

# COMPETITIVE ABILITIES OF NATIVE EUROPEAN AND NON-NATIVE NORTH AMERICAN POPULATIONS OF *Lythrum salicaria* L.

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## Abstract

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As expressed by the evolution of increased competitive ability (EICA) hypothesis, non-native invasive plants are larger than plants of the same species growing in their native range as a result of changed dry weight allocation patterns. This should result in a greater competitive ability for the non-native populations. Competitive abilities and dry weight allocation patterns for North American non-native and native European *Lythrum salicaria* populations were tested against each other in a three-year common garden experiment using a replacement series design. Plants were grown across a range of nutrient and water levels to determine differential environmental effects of these two factors. Shoot height, stem number and flowering phenology were measured annually. The plants were harvested after three years and their dry weight allocation patterns determined. Shoot heights and stem numbers were positively related to nutrient levels but few significant between-population differences were found. The non-native North American plants flowered significantly later than those from native European populations. Competitive ability, measured as relative yield and relative yield total, was also not significantly different in most cases. Differences in dry weight allocation patterns depended upon the particular populations being analyzed. The results of this study do not support the predictions of the EICA hypothesis for this species under the tested conditions. Other factors, such as where a population falls along environmental and latitudinal gradients, daylength, or adaptation to local conditions, may be more important in explaining the greater growth and later flowering phenology seen in the non-native populations.

*Key words:* allometric analysis, competition, dry weight allocation, EICA hypothesis, *Lythrum salicaria*

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## Introduction

Plants of successful invasive populations tend to be larger than plants of the same species growing in their native range (Crawley, 1987, however see Thébaud, Simberloff, 2001). This seems to be one of the few generalizations that can be made about invasive plant species. However, no general mechanism has been found that would explain this difference.

The greater growth of the non-native plants may increase their competitive ability, allowing them to dominate newly colonized habitats in their region of secondary distribution. Such an apparent increase in competitive ability, which is usually lacking in their native range, allows the non-native plants to overshadow and crowd out native plants, leading to decreased native plant density and diversity (Mooney, Drake, 1986; Lodge, 1993; Cronk, Fuller, 1995; Williamson, 1996).

One possible mechanism is expressed by the Evolution of Increased Competitive Ability (EICA) hypothesis (Blossey, Nötzold, 1995). The increased growth of the invasive plants, compared to plants of the same species in their native range, is the result of a change in dry weight allocation patterns due to a micro-evolutionary event that occurred after the successful introduction of the species into its new region. It is thought that the greater growth and production is a response to the long-term absence of natural control agents.

However, differences in dry weight allocation patterns within a species are connected usually to where the populations fall along environmental gradients. An alternative hypothesis is that species which successfully invade new geographic areas come from more competitive genotypes of the species in its native area (Mooney, Drake, 1986; Di Castri et al., 1990). This is more likely to occur when the species involved has a wide geographic distribution (Peacock, McMillan, 1965, 1968). In this way, the successful invasive populations may come from native genotypes that have certain morphological and life history characteristics, which evolved in response to particular local conditions in the home range, such as day length (Bastlová, 2001; Bastlová, Květ, 2002).

*Lythrum salicaria* L. is a good example of a successful invasive species that appears to be more competitive in its area of secondary distribution (North America, Australia) than in its native range of Eurasia (Thompson et al., 1987; Malecki et al., 1993; Edwards, 1996). It also has a large geographic distribution in its native range, from the southern Mediterranean coast to the northern parts of Scandinavia (25–67° N) and from the British Isles to Japan (Edwards et al., 1999; Olsson, Agren, 2002; Bastlová et al., 2004). This makes *L. salicaria* a good species in which to test the validity of the two alternate hypotheses.

Here we report on a small study investigating dry weight allocation patterns and competitive ability between native European and non-native US populations of *L. salicaria*. The objective of this study was to directly test whether the US population is competitively superior to the native European populations, as according to the EICA hypothesis. If the EICA hypothesis is correct, then the US population should retard the growth of the European populations when grown in mixture, as well as having different dry weight allocation patterns.

## Methods

A common garden experiment was established at the Institute of Botany, Třeboň, the Czech Republic in 1996. Seeds from one non-native US and two native European populations of *Lythrum salicaria* were sown, and seedlings germinated, in a solar glasshouse in May 1996. The populations were part of an earlier field study of the population dynamics of native and non-native *L. salicaria* populations (Edwards, 1996; Edwards et al., 1998). The US population, from Indiana Dunes National Lakeshore (41°50' N, 87° W), grows in organic and always water-saturated substrates in the middle of the north-south distribution of *L. salicaria* in North America (Thompson et al., 1987). One of the native European populations grows in similar conditions (Gbelce, Parížske močiare National Nature Reserve, the Slovak Republic, 48° N, 18° E), while the other (Opatovický, Třeboň Basin Biosphere Reserve, the Czech Republic, 49° N, 14°50' E) grows in a sandy, nutrient-poor habitat, with fluctuating water levels (see Edwards et al., 1999 for a more detailed description of the field sites). The populations selected grow under similar climatic conditions, but differing daylength, in the field.

The germinated seedlings were transplanted into outdoor tubs (187x106x50 cm) in June 1996, after the emergence of the second leaf pair. The tubs were filled with sand and divided into plots of 34x30 cm (= 0.102 m<sup>2</sup>). The seedlings were planted in three replicate rows per tub, with a plant density of four seedlings per plot, confined to a central 0.01 m<sup>2</sup> area (plant density = 400 plants/1.0 m<sup>2</sup>); this is at the high range of plant densities used by Mal et al. (1997), when they compared the competitive ability of *L. salicaria* and *Typha angustifolia* L. Thus, any competitive interactions between the North American and European populations should be noticed at this planting density.

Plants within one plot were separated from plants in adjacent plots by 30 cm wide buffers, so to minimize between-plot interactions. Above- and below-ground plant structures were found not to overlap in low and medium nutrient treatments (see below). Although the roots of plants in neighboring plots in the high nutrient treatments did intermingle, the supplied nutrient levels were assumed to be high enough so plant growth was not affected adversely. The plants were grown in tubs and not in separate pots, because the greater volume afforded by use of the tubs minimized the chance of root binding, which would be more likely to occur if pots were used.

The full experiment was designed as a competition experiment, using a replacement series design (de Wit, van den Bergh, 1965); shoot height, dry weight allocation, and flowering data were taken as part of this experiment. Plant frequencies were 4 European plants: 0 US plants, 3:1, 2:2, 1:3, and 0:4 (frequencies = 1.0, 0.75, 0.5, and 0.25 for both the European and US populations). Replacement series keep planting densities constant, for which they have been criticized (Connolly, 1997), but are also a good means for determining the relative competitive superiority of species or, in this case, populations of the same species but growing in different continents (Engelhardt, Ritchie, 2002). In each tub, seedlings from the US population were planted with seedlings from one of the two European populations, so that there were two tubs for each treatment combination; one with plants from the Opatovický population and the other with plants from the Gbelce population (Table 1). There were no Opatovický vs. Gbelce plots due to space and time limitations. The extra number of plants and tubs would have made the experiment unmanageable.

Table 1. Experimental treatments for each of the 12 tubs in the common garden tub experiment.

Acronym	Native population	Nutrient	Water
OPLL	Opatovický	LOW	LOW
OPLH	Opatovický	LOW	HIGH
OPML	Opatovický	MID	LOW
OPMH	Opatovický	MID	HIGH
OPHL	Opatovický	HIGH	LOW
OPHH	Opatovický	HIGH	HIGH
GBLL	Gbelce	LOW	LOW
GBLH	Gbelce	LOW	HIGH
GBML	Gbelce	MID	LOW
GBMH	Gbelce	MID	HIGH
GBHL	Gbelce	HIGH	LOW
GBHH	Gbelce	HIGH	HIGH

Three nutrient and two water level treatments were assigned randomly to the tubs, using a factorial design, in order to simulate field conditions. A commercial fertilizer (Substral: 67 kg/l N; 30 P; 66 K) was used for the nutrient treatments. Different nutrient concentrations were created by diluting the stock nutrient solution (low = 1/250 strength; mid = 1/100; high = 1/10). These concentrations were similar to those found in the field sites (Edwards et al., 1999). During each growing season, 10 ml of the appropriate nutrient solution was added around the base of each plant at two week intervals, using a plastic syringe.

In addition, each tub was subjected to one of two water level treatments. In the high water treatment, the water level was kept at, or just above, the soil surface, with little or no fluctuation. Treatment 2 consisted of the water levels being allowed to fluctuate, but not to rise above (-)10 cm below the soil surface. Again, the water level treatments simulated field conditions (Edwards et al., 1999).

Shoot height and flower phenology were measured for all plants in the 1997 and 1998 growing periods. All plants were harvested in late July–early August 1998, after flowering had occurred, but before leaf senescence. Sand was washed carefully from the roots, followed by separation of the plants into their respective plant parts. These were dried for 24 hours at 70 °C and then weighed. Stem, leaf, inflorescence, and root dry weights were determined from these data. Aboveground dry weight was determined by adding the stem, leaf, and inflorescence weights together for each plant. Total plant dry weight was determined by adding the aboveground and root dry weights together. Prior to drying, final shoot height and stem number were measured for each plant.

## *Analyses*

All statistical analyses comparing native and non-native plants were done within each tub; no between-tub analyses were performed because such an analysis would represent pseudoreplication (Hurlburt, 1984). All analyses were done using SYSTAT (Wilkinson, 1990).

Between-population differences in final shoot height (after three growing seasons) and flower phenology (1997 and 1998 growing seasons) were analyzed by t-test (Snedecor, Cochran, 1989). Data from the 1997 and 1998 growing periods were tested separately for flower phenology. Results of the t-tests were similar for both years, therefore only the 1998 results will be presented. Comparison of the dry weight (DW) ratios (stem weight = SWR, leaf weight = LWR, root weight = RWR, and reproductive effort = RE), root-to-shoot (R/S), and total DW between the populations in each tub were also analyzed by t-tests. Classic allometric analysis calculates the ratio of a particular plant part DW to the total plant DW in plants of the same age (Hunt, 1978). Root-to-shoot (R/S) ratios were determined from the harvest data. Reproductive effort (RE) was defined as the inflorescence dry weight divided by total plant dry weight (Dunn, Sharitz, 1991). Differences in the allocation ratios and total plant DW, between native European and non-native US populations within each treatment tub, were first analyzed by oneway ANOVA, so to determine whether plant frequency affected the allocation patterns. Plant frequency ratio was not a significant factor ( $p = 0.05$ ), thus all plants of each population in a particular tub were grouped together and then compared to the other population using t-tests.

Relative yields (RY) and relative yield totals (RYT) were calculated for the populations within a tub so to determine whether the non-native North American population was competitively superior to the two native European populations under differing environmental conditions. RY and RYT were determined only for the 2:2 frequency plots, for ease of calculation and because frequency effects were found to be not significant. In order to determine RY, the dry weight of a population in mixture was divided by its dry weight when grown in monoculture, after standardizing for the differences in the number of plants planted in monoculture vs mixed plots. In this case, the mean dry weight of a population in monoculture was divided by two (Engelhardt, Ritchie, 2002). RYT was determined by calculating the mean of the RYs in a replicate series. The populations are not competing when RYT > 1 and the RYs of each population are > 1. Competitive interactions may be shown when RYT > 1 but there must be a clear difference in the RY values of the two populations (Engelhardt, Ritchie, 2002).

Confidence intervals (95%, 99%, and 99.9%) were constructed for all of the RY and RYT values (Snedecor, Cochran, 1989; Engelhardt, Ritchie, 2002). This was done to determine whether these values were significantly different from 1.

As a check on the first competition analysis, input-output ratio diagrams were constructed for each treatment in each growing period. These ratio diagrams may be used to infer the results of competition between species or genotype pairs, as well as frequency-dependent competitive interactions (Harper, 1977; Mal et al., 1997). The use

of shoot number provides a quick and easy method for estimating the competitive abilities between pairs of species or populations. Natural logarithm transformed proportions of non-native-to-native shoot number at the end of each growing period were plotted against the log-transformed proportions at the beginning of the experiment. Only those plots that originally contained both native and non-native plants (frequencies of 3:1, 2:2, 1:3) were included in the analysis as natural logarithm transformation of the ratios for the monocultural plots (frequencies of 4:0 and 0:4) would produce undefined numbers. The non-native population would be considered the better competitor if the subsequent line is significantly above a 45° threshold line, which denotes no competitive interaction. If the line is significantly below the threshold line, then the native population is more competitive.

All treatments were analyzed for shoot height and flower phenology. However, the mid nutrient-high water treatments (OPMH, GBMH; Table 1) were omitted from the allocation and competition analyses because of high plant mortality, while the OPLH and OPHL treatments were omitted from the competition analyses.

## Results

### *Shoot height and flower phenology*

The final shoot height of the plants increased with increasing nutrient and water availability (Fig. 1). Non-native US plants were significantly taller than native European plants in three

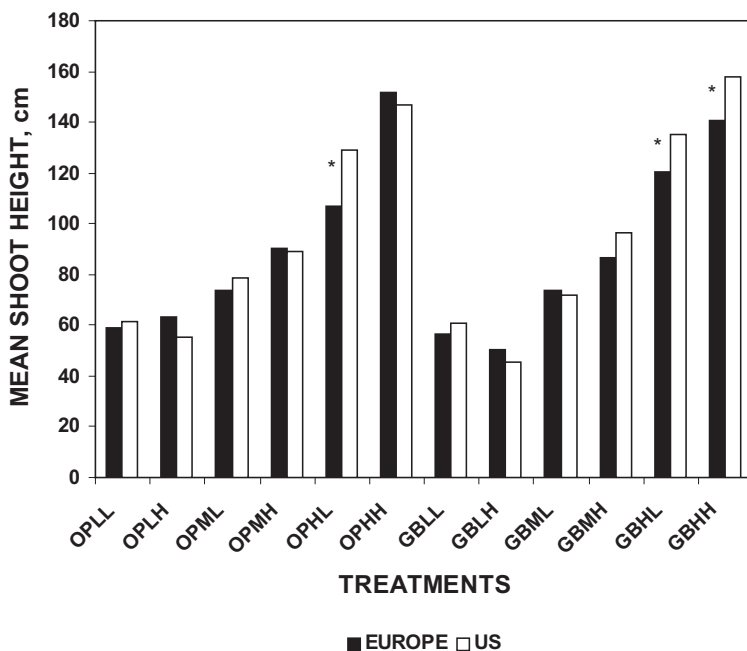


Fig. 1. Mean shoot height (cm) of native European and non-native US populations of *Lythrum salicaria* for the 1998 growing season. Treatments with asterisks had significant differences between native and non-native populations ( $p < 0.001$ ). Treatment names: OP = Opatovický; GB = Gbelce; L = low; M = medium; H = high (see Table 1 for more details concerning treatment names).

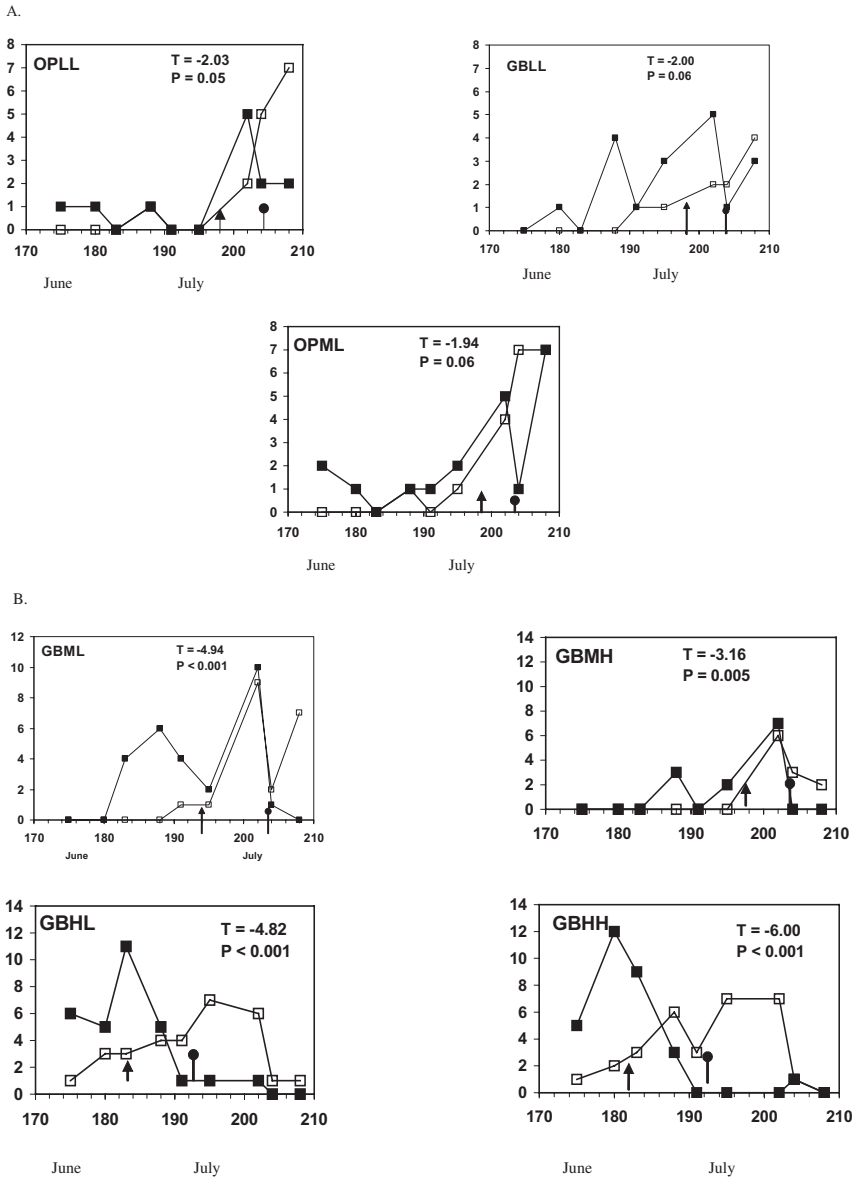


Fig. 2. Frequency of native and non-native plants commencing to flower on particular days during the 1998 growing season. The Y-axis is the number of plants beginning to flower while Julian calendar dates (day 1 = January 1) comprise the x-axis. Only those treatments showing A. borderline significant or B. significant differences ( $p < 0.05$ ) are shown. Black arrows represent the mean date of flowering for native plants, while a black circle shows the mean flowering date for non-native plants. Treatment names: OP = Opatovický; GB = Gbelce; L = low; M = medium; H = high (see Table 1 for more details concerning treatment names).

treatments, but only under high nutrient conditions. US plants were taller on average in four of the other treatments, while European plants were taller in the other five treatments; however, these differences were not significant at the 0.05 level. There was no difference in average shoot height with plant frequency within each treatment condition.

Native European plants flowered about a week earlier in the growing season than non-native plants in both 1997 and 1998 (Fig. 2). These differences were significant especially when comparing the US and Gbelce populations; the Gbelce plants flowered significantly earlier than the US plants in all treatment conditions, except for the low nutrient-high water treatment in 1998. In contrast, flower phenology was statistically similar between the Opatovický and US plants in both years.

The mean date of flowering was different among nutrient treatments. Native plants flowered in mid-July in the low and medium nutrient treatments, with the US plants flowering around July 22 or 23 under the same treatment conditions. However, in the high nutrient treatment, both native and US plants flowered almost two weeks earlier (Fig. 2).

### *Dry weight allocation*

The dry weight ratios, as well as R/S and total plant DW, did not differ significantly when comparing plants from the non-native US population to those from the Opatovický site in all treatment conditions (Table 2). The situation was quite different when comparing the US plants to those from Gbelce. R/S and RWR ratios were significantly different at the  $p < 0.05$  level. A stronger difference ( $p < 0.001$ ) was seen in RE, where much more biomass was allocated to reproductive tissues in the Gbelce plants compared to those from the US in all treatment conditions (Table 2). While there was no significant difference between the US and Opatovický populations in time of initial flowering, the Opatovický plants usually began to flower earlier in most of the treatments. On average, more dry weight was allocated to the inflorescences in the Opatovický plants compared to those from the US, but these differences were not statistically different.

### *Competitive interactions*

The RY and RYT values for each treatment are given in Table 3, along with the conclusions of the competition analyses. In all cases, except for the GBLH treatment, the RYT values were significantly greater than 1 ( $p < 0.01$ ). The RY values were also  $> 1$ , although usually not significantly greater than 1 (Table 3). Differences in RY values between the native and non-native populations were not significantly different from each other in all treatments. This means that the three populations grew the same in mixture as in monoculture. Therefore, the populations either did not compete against each other or the competitive strengths of the populations were equal.

Just as with the RY and RYT values, no competitive advantage for non-native *L. salicaria* plants was noticed in most treatments when constructing the input-output ratio diagrams (Fig. 3). The regression lines were very close and parallel to the 45° threshold line, which

Table 2. Mean dry weight allocation values ( $\pm 1$  SD) in native European and non-native US populations of *L. salicaria*.

Treat		Tot DW, g	SWR	LWR	RE	RWR	R/S
OPLL	E	7.56 $\pm$ 3.30	0.16 $\pm$ 0.05	0.18 $\pm$ 0.04	0.04 $\pm$ 0.05	0.63 $\pm$ 0.06	1.76 $\pm$ 0.50
	U	8.28 $\pm$ 3.40	0.15 $\pm$ 0.04	0.18 $\pm$ 0.03	0.03 $\pm$ 0.03	0.64 $\pm$ 0.06	1.85 $\pm$ 0.52
	T	0.79	0.69	0.72	1.10	0.85	0.69
OPLH	E	9.30 $\pm$ 3.89	0.17 $\pm$ 0.04	0.20 $\pm$ 0.03	0.02 $\pm$ 0.02	0.60 $\pm$ 0.08	1.64 $\pm$ 0.54
	U	7.52 $\pm$ 3.54	0.17 $\pm$ 0.06	0.19 $\pm$ 0.04	0.02 $\pm$ 0.03	0.62 $\pm$ 0.09	1.83 $\pm$ 0.97
	T	1.51	0.20	0.94	0.06	0.54	0.75
OPML	E	12.29 $\pm$ 4.39	0.17 $\pm$ 0.05	0.18 $\pm$ 0.04	0.06 $\pm$ 0.06	0.59 $\pm$ 0.09	1.56 $\pm$ 0.61
	U	14.82 $\pm$ 5.28	0.16 $\pm$ 0.04	0.18 $\pm$ 0.04	0.04 $\pm$ 0.02	0.62 $\pm$ 0.06	1.71 $\pm$ 0.42
	T	2.01 *	0.93	0.40	1.54	1.64	1.74
OPHL	E	46.61 $\pm$ 24.35	0.27 $\pm$ 0.08	0.14 $\pm$ 0.04	0.08 $\pm$ 0.06	0.52 $\pm$ 0.12	1.35 $\pm$ 1.34
	U	79.34 $\pm$ 37.34	0.31 $\pm$ 0.05	0.12 $\pm$ 0.02	0.06 $\pm$ 0.04	0.51 $\pm$ 0.08	1.14 $\pm$ 0.51
	T	3.414 ***	1.80	1.22	1.32	0.13	0.75
OPHH	E	82.56 $\pm$ 36.45	0.34 $\pm$ 0.05	0.12 $\pm$ 0.03	0.14 $\pm$ 0.05	0.40 $\pm$ 0.06	0.69 $\pm$ 0.18
	U	84.07 $\pm$ 25.98	0.31 $\pm$ 0.04	0.11 $\pm$ 0.02	0.14 $\pm$ 0.03	0.43 $\pm$ 0.05	0.78 $\pm$ 0.19
	T	0.18	1.80	1.86	0.39	2.02 *	1.80
GBLL	E	6.07 $\pm$ 2.72	0.15 $\pm$ 0.04	0.20 $\pm$ 0.06	0.10 $\pm$ 0.05	0.56 $\pm$ 0.06	1.30 $\pm$ 0.36
	U	8.68 $\pm$ 4.62	0.16 $\pm$ 0.04	0.20 $\pm$ 0.05	0.06 $\pm$ 0.05	0.57 $\pm$ 0.06	1.35 $\pm$ 0.32
	T	2.66 **	0.72	0.90	2.33 *	0.69	0.58
GBLH	E	4.44 $\pm$ 1.95	0.20 $\pm$ 0.04	0.17 $\pm$ 0.04	0.05 $\pm$ 0.04	0.59 $\pm$ 0.07	1.50 $\pm$ 0.47
	U	5.32 $\pm$ 2.73	0.17 $\pm$ 0.04	0.19 $\pm$ 0.04	0.01 $\pm$ 0.02	0.63 $\pm$ 0.07	1.78 $\pm$ 0.51
	T	1.39	2.17 *	1.76	4.39 ****	2.21 *	2.10 *
GBML	E	10.02 $\pm$ 4.33	0.19 $\pm$ 0.04	0.16 $\pm$ 0.05	0.14 $\pm$ 0.05	0.51 $\pm$ 0.07	1.07 $\pm$ 0.29
	U	12.40 $\pm$ 5.34	0.18 $\pm$ 0.05	0.19 $\pm$ 0.04	0.07 $\pm$ 0.04	0.56 $\pm$ 0.08	1.33 $\pm$ 0.47
	T	1.87	0.61	2.57 *	6.06 ****	2.61 *	2.58 *
GBHL	E	53.69 $\pm$ 20.60	0.28 $\pm$ 0.04	0.14 $\pm$ 0.03	0.11 $\pm$ 0.05	0.47 $\pm$ 0.06	0.92 $\pm$ 0.26
	U	70.70 $\pm$ 23.41	0.27 $\pm$ 0.04	0.15 $\pm$ 0.02	0.08 $\pm$ 0.04	0.51 $\pm$ 0.07	1.06 $\pm$ 0.29
	T	2.95 ***	0.47	0.82	3.21 ***	2.11 *	2.03 *
GBHH	E	69.08 $\pm$ 25.67	0.33 $\pm$ 0.04	0.11 $\pm$ 0.02	0.18 $\pm$ 0.06	0.38 $\pm$ 0.06	0.63 $\pm$ 0.16
	U	98.64 $\pm$ 42.81	0.34 $\pm$ 0.04	0.14 $\pm$ 0.02	0.13 $\pm$ 0.04	0.40 $\pm$ 0.06	0.67 $\pm$ 0.16
	T	3.24 ***	0.60	5.41 ****	3.84 ****	0.97	0.91

Legend: Treat = Treatment; E = Europe; U = US; T = T-statistic; SWR = stem weight ratio; LWR = leaf weight ratio; RE = reproductive effort; RWR = root weight ratio; R/S = root-to-shoot ratio. The ratios are given as proportions of plant parts to total plant DW. Treatment names: OP = Opatovický; GB = Gbelce; L = low; M = medium; H = high (see Table 1 for more details concerning treatment names). Significant T-test statistics are in bold type. P values: \* < 0.05; \*\* < 0.01; \*\*\* < 0.005; \*\*\*\* < 0.001

denotes no or equal competitive interaction. The input-output lines were significantly below this threshold line in the OPLL treatment for both growing periods, indicating that



Table 3. Relative yield (RY) and relative yield total (RYT) values (mean  $\pm$  SE) for the non-native (Indiana Dunes National Lakeshore, USA) and native (Opatovický, the Czech Republic; Gbelce, the Slovak Republic) populations of *Lythrum salicaria* grown under different nutrient and water level treatments. RY and RYT values were calculated using the method of Engelhardt and Ritchie (2002). Treatment acronyms are as given in Table 1. High plant mortality prevented calculation of the competitive abilities in the OPLH, OPMH, OPHL, and GBMH treatments. T-tests were used to determine whether the RY and RYT values were significantly different from 1. \* < 0.01, \*\* < 0.001

Treatment	RY, Native	RY, Non-native	RYT
OPLL	2.27 $\pm$ 0.69	1.52 $\pm$ 0.36	1.89 $\pm$ 0.19 **
OPML	2.05 $\pm$ 0.35 *	1.63 $\pm$ 0.62	1.84 $\pm$ 0.31 *
OPHH	1.91 $\pm$ 0.26 **	1.82 $\pm$ 0.05 **	1.86 $\pm$ 0.15 **
GBLL	2.45 $\pm$ 0.52 *	1.74 $\pm$ 0.49	2.10 $\pm$ 0.19 **
GBLH	1.07 $\pm$ 0.35	1.83 $\pm$ 0.32 *	1.45 $\pm$ 0.28
GBML	1.32 $\pm$ 0.17	1.75 $\pm$ 0.21 *	1.54 $\pm$ 0.03 **
GBHL	1.33 $\pm$ 0.22	2.06 $\pm$ 0.22 **	1.70 $\pm$ 0.22 *
GBHH	1.75 $\pm$ 0.16 **	2.03 $\pm$ 0.21 **	1.89 $\pm$ 0.18 **

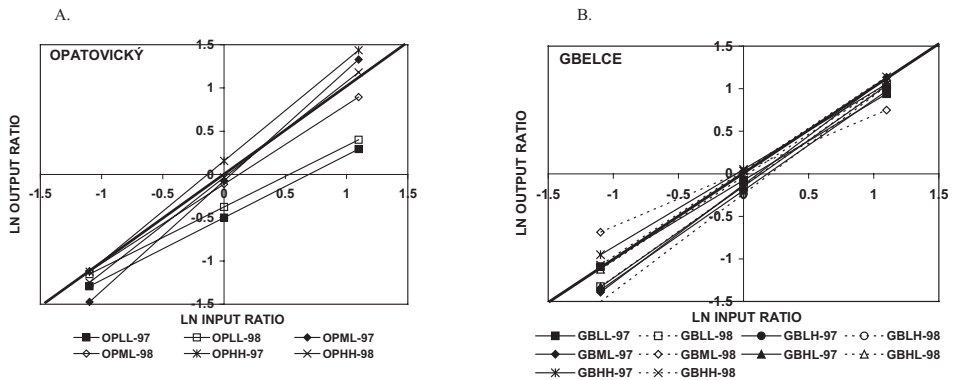


Fig. 3. Input-output regression lines for the A. Opatovický and B. Gbelce competition experiments. The non-native US population is more competitive if the treatment line is significantly above the 45° threshold line; if the regression line is significantly below the threshold line, then the native population is the better competitor. Treatment names: OP = Opatovický; GB = Gbelce; L = low; M = medium; H = high (see Table 1 for more details concerning treatment names).

the native Opatovický population is more competitive than the US population under these habitat conditions.

## Discussion

The number of populations used in this study was quite small, thus precluding the formation of any general, conclusive statements concerning the validity of the mechanistic hypotheses presented. Any full test of the validity of these hypotheses would require larger experiments, using more populations. Still, some general trends can be ascertained from this small study.

There are little data to support the idea that the invasive population of *L. salicaria* is competitively superior to the native European populations used in this study. An increased competitive ability in invasive populations, compared to native populations of the same species, was one of the main predictions of the EICA hypothesis (Blossey, Nötzold, 1995). But in this particular case, either the populations did not compete against each other, which would imply a complementary relationship (Engelhardt, Ritchie, 2002), or the competitive strengths of the populations were equal in all treatments. It is unlikely that there was a lack of competition among the populations, as intraspecific competition is quite strong in *L. salicaria* (Gaudet, Keddy, 1988; Mal et al., 1997; Weihe, Neely, 1997; Farnsworth, Ellis, 2001). The planting density used in this experiment was in the high part of the range used by Mal et al (1997). These authors found that *L. salicaria* was the stronger competitor than *Typha angustifolia* at all planting densities, with both species showing high inter and intraspecific competitive abilities.

The EICA hypothesis also predicts that, as a consequence of the long-term absence of any control agents, such as herbivores, less photosynthate would be allocated to defense in the non-native populations, compared to native populations of the same species. Instead, the photosynthate would be used for increased growth, resulting in the taller and more competitive plants seen in non-native populations (Blossey, Nötzold, 1995). Neither herbivore preference nor plant resistance were investigated explicitly in this study. However, we did note on which plants and populations known insect herbivores of *Lythrum salicaria* were found. Analysis of these data found no preference by herbivores for any of the populations (unpublished data).

Our preliminary results about herbivore preference agree with the findings of the much more in-depth study done by Willis et al. (1999). These authors studied herbivore resistance and plant growth in *L. salicaria* using many more native and non-native populations. Herbivore resistance was found to differ little between the native and non-native populations. Willis et al. (1999) did find that the native populations had higher concentrations of phenolic compounds in their leaves, compared to the non-native populations (as predicted by the EICA hypothesis). But, these concentrations were far below levels considered to be effective for providing any protection from herbivores.

The results from our study and that of Willis et al. (1999) bring into question the explanatory power of the EICA hypothesis. Non-native populations of *L. salicaria* are not more competitive than native European populations (this study), while there is no difference in herbivore resistance between native and non-native populations of this species (Willis et al., 1999). Also, shoot height, plant biomass, and dry weight allocation patterns were affected by nutrient and water level conditions, with little differences between the native and non-native

populations seen in the low and intermediate nutrient treatments. Other mechanisms may be more relevant in explaining the increased size of non-native populations of successful invasive plant species than the EICA hypothesis.

Changes in dry weight allocation patterns may be the result of positive effects of environmental factors on the non-native populations (Bastlová, Květ, 2002). Phenotypic differences among populations of a species are associated with where the population falls along environmental as well as latitudinal gradients (Mooney, Drake, 1986; di Castri et al., 1990). Weber, Schmid (1998) showed that populations of two *Solidago* species differed in dry weight allocation patterns depending on where the populations originated from along a latitudinal gradient. Similar results have been found by Bastlová, Květ (2002) and Olsson, Agren (2002) for *L. salicaria*. The differences in allocation patterns may be due to the populations being adapted to local conditions, such as daylength (Peacock, McMillan, 1968). Daylength is known to be a very important factor in plant development (Bastlová, Květ, 2002). When these plants then establish in new, more southerly, geographic areas, the local conditions at the new habitat may select for larger phenotypes. Nutrient conditions can also be important in ameliorating differences between native and non-native populations, as shown in this study.

The US population used in this study grew in an area at least 7° further south in latitude than the native European populations, with a concomitant greater daylength. The differences in flower phenology seen in this study support the idea that adaptation to local conditions in the native range, and the effects of changed daylength in the new geographic area, may be more likely to have caused the change in biomass allocation patterns in the non-native populations than any rapid evolutionary event post-invasion, as hypothesized in the EICA hypothesis (Blossey, Nötzold, 1995). Further research on the effects of latitude and daylength seems to offer a more productive approach to determining the underlying mechanism for increased growth in non-native populations.

*Original English by K.R.Edwards*

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