A comprehensive test of evolutionarily increased competitive ability in a highly invasive plant species

Srijana Joshi1†, Michal Gruntman1*, Mark Bilton1, Merav Seifan2 and Katja Tielbörger1

1Plant Ecology Group, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany and 2Mitran Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 84990, Israel

* For correspondence. E-mail michal.gruntman@bot.uni-tuebingen.de
† Present address: International Centre for Integrated Mountain Development, GPO Box 3226, Kathmandu, Nepal

Received: 21 May 2014 Returned for revision: 11 July 2014 Accepted: 26 August 2014 Published electronically: 9 October 2014

• Background and Aims A common hypothesis to explain plants’ invasive success is that release from natural enemies in the introduced range selects for reduced allocation to resistance traits and a subsequent increase in resources available for growth and competitive ability (evolution of increased competitive ability, EICA). However, studies that have investigated this hypothesis have been incomplete as they either did not test for all aspects of competitive ability or did not select appropriate competitors.

• Methods Here, the prediction of increased competitive ability was examined with the invasive plant Lythrum salicaria (purple loosestrife) in a set of common-garden experiments that addressed these aspects by carefully distinguishing between competitive effect and response of invasive and native plants, and by using both interspecific and intraspecific competition settings with a highly vigorous neighbour, Urtica dioica (stinging nettle), which occurs in both ranges.

• Key Results While the intraspecific competition results showed no differences in competitive effect or response between native and invasive plants, the interspecific competition experiment revealed greater competitive response and effect of invasive plants in both biomass and seed production.

• Conclusions The use of both intra- and interspecific competition experiments in this study revealed opposing results. While the first experiment refutes the EICA hypothesis, the second shows strong support for it, suggesting evolutionarily increased competitive ability in invasive populations of L. salicaria. It is suggested that the use of naturally co-occurring heterospecifics, rather than conspecifics, may provide a better evaluation of the possible evolutionary shift towards greater competitive ability.

Key words: Competitive effect, competitive response, evolution of increased competitive ability, EICA, intraspecific competition, interspecific competition, invasive species, Lythrum salicaria, purple loosestrife, stinging nettle, Urtica dioica.

INTRODUCTION

Invasive success has often been suggested to result from species’ post-invasion evolution and their resulting adaptations to novel environments (Sakai et al., 2001; Müller-Schärer et al., 2004; Prentis et al., 2008; Drenovsky et al., 2012). For example, the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold, 1995) proposes that plants in their introduced range experience reduced damage by natural enemies, such as pathogens and specialist herbivores, which selects for reduced allocation to resistance traits and a consequent increase in resources available for growth and competitive ability (Blossey and Nötzold, 1995; Maron et al., 2004; Bossdorf et al., 2005; Doorduin and Vrieling, 2011). The EICA hypothesis therefore predicts that, compared with their native conspecifics, invasive genotypes should exhibit an inherently reduced resistance to native-range enemies and a greater competitive ability when these enemies are excluded (Blossey and Nötzold, 1995; Doorduin and Vrieling, 2011).

These predictions have been examined, often separately, in several studies (Vilà et al., 2003; Franks et al., 2008; Huang et al., 2010; Beaton et al., 2011; Alba et al., 2012; Hanley, 2012; Wang et al., 2013), but no general pattern has emerged, particularly regarding the evolution of increased competitive ability (Bossdorf et al., 2005; van Kleunen et al., 2010; Dostal, 2011; Felker-Quinn et al., 2013). This may be due to the fact that, despite being a key component of the hypothesis, competitive ability has rarely been addressed in a manner consistent with current approaches in community ecology. Particularly, previous plant competition studies have suggested that a distinction should be made between the ability of plants to suppress the growth of their neighbours (i.e. competitive effect) and to tolerate their impact (i.e. competitive response) (Goldberg and Fleetwood, 1987; Goldberg and Landa, 1991; Cahill et al., 2005). Competitive effect and response are not necessarily correlated (Goldberg and Landa, 1991; Keddy et al., 1994; Cahill et al., 2005) and could be governed by different traits, such as high resource-capture rate and resource-use efficiency, respectively (Cahill et al., 2005). In an invasion context, it is particularly important to distinguish between these components because they could characterize different invasion stages: while traits related to competitive effect may be important for outcompeting...
native plants at the establishment phase of invasion, competitive response is likely to be important at later stages when it enables stable persistence. To date, however, this distinction has been applied in only a few studies that have examined the predictions of the EICA hypothesis (Suding et al., 2004; Ridenour et al., 2008; He et al., 2009). Furthermore, these previous experimental setups did not provide an independent evaluation of competitive effect versus response.

Another key element that should be considered when studying the predictions of the EICA hypothesis is the choice of neighbour species. Ideally, evolutionary changes in competitive ability of invasive plants should be examined using heterospecifics that co-occur naturally with the invasive species. However, to provide unbiased evaluation of such competitive ability, this interspecific approach requires neighbours that are similar to the invasive species in size, life form and phenology and that occur with it in both ranges (Bossdorf et al., 2004; Vilà and Weiner, 2004). Unfortunately, only a few studies were able to use an appropriate competitor (Blair and Wolfe, 2004; Barney et al., 2009; He et al., 2009; Dostal, 2011), and no study to date has used a competitor that occurs in both ranges, making a direct comparison of competitive ability between ranges difficult. In an attempt to overcome these limitations, another approach has been applied in a few studies, where conspecifics from the native and invasive ranges were used as competing neighbours (Leger and Rice, 2003; Bossdorf et al., 2004; Zou et al., 2008). Although this intraspecific approach avoids the problem of choosing an appropriate neighbour (Bossdorf et al., 2005), it cannot fully test the EICA hypothesis because native and invasive plants rarely co-occur in nature. A possible way of addressing the limitations of each approach is to use both intra- and interspecific competition, but this has been rarely applied so far (Barney et al., 2009).

Here, the prediction of evolutionarily increased competitive ability was examined in the invasive plant Lythrum salicaria, which is native to Europe and highly invasive in North America (Thompson et al., 1987). In a previous study we have shown that invasive-range L. salicaria plants exhibit increased growth rate and biomass allocation (Joshi and Tielbörger, 2012) while other studies have shown that they outcompete conspecifics (2) do invasive plants exhibit greater competitive ability? (3) do potential origin-dependent differences in competitive ability depend on the competition setting (i.e. competitive effect versus response)? (4) do these origin-dependent differences in competitive ability depend on neighbour identity (i.e. intra- versus interspecific competition)?

MATERIALS AND METHODS

Study species

Lythrum salicaria is a herbaceous perennial plant. It was introduced to eastern North America in the early 19th century (Thompson et al., 1987) and has become highly invasive in North American wetland habitats, where it often forms large monospecific stands (Thompson et al., 1987), which have been shown to prevent the growth and establishment of local species and suppress their colonization (Mal et al., 1997; Hager, 2004; Flanagan et al., 2010; Hovick et al., 2011). Genetic evidence supports parallel introductions of this species (Houghton-Thompson et al., 2005; Chun et al., 2009), but rapid evolution in the introduced range rather than the introduction of preadapted populations (Colautti and Barrett, 2013).

Urtica dioica (Urticaceae) is a tall dioecious perennial herb. It is native to and widely distributed in Europe, Asia, North America and northern Africa, where it inhabits riparian and open areas (Taylor, 2009). Urtica dioica naturally co-occurs with L. salicaria in both its invasive and native ranges (Wolin and MacKeigan, 2005), and has been classified as a classical competitor (C) species in Grime’s (1977) model of plant strategy types.

Plant sources and seed handling

Seeds of L. salicaria were collected in summer 2006 from four native and four introduced populations in Germany (two from the northeast of Germany and two from the southwest) and the USA, respectively (Table 1). In the invasive range, the sampled populations were chosen so as to depict a range of invasion history, as two were from New Jersey, representing the eastern-most and oldest invasion range of L. salicaria in the USA, and two from Iowa, representing a much younger invasion range (Chun et al., 2009). Urtica dioica seeds were collected from three

<p>| TABLE 1. Sources of native and invasive populations of Lythrum salicaria used in the experiments, as well as of Urtica dioica |
|---------------------------------|---------------------------------|-----------------|-----------------|</p>
<table>
<thead>
<tr>
<th>Origin</th>
<th>Population (code)</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>Golm (GO)</td>
<td>48°52′N</td>
<td>8°9′E</td>
</tr>
<tr>
<td></td>
<td>Grube (GR)</td>
<td>48°32′N</td>
<td>9°0′E</td>
</tr>
<tr>
<td></td>
<td>Hagelloch (HA)*</td>
<td>52°43′N</td>
<td>12°9′E</td>
</tr>
<tr>
<td></td>
<td>Unterjessen (UN)*</td>
<td>52°40′N</td>
<td>12°9′E</td>
</tr>
<tr>
<td></td>
<td>Tübingen (TU)*</td>
<td>48°31′N</td>
<td>9°0′E</td>
</tr>
<tr>
<td>Invasive</td>
<td>Boone Forks, Iowa (BF)</td>
<td>40°51′N</td>
<td>79°55′W</td>
</tr>
<tr>
<td></td>
<td>Manly, Iowa (MA)</td>
<td>41°25′N</td>
<td>74°80′W</td>
</tr>
<tr>
<td></td>
<td>Beaver Run, New Jersey (BR)</td>
<td>42°17′N</td>
<td>93°56′W</td>
</tr>
<tr>
<td></td>
<td>Hainesville county, New Jersey (HV)</td>
<td>43°10′N</td>
<td>93°07′W</td>
</tr>
</tbody>
</table>

*Source populations of both U. dioica and L. salicaria.

*Source populations of only U. dioica.
populations in Germany in summer 2007 (Table 1). Seeds of both species were sampled from \( \sim 20 \) randomly selected mother plants per population and bagged separately for each mother plant. As \( L. \ salicaria \) is an obligate outcrosser (Agren and Ericson, 1996) and \( U. \ dioica \) is dioecious (Taylor, 2009), seeds within maternal families of both species were essentially half-sibs. All seeds were cold-stratified during winter at Tübingen University.

**Intraspecific competition experiments**

In May 2007, \( L. \ salicaria \) seeds were germinated in 2-L pots filled with standard potting soil (Topferde, Einheitserde, Kreuztal, Germany), following which they were transplanted into 18-L experimental pots. Our overall aim was to evaluate the performance of conspecific invasive and native plants in a competitive situation. In total we had eight populations \( [4 \times 2 \text{ origins}: \text{native (German); invasive (USA)}] \), with each population represented by five maternal genotypes. In competition pots (containing two plants per pot) we used a full factorial design to include all 36 possible combinations of populations (Fig. 1). These were directly compared with individuals in control pots (no neighbour; one plant per pot) containing their maternally related individuals. This experimental design resulted in a total of 400 individuals \( (8 \text{ populations} \times 5 \text{ maternal genotypes} \times 10 \text{ replicates per genotype}) \) planted in 220 pots \( (5 \text{ replicated pots} \times 8 \text{ control pots} + 36 \text{ competition pots}) \) (Fig. 1).

Following transplant, the pots were placed in a common garden at Tübingen University \( (48^\circ 32' \text{N}, 9^\circ 02' \text{E}) \). As \( L. \ salicaria \) grows in wetland habitats, the pots were constantly waterlogged, with one 20-g application of a slow-release fertilizer (Osmocote 18–10–11 NPK; Scotts, Geldermalsen, The Netherlands). Preliminary experiments showed that the use of an insecticide has potential side effects on the performance of \( L. \ salicaria \). Moreover, with concurrent studies we found a 50 % reduction in herbivore attack in the common garden compared with natural habitats, which reduced leaf damage to only 5 % at the common garden (R. Wegerer, Plant Ecology Group, University of Tübingen, Germany, unpubl. data). An insecticide was therefore not applied in this experiment as well as in the following interspecific experiment.

**Interspecific competition experiment**

In May 2008, seeds of \( L. \ salicaria \) from five maternal genotypes per population, as well as seeds of \( U. \ dioica \) from five maternal genotypes chosen randomly from the three populations, were germinated as described above for the intraspecific competition experiment. Seedlings from each maternal genotype were then transplanted into 18-L pots filled with the same standard potting soil and randomly assigned to one of the following four treatments: \( L. \ salicaria \) control with a single plant per pot; \( U. \ dioica \) control with a single plant per pot; competitive response, with \( L. \ salicaria \) as a single target plant surrounded by three \( U. \ dioica \) neighbours; competitive effect, with \( U. \ dioica \) as a single target plant surrounded by three \( L. \ salicaria \) neighbours. For the \( U. \ dioica \) control treatment, five pots were used in total, one per full treatment combination, and each corresponded to its maternal half-sib in the competitive-effect treatment. This experimental design resulted in a total of 125 pots \( [2 \text{ \( L. \ salicaria \) origins (native, invasive) } \times 3 \text{ competition treatments (\( L. \ salicaria \) control, competitive response and competitive effect) } \times 20 \text{ maternal genotypes } + 5 \text{ \( U. \ dioica \) controls}] \).

As in the intraspecific competition experiment, the pots were placed in the common garden at Tübingen University, where they were constantly waterlogged and 20 g of a slow-release fertilizer was applied.

**Response variables**

Plant performance in the two experiments was quantified with above-ground biomass and seed output per individual plant as the response variables. In both experiments, above-ground biomass of control and target plants was harvested following seed ripening at the end of October and measured after oven-drying at 60 °C for 24 h. Prior to that, total seed number of \( L. \ salicaria \) was estimated as \([\text{mean number of seeds per capsule (derived from a total of three capsules from apical, middle and basal stalks) } \times \text{ mean number of capsules per flowering stalk (derived from six randomly chosen stalks) } \times \text{ total number of stalks]}\) for \( U. \ dioica \), which is a dioecious plant, seed output could not be estimated as many individuals were androecious and performance was thus quantified only with above-ground biomass.

Competitive effect and response were estimated using the relative interaction index (RII) (Armas et al., 2004), which calculates the relative change in the performance of a target individual with neighbours \((P_w)\) compared with that under control conditions without neighbours \((P_{w/o})\) [RII = \( (P_w - P_{w/o})/(P_w + P_{w/o}) \)]. RII values range from \(-1 \) to \(+1 \), where negative and positive
values indicate suppressive and facilitative effects in the response variable, respectively. In both the intra- and interspecific competition experiments, calculations were carried out between control ($P_{w/o}$) and competition pots ($P_{w}$) which contained individuals of the same maternal family. In both experiments competitive response was measured using the identity of the target [i.e. the measured plant ($P_{w}$)], whereas competitive effect is given by the identity of the neighbour. For the intraspecific competition experiment, both individuals in the competition pots acted as either target or neighbour, whereas in the interspecific competition experiment the central plant always acted as the target ($P_{w}$), with the identities of *L. salicaria* targets giving the competitive response when surrounded by *U. dioica* and the identities of *L. salicaria* neighbours giving competitive effect when surrounding *U. dioica*.

**Data analyses**

For both experiments, differences in performance (biomass and seed output) between invasive and native plants with or without neighbours were examined using linear mixed models (LMMs), with data square-root-transformed to match model assumptions. For the intraspecific competitive response, origin and competition were used as fixed factors and populations as random intercepts nested within origin. For the interspecific competition experiment as well as for the competitive effect in the interspecific experiment, the competition factor with and without neighbours was unbalanced, and therefore the data were analysed separately to determine the origin effect in the no-competition treatment (intraspecific – random intercepts for populations within origin) and competition treatments (interspecific – crossed random intercepts for populations within target origin and populations within neighbour origin and pot; and interspecific – random intercepts for populations within neighbour origin).

For the intraspecific competition experiments, origin differences in RII values were examined using LMMs, with competitive response (target origin) and competitive effect (neighbour origin) as fixed factors using the crossed random intercepts for populations within target origin and populations within neighbour origin and pot. For the interspecific competition experiment, origin differences in RII values were analysed separately for competitive response and effect using LMMs, with origin as a fixed factor and populations as random intercepts nested within origin. All statistical analyses were performed using the lmer function in package lme4 (Bates, 2012) of R version 2.15 (R Development Core Team 2012), employing a likelihood ratio test to assess factor significance ($\chi^2$ test; d.f. = 1).

**RESULTS**

**Intraspecific competition experiment**

Invasive *L. salicaria* plants exhibited greater performance compared with their native conspecifics under competition-free conditions in both biomass (LMM: $\chi^2 = 12.580$, $P < 0.001$; Fig. 2A) and seed production (LMM: $\chi^2 = 9.849$, $P < 0.01$; Fig. 2B), as well as under intraspecific competition in both biomass (LMM: $\chi^2 = 11.72$, $P < 0.001$; Fig. 2A) and seed production (LMM: $\chi^2 = 7.32$, $P < 0.01$; Fig. 2B). However, this greater performance did not translate into any overall origin-related differences in competitive ability, i.e. when grown under intraspecific competition there were no significant differences in biomass (LMM: $\chi^2 = 2.86$) or seed production (LMM: $\chi^2 = 0.07$) values in relation to neighbour origin, and no significant interactions between target origin and neighbour origin (LMM: biomass, $\chi^2 = 3.58$; seed, $\chi^2 = 0.36$). In addition, for statistical models run on RII values, all origin-level effects and their interactions were non-significant, using either target origin response to or neighbour origin effect on conspecifics (Table 2; Fig. 3).

**Interspecific competition experiment**

Matching the results from the intraspecific competition, the interspecific competition experiment revealed greater overall performance of invasive compared with native *L. salicaria* in both biomass (LMM: $\chi^2 = 13.159$; $P < 0.01$; Fig. 4A) and seed production (LMM: $\chi^2 = 9.66$; $P < 0.01$; Fig. 4B), in both the absence and presence of *U. dioica* competitors.

However, unlike the intraspecific competition results, the greater performance of invasive plants did correspond here with their reduced response to competition. This is revealed both in the interaction between neighbour and origin effects on above-ground biomass (LMM: $\chi^2 = 4.575$; $P < 0.05$; Fig. 4A) and in the RII competitive response in both biomass and seed production (Table 3; Fig. 5A, B). Similarly, invasive *L. salicaria*
exerted a greater competitive effect on the biomass production of *U. dioica* compared with their native conspecifics, as revealed in both the neighbour origin effect on *U. dioica* biomass (LMM: \( \chi^2 = 4.338; P < 0.05; \) Fig. 4C) and in the RII competitive effect on biomass and seed production (Table 3; Fig. 5C).

### TABLE 2. LMM results for the intraspecific competition experiment, showing the lack of effects of target origin (competitive response) and neighbour origin (competitive effect) of *Lythrum salicaria* when grown with conspecifics. Competitive ability was estimated with the relative interaction index (RII) and population effects were accounted for in the statistical model (see Materials and methods)

<table>
<thead>
<tr>
<th>(A) Fixed effects</th>
<th>Above-ground biomass (g)</th>
<th>Seed number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Target origin (competitive response)</td>
<td>0.2183</td>
<td>3.5466</td>
</tr>
<tr>
<td>Neighbour origin (competitive effect)</td>
<td>3.2291</td>
<td>0.0420</td>
</tr>
<tr>
<td>Target origin <em>×</em> neighbour origin</td>
<td>2.6209</td>
<td>0.0357</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(B) Error variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pot intercept (<em>n</em> = 180)</td>
</tr>
<tr>
<td>Target population intercept (<em>n</em> = 8)</td>
</tr>
<tr>
<td>Neighbour population intercept (<em>n</em> = 8)</td>
</tr>
<tr>
<td>Residual</td>
</tr>
</tbody>
</table>

Values are \( \chi^2 \) (d.f. = 1; \( P > 0.05 \)); total \( N = 360 \).

**DISCUSSION**

The invasive success of plants has been attributed to the purported evolution of increased competitive ability in the introduced range (Blossey and Nötzold, 1995). In this study, we examined this prediction for the invasive plant *L. salicaria* using both intra- and interspecific competition settings and separating competitive effect and response. Our results suggest that inferences of genetically determined increase in competitive ability of invasive plants could depend highly on the choice of competition setting and neighbouring plants.

In particular, we show that under interspecific competition invasive *L. salicaria* exhibited greater competitive ability compared with their native conspecifics, but that this divergence was not apparent under intraspecific competition with native or invasive plants.

In the interspecific competition experiment, the competitive dominance of invasive *L. salicaria* plants was evident in their greater ability both to suppress *U. dioica* plants (competitive effect) and to tolerate their impact (competitive response). Superiority in both components of competition might indicate that *L. salicaria*’s invasiveness could be fuelled by its ability to outcompete native plants, and thus successfully establish at...
the initial stages of invasion, as well as to persist following establishment. Previous experiments with invasive *L. salicaria* reveal similar results of a strong competitive effect on co-occurring species (Hager, 2004; Hovick *et al.*, 2011), although Hager (2004) found the plants not to be as superior in their competitive response. However, these studies were limited to *L. salicaria* from the invaded range and thus provide limited inference regarding the possible evolution of competitive ability in this species. Here, we could demonstrate that invasive *L. salicaria* plants exhibit greater competitive response and effect compared with their native conspecifics in both seed production and vegetative growth, implying genetic diversion in these traits following introduction. While our interspecific setting indicates that invasive *L. salicaria* plants might have evolved into 'super-competitors', their greater competitive ability was less apparent under intraspecific competition. Differences in the results of these experiments could have stemmed from their different designs, i.e. the greater neighbour density in the interspecific experiment may have exerted greater competitive impact. However, contrary to these expected density-dependent effects, the competitive response values were much lower in the less dense intraspecific experiment, suggesting that competition here was stronger and therefore that *L. salicaria* might be a stronger overall competitor than *U. dioica*. To some extent this supports the commonly proposed idea that intraspecific interactions should be more intense than interspecific interactions due to greater similarities in the resource requirements of conspecifics (MacArthur and Levins, 1967; Farrer and Goldberg, 2011). Whilst we would not conclude that intra- is stronger than interspecific competition in all cases, our findings do suggest that in our case the greater similarity between conspecifics may have an additional impact on their interactions than mere size-related depletion of resources. Other components, such as plant–soil feedbacks, which have been shown to be more negative under intra- compared with interspecific competition (Kulmatiski *et al.*, 2008), or requirements for specific nutrients could be overriding some of the size-related elements for this highly competitive species, making the responses in origin more similar.

**Bossdorf *et al.*, (2004)** suggested that the use of conspecific competitors offers an advantage when comparing invasive and native genotypes as it avoids the problem of choosing neighbour species from either range. However, our results indicate that this approach could be misleading; had we examined only intraspecific competition, we would have inferred no evolutionary change in invasive *L. salicaria*. Interestingly, the few studies that found a decrease in the competitive ability of invasive genotypes were also performed with conspecific neighbours, and a new 'evolution of reduced competitive ability hypothesis' has been generated from these findings (van Kleunen and Schmid, 2003; Bossdorf *et al.*, 2004). We suggest that our
interspecific competition results might provide a more factual evaluation of the competitive ability of invasive L. salicaria, particularly as U. dioica co-occurs in both its native and invasive ranges, where it is one of its most vigorous competitors. Accordingly, despite its merits in terms of experimental design, the use of conspecific neighbours should be considered with care when estimating the competitive ability of invasive plants, especially as invasive and native plants do not co-occur in nature.

A possible caveat of our study is that competitive interactions were examined with co-occurring individuals from only the native range rather than from both. This implies that the greater tolerance of U. dioica to competition with native compared with invasive L. salicaria might be due to their common evolutionary history (Aarssen and Turkington, 1985; Ehlers and Thompson, 2004; Lankau, 2012) rather than to the evolution of increased competitive ability. However, such co-evolution between neighbouring plants has commonly been shown to be mediated by toxic effects on plants (Callaway and Ridenour, 2004) or soil communities (Lankau, 2012). As L. salicaria plants possess no such effects (Nakai et al., 2010; Scharfy et al., 2011) it seems unlikely that such interactions govern the interspecific pattern observed in this study. Nonetheless, while our study goes further than most in terms of determining the competitive ability of an invasive species, an even more comprehensive test could be garnered with the inclusion of U. dioica from both ranges, preferably with additional species as well.

In conclusion, our interspecific results demonstrate that introduced populations of L. salicaria express a genetically inherent increased competitive ability, which encompasses both strong negative effects on neighbours and the ability to withstand displacement. Combined with our previous findings of a decrease in the resistance of invasive L. salicaria to native-range herbivores (Joshi and Tiellbörger, 2012), these results provide compelling evidence for the EICA hypothesis within L. salicaria, showing that release from enemies may induce an evolutionary shift in resource allocation from traits related to herbivory resistance to those of competitive ability. To date, we know of only a few studies that provide support for both predictions of the EICA hypothesis (Beaton et al., 2011; Huang et al., 2012).

However, the fact that this trend was not apparent under intraspecific competition suggests that these interactions might be species-specific and that our ability to test these predictions may be best served by both an appropriate choice, and preferably multiple numbers, of neighbouring species.

ACKNOWLEDGEMENTS

We thank Ortrun Ebinger for her technical help. We also thank Mick Hanley and two anonymous reviewers for valuable comments on a previous version of this manuscript. This work was supported by the German Research Foundation to K.T. (DFG; TI-338/8–1) and to M.G (DFG; GR-4325/1–1) and by a fellowship of the Minerva Foundation to M.G.

LITERATURE CITED


