived, with large differences among populations. Partly due to the initial clipping most plants were rather small (93 ± 2 cm, mean ± SE) and highly branched; the leaves were reddish and wrinkled, and flowering and fruiting were low. Above-ground biomass (27.4 ± 1.9 g; $n = 55$) was much less than that of the common garden experiment (73.7 ± 2.6 g; $n = 140$).

Partitioning of variation in growth and phenology
In the nested ANOVA most variation in above-ground biomass, plant height and time till flowering was explained by differences among regions (96–98%, Tables 3 and 4). The effect of populations within region was only significant for time till flowering, but even so 98% of the variance was due to regional effects. No differences among regions were observed in relative biomass of leaves, flowers and fruits ($F_{8,36} = 0.64, P > 0.05$), but about 36% of trait variance was explained by differences among populations within regions ($F_{8,36} = 3.8, P < 0.004$).

Correlation with site and population traits
In the common garden experiment, the differences between regions in above-ground biomass, plant height and time till flowering followed a clear latitudinal gradient with lower values in the northern populations ($r^2 = 0.36–0.63, P < 0.02$; Fig. 1). The Swedish, Danish and English plants had about half the biomass compared with plants from the Swiss, Czech and French populations. Time till flowering was about 10–15 days shorter in the northern populations.

Latitude was correlated with some of the site variables, for example, average annual temperature, minimum temperature and elevation ($P < 0.02$). Therefore, we did not calculate correlations with these variables as the results would not be independent. No other regional or local factor, including maximum temperature, annual precipitation and population size, showed any relationship with the measured plant traits ($r^2 = 0.22, P > 0.32$).

In the field experiment, the differences among the nine European regions in plant survival ($r^2 = 0.01, P > 0.05$) and biomass revealed no significant latitudinal pattern ($r^2 = 0.05, P > 0.05$). Because of the high mortality all plants per region were pooled for this analysis.

DISCUSSION
This is one of the first reports on latitudinal trends in growth and flowering phenology of an invasive alien annual plant, showing a
increase in size and time till flowering for southern populations in a common garden experiment. Similar latitudinal patterns in growth have been observed in the invasive alien biennials Verbascum thapsus and Daucus carota in North America (Reinartz, 1984; Lacey, 1988) and in the invasive alien perennials Solidago altissima and S. gigantea in Europe (Weber & Schmid, 1998), but also in native populations of Arabidopsis thaliana (Li et al., 1998) and Lythrum salicaria (Olsson & Ågren, 2002; Bastlová & Květ, 2003). In biennials and perennials the pre-reproductive period is often longer for plants from high latitudes (Lacey, 1988), whereas the opposite could be true for annuals where reproduction must be completed within one growing season. Reciprocal transplant experiments would be necessary to prove this hypothesis. Most of the above studies used only one transplant site which is unfortunate since the results can change depending on site conditions. Even better would be reciprocal transplant experiments among natural populations which could help to assess more precisely the degree of regional and local adaptation along the geographical gradient (Lacey, 1988; Rice & Mack, 1991). Obviously, such experiments are prohibitive in invasive plants as they may hybridize and spread if not done in common gardens (Parker et al., 2003). In our study the latitudinal patterns disappeared in the arable field which was apparently less suitable for I. glandulifera because of episodic drought and windy conditions which are unusual in natural populations of the species (Demuth, 1993). However, the same latitudinal patterns of growth and phenology as in the common garden were also observed in a greenhouse experiment where conditions were milder than in natural populations (J. Kollmann, unpublished data). The variation of plant traits among and within regions helps to understand the main result of clinal variation in I. glandulifera. Because variation among regions was markedly higher than variation within regions, the latitudinal trends in growth and flowering may largely be interpreted as adaptation to length of the growing season. No other site and population characteristic was correlated with postemergence heat temperature, as transplants were smaller and produced fewer seeds with increasing elevation; maximum height and pod production in this study were correlated with increasing postemergence heat temperature.
sum (i.e. degree days > 5 °C). The factors explaining altitudinal variation may be similar for the latitudinal gradient reported in our study. Bastlová & Kvet (2003) also found higher variability among than within regions in 10 (of 12) above-ground traits of *Lythrum salicaria*. These authors observed higher variability within regions only for 2 (of 2) root traits, which might be less dependent on variation of the growing season and more on local conditions. As a next step, native east-Asian populations of *I. glandulifera* should now be investigated, because it is often observed that plants differ in their native and in the introduced range (Bastlová & Kvet, 2002; Keane & Crawley, 2002; Jakobs *et al.*, 2004).

Lower plant biomass in the northern populations may reduce the competitive ability of *I. glandulifera* in case of transfer to central Europe, because high competitiveness is a key factor for the success of the species in central European floodplains and lakeshores (Demuth, 1993). In these moist and relatively nutrient-rich sites other tall herbs (e.g. *Epilobium hirsutum*, *Phalaris arundinacea*, *Urtica dioica*) may outcompete small-statured genotypes of *I. glandulifera* (Tickner *et al.*, 2001). This should lead to lower fecundity of these plants, as above-ground biomass and seed production are often correlated in annual species (Primack, 1979; Thompson *et al.*, 1991). However, many plant species do not show linear relationships between size and fecundity (Samson & Werk, 1986; Aarssen & Taylor, 1992), and so far no information is available for *I. glandulifera*. Plant size has also been found to be critical for determining whether plants reproduce at all, and many species have a minimum threshold size before flowering (Weiner, 1988; Klinkhamer *et al.*, 1992), although not so much in annuals. In fact, none of the populations in our study remained under this threshold, and flowering has been observed even in individuals only 5 cm tall (K. Prach, pers. comm.).

Southern populations transferred to northern sites, on the other hand, flower late in the face of a short growing season. Further experiments are needed to predict more details of population- and site-specific reproductive success, because late-flowering individuals achieved a larger size before flowering and consequently possessed more resources for seed production, as observed in *Prunella vulgaris* by Winn & Gross (1993). Unfortunately, flower and fruit production could not be quantified in the present study. Seed production must be a key factor for population dynamics of *I. glandulifera* as this annual species develops no seed or seedling bank (Beerling & Perrins, 1993).

As *I. glandulifera* has been in Europe for about 150 years, many generations could have been involved in potential adaptations to the length of the growing season. However, the species might be a more recent invader in some parts of its current European range, but no precise information exists about its exact dispersal history. Genotypic changes in height and timing of flowering are relatively fast and often correlated because growth is markedly reduced with onset of flowering. Recent research in the annual weed *Capsella bursa-pastoris* revealed that only a few genes are involved in flowering time, which is an important trait for colonizing different habitats (Linde *et al.*, 2001). Genotypes flowering too late or too early at a certain latitude will most likely

![Figure 1](image-url)  
**Figure 1** Latitudinal trends in above-ground biomass, plant height and time till flowering in 26 populations of *Impatiens glandulifera* from nine European regions (mean values from five plants per population). Results of a common garden experiment at latitude 55°41′ N; for origin of the populations see Table 1 (*P < 0.05*).
produce fewer seeds and thus are negatively selected (O’Neil, 1999). Regional adaptation to differences in photoperiod has been shown in a number of native non-invasive species, e.g. Cardamine flexuosa (Kudoh et al., 1995) and Arabidopsis thaliana (Pollard et al., 2001) but more rarely in invasive alien plants (Weber & Schmid, 1998). We suspect that the observed variation in growth and flowering initiation could actually be related to initial seed size. Seeds from northern populations might be smaller due to less favourable growth conditions, in contrast to observations in Prunella vulgaris (Winn & Gross, 1993). Although we cannot tell whether or not variation in seed mass and plant performance are the result of different genotypes or phenotypic plasticity (cf. Winn & Gross, 1993), they will translate into differential reproductive output in case of large-distance seed dispersal as in the study by Keller et al. (2000).

Impatiens glandulifera is a major problem for habitat management in Europe, because of the associated economic costs and because of local extinction of native species. Control is difficult, and suitable management strategies are still lacking for many habitat types (Dawson & Holland, 1999; Wadsworth et al., 2000; Shaw, 2003). Due to increasing mobility, new genotypes are likely to be introduced and spread within Europe, and at least some will become invasive. So far, most management plans ignore regional and local differentiation of populations which could reduce, for example the success of biological control. In addition, mowing regimes need to be adapted to the flowering phenology of the respective genotype. Regionally adapted populations may be dispersed due to increasing human transport, and dispersal of such genotypes could result in the formation of new hybrids with increased invasiveness (Nagy, 1997; Vilà & D’Antonio, 1998). These topics should be targeted by future research initiatives (cf. Rice & Emery, 2003).

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