ORIGINAL PAPER

Evidence for a shift in life-history strategy during the secondary phase of a plant invasion

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Received: 14 March 2008 / Accepted: 14 April 2008 / Published online: 25 April 2008 © Springer Science+Business Media B.V. 2008

Abstract We investigated the correlated response of several key traits of Lythrum salicaria L. to water availability gradients in introduced (Iowa, USA) and native (Switzerland, Europe) populations. This was done to investigate whether plants exhibit a shift in life-history strategy during expansion into more stressful habitats during the secondary phase of invasion, as has recently been hypothesized by Dietz and Edwards (Ecology 87(6):1359, 2006). Plants in invaded habitats exhibited a correlated increase in longevity and decrease in overall size in the transition into more stressful mesic habitats. In contrast, plants in the native range only exhibited a decrease in height. Our findings are consistent with the hypothesis that secondary invasion is taking place in L. salicaria, allowing it to be more successful under the more stressful mesic conditions in the invaded range. If this trend continues, L. salicaria may become a more problematic species in the future.

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H. Dietz e-mail: hansjoerg.dietz@env.ethz.ch **Keywords** Secondary invasion · *Lythrum* salicaria · Invasive species · Herb-chronology · Life-history evolution · Purple loosestrife · Moisture gradient

Introduction

Attempts to explain the success of invasive species have generated a broad variety of hypotheses that have generally met with mixed support, depending on the plant species, habitat or abiotic resources examined (Williamson 1999; Lambrinos 2004). These empirical inconsistencies have inhibited the development of a general theory of invasive species. Recently, Dietz and Edwards (2006) have suggested that one way around this problem is to develop a more sophisticated conceptual framework, accounting not only for the broad array of factors involved, but also for changes in the relative importance of these factors during the process of invasion. In particular they state that it must be recognized that the ecological and evolutionary processes responsible for successful invasions in new habitats change during the course of an invasion. They suggest dividing the process of invasion into a primary phase, in which pre-adapted species increase rapidly in abundance due to favorable growth conditions in relatively resource-rich habitats, and a secondary phase, during which plants expand their range into more resource poor, invasion resistant habitats. Dietz and Edwards (2006) hypothesize that the secondary expansion is a result of strategic shifts in crucial lifehistory traits either through a plastic response or by adaptive evolution. (We will hereafter refer to this as the Dietz–Edwards hypothesis.)

During a successful invasion, plants would be expected to decrease in vigour and shift towards a more conservative life-history strategy as they expand into novel habitats presenting more stressful conditions. Individuals should decrease in size, place more photosynthate into root storage, increase in longevity, and reduce flowering or postpone it to a later stage to optimize lifetime reproductive success under more stressful conditions (cf., Grime 2001; Chapin et al. 1993). Baret et al. (2004) present one of the few studies so far that can be used as evidence in support of this idea. They partly explain the success of the invasive plant Rubus alceifolius as a plastic shift towards a more conservative growth strategy (i.e., an increase in asexual versus sexual reproduction) under more severe conditions along an altitudinal gradient. However, shifts in life-history strategies along environmental gradients are certainly not restricted to the introduced range. For example, Maron et al. (2004) demonstrated that the invasive species Hypericum perforatum can show significant genetic and phenotypic variability in response to broad scale changes in environmental conditions (i.e., latitude) that is similar in pattern in the native and introduced ranges. Other authors have shown a correlation between various life-history characteristics and environmental gradients in either the native or the introduced range (Olsson and Agren 2002; Sexton et al. 2002; Willis and Hulme 2002; Kollmann and Bañuelos 2004). These results suggest that it is necessary to compare possible shifts in lifehistory strategies along environmental gradients between the native and introduced range. This would reveal whether invasive species show novel responses in more restrictive habitats in the introduced range that could explain a higher invasiveness in such habitats compared to the native range.

We studied several key life-history traits of *Lythrum salicaria* L. (purple loosestrife) along a strong water availability gradient in the introduced (North America) and native (Europe) range to investigate whether invasions of this wetland species into more mesic habitats in North America are due to a shift in life-history response not present in the

native range. Lythrum salicaria is an important invasive species in North America that grows much larger in the invaded range than in the native range. It can also exhibit a significant shift in stem height and biomass production in response to varying soil water conditions (Edwards et al. 1995; Mal et al. 1997; Mal and Lovett-Doust 2005; Chun et al. 2007). These shifts, however, have not been considered in connection with other life-history traits (although see Chun et al. (2007)). Thus, the demonstrated plasticity could simply be indicative of a short-term response to changing growth conditions rather than a shift in lifehistory strategy. To provide evidence for an effective shift in life-history strategy, at least two life-history traits connected by a trade-off have to be investigated (cf., Grime 2001). In order to accomplish this, we investigated stem height, number of stems, root size and plant age in L. salicaria.

Given the above considerations, we hypothesized that L. salicaria would decrease in overall size (stem height and number of stems), but be longer lived with greater root size in going from wet habitat to the more stressful mesic habitat in the invaded range. In contrast, we also hypothesized that the corresponding changes would be less pronounced or non-existent in the native range. We were particularly interested in examining the age response, because plant age is an important life-history trait of perennial plant species and it has been an understudied component in the examination of herbaceous plants (cf., Von Arx et al. 2006). Fortunately, there have been recent advances in aging herbaceous forbs using the techniques of herb-chronology (e.g., Dietz and Ullmann 1997, 1998; Dietz and von Arx 2005), which allow us to determine if there has been a systematic shift towards greater longevity in the introduced range, under more stressful environmental conditions.

Methods

Study species

Lythrum salicaria L. (purple loosestrife) is a fast growing perennial herb native to Eurasia and invasive to North America, where it was introduced in the early 19th century. In both areas it is predominately found in nutrient rich wetland habitats, growing on a broad range of soil types (Thompson et al. 1987).

Although growing in drier habitats (Dietz 2002), L. salicaria is most successful on nutrient rich, moist sandy soils (Shamsi and Whitehead 1974; Thompson et al. 1987). Under these conditions the invasive form of the plant grows much larger and is more fecund than the native form (Edwards et al. 1995). In its native range, L. salicaria does not usually form dense populations, whereas in the introduced range populations can form monospecific stands, altering or completely displacing the native vegetation and modifying ecosystem composition and properties (Thompson et al. 1987, but see Hager and McCoy 1998). There is also some circumstantial evidence that L. salicaria is expanding to occupy more mesic conditions in the invaded range (Dietz 2002; personal observations of the authors).

Study areas

We selected six *L. salicaria* populations from two provenances for our study, three from Switzerland (CH) and three from Iowa, USA (US; Table 1). Each population spanned a soil water availability gradient ranging from hydric to mesic. We chose populations from both provenances that were as similar as possible in terms of landscape position and management. All study areas were situated at approximately the same elevation with no indication of recent mowing (Table 1). Each study site was surrounded by

Table 1 General characteristics of the study sites sampled

intensely managed agricultural fields ensuring that nutrient inputs would be consistently high. Populations in Switzerland were located along creeks, with hydric habitats lying directly on the edge of the creek and mesic habitats occurring at slightly higher elevations. Iowa populations were located in wetland basins with the more mesic parts of the population occurring at slightly higher elevations, grading into grasslands.

Mesic and hydric habitats in each study area were first identified by determining the orientation of the local water availability gradient, either by means of micro-topography (i.e., elevation along a slope) or, in the case of relatively flat areas (Black Hawk Marsh and Manly in Iowa) by means of indicator species that characterize the change from hydric towards mesic soil conditions (e.g., *Phragmites australis* and *Typha* sp. at the hydric end of the gradient changing into *Solidago* sp. dominated plant communities at the mesic end). Hydric and mesic habitats used in this study were located at the two extremes of the soil water availability gradient within the respective *L. salicaria* populations.

Data collection

Data were collected during July and August 2006 (Table 1). At each study site, two band transects were placed perpendicular to the water availability

Population	Sample date	Location	Elevation (m)	Mean annual temperature (°C)	Mean annual rainfall (mm)	Approx. distance between transects (m)
Iowa, USA						
Boone Forks	July 22, 2006	42°17′13″ N 93°56′19″ W	332	8.3	866	20
Black Hawk Marsh	July 29, 2006	42°16′03″ N 95°02′40″ W	374	8.3	786	15
Manly	August 1, 2006	43°16′58″ N 93°07′13″ W	346	7.2	816	30
Switzerland						
Adlikon (Furtbach)	July 4, 2006	47°42′02″ N 8°27′27″ E	425	8.5	1086	2
Rümlang (Eichriedgraben)	July 3, 2006	47°25′54″ N 8°30′44″ E	438	8.5	1086	4
Schlattingen (Furtbach)	August 23, 2006	47°39′43″ N 8°47′00″ E	423	8.5	883	1

gradient, one in the hydric habitat and one in the mesic habitat. The hydric and mesic transects were much further apart in the Iowa sites than in Switzerland due to differences in topography. The transects were 50 m in length in the denser Iowa populations, whereas they were 300 m long in the more widely scattered Swiss populations. The differences in transect length were required to obtain equal sample sizes in both provenances. All *L. salicaria* plants positioned within 30 cm to either side of a transect were located and assigned a unique number. Thirty plants were then chosen at random from each transect for further study. For each of the thirty plants, height of the tallest stem was measured from the soil surface and total number of stems per rootstock was counted.

Age for each plant was determined by first excavating the rootstock and obtaining a 10 cm long section of root, which came from the largest intact root proximal to the aboveground stem. These root segments were found to provide the oldest estimate of plant age in a preliminary study (Knaus, unpublished data). The shortest diameter of the section at the proximal end to the aboveground stem was then measured and recorded as an estimate of root size. Roots were stored in alcohol after excavation and an estimate of the age of the plant was obtained by applying the techniques of herb-chronology (see Dietz and Ullmann (1997) for an explanation of the technique). Ages identified using these techniques should be interpreted as indicating a minimum estimate of the overall age of the plant; it is possible that we did not actually obtain the oldest root segment.

Data analyses

Univariate analysis

Height (*height*), number of stems (*stems*) and root diameter (*root*) were analyzed in R using a mixedeffects modeling approach (see Pinheiro and Bates 2004; Venables and Ripley 2002). *Stems* and *root* were \log_{10} transformed prior to analysis, resulting in well behaved residuals as assessed with Q-Q plots and plots of the residuals against model predicted values. Independent variables used in the analyses included the categorical fixed-effects of provenance (*P*) and habitat (*H*) and covariates of age (*a*) and relative date (*d*). Relative date was the number of days after July 3, 2006 (the day the first sample was collected; d = 0 for July 3, 2006). Population nested within country (π) was treated as a random effect.

The first step in model construction involved fitting a fully specified, mixed-effects model incorporating the random effect of population nested within country and all interactions between the fixedeffects, with the exception of date. Date was only entered in the model as a main effect.

The models were fit using *lmer* in R, as provided through the *lme4* package (Pinheiro and Bates 2004; Venables and Ripley 2002). The model statement for the fully specified model following R notation was *lmer* ($y \sim P * H * a + d + (I|\pi)$)), where y was the response variable and the independent variables were as defined above.

After fitting the full model, the model was reduced using methods following the recommendations of Venables and Ripley (2002). Terms identified as being potential candidates for removal were eliminated from the model one at a time, the model was reanalyzed and results were compared with and without the newly removed term using the *anova* protocol in R. If there was no significant difference between the models (P > 0.05), the parameter thus identified was removed from the model in further analyses. This procedure was continued until no more terms could be dropped.

Multivariate analysis

We conducted a PCA analysis of the data to explore allometric relationships between the four main variables (*height*, *stems*, *root*, and *age*). A shift in lifehistory strategy is indicated by a correlated change in allometric relationships among key traits, e.g., tradeoffs in above ground growth (*height* and *stems*) versus below ground growth (*root*). *Root*, *stems* and *age* were log₁₀-transformed prior to analysis. The analysis was conducted on the correlation matrix, giving equal weighting to the four variables.

Results

Age

Age distributions were quite similar in comparing hydric and mesic populations within and between

Fig. 1 Response of four life-history traits in L. salicaria to a moisture gradient in the native and invaded ranges. Notched box-plots were produced using the boxplot routine in R. The central line is the median, hinges are at the 1st and 3rd quartiles and the whiskers extend out from the box to either the most extreme data point or to a maximum of 1.5 times the length of the box. Extreme data values extending beyond the whiskers are drawn as points. Nonoverlapping notches indicate that there is "strong evidence" that the medians differ (Chambers et al. 1983)



countries, with one exception: the age distribution for plants from mesic populations in Iowa (IA-M) was skewed towards older age classes (Figs. 1 and 2). Plants in the mesic habitat of Iowa (IA-M) had a mean age of 5.4 years (Fig. 2), at least 1.3 years older than any other category. The IA-M populations also contained the oldest plant found in this study, an 11-year-old individual. The previous record was a 13-year-old individual, which was also found in a mesic site in Iowa (unpublished result). Pairwise comparisons of distributions using a Wilcoxon Rank Sum test indicated that IA-M had a significantly different distribution when compared to the three other population categories (Table 2), due primarily to a greater number of individuals in the older age classes (>5 years; Fig. 2). In all cases, there were fewer 1-year-old individuals than would be expected for a population with annual recruitment, at least based on the number of individuals found in the older age classes. One reason for the paucity of 1-year-old individuals in the data set might be that they were small and hard to find.

Height

Plants in the invaded range were systematically taller than plants in the native range when comparing similar habitats (Fig. 1 and Table 1) Plants in wet habitats were also consistently taller than plants in mesic habitats, independent of provenance (Fig. 1). Mixed-model analysis for height produced a purely additive model that included all of the fixed-effect terms and covariates originally entered into the full model, but no significant interactions with age (Table 3). Although age (a) was included in the final model, it does not appear to contribute much to the height of the plant, adding only 2.2 cm (approximately) per year, roughly 4% of the overall height of the smallest plants (46.9 cm intercept).

Stems

Plants in Iowa had significantly more stems originating from rootstock than did plants in Switzerland (Table 3; Fig. 1). There were also subtle differences in stem

Fig. 2 Frequency distributions of age in *L.* salicaria in response to a moisture gradient in the native and invaded ranges. Mean age (\bar{x}) is indicated in each figure



 Table 2
 Wilcoxon rank sum tests comparing age distributions

 between provenances and habitats (Fig. 2)
 2

AGE		US	СН		
		Mesic	Wet	Mesic	Wet
US	Mesic				
	Wet	5440***			
СН	Mesic	5740***	4422 ^{ns}		
_	Wet	5802***	4528 ^{ns}	4169 ^{ns}	

Values are the rank sums (*W*) for the comparisons. Analyses were conducted in *R* using the *wilcox.test* routine. Significance levels were assessed using two-sided tests. (ns, non-significant; ** P < 0.05; *** P < 0.001 indicated by. Bonferonni corrections for multiple comparisons were applied)

production between habitats (*H*) that shifted between provenances, as indicated by the significant P^*H interaction effect (Table 3). There were slightly more stems per plant in the mesic habitats for Swiss plants (1.6 stems per plant in mesic habitats versus 1.4 in hydric), whereas the opposite was the case for Iowa plants (2.7 stems per plant in mesic habitats versus 3.8 in hydric; values represent back-transforms of mean values calculated on \log_{10} transforms). The significance of this interaction effect, however, should not be overstated, since there is a great deal of variability in the number of stems produced by plants both within and between treatments. Because of this variability, the regression model fit to the data was only able to explain 27% of the overall variance in the data.

Roots

Root diameters were uniformly larger in the invaded (IA) as compared to the native (CH) provenance (Fig. 1), with no significant differences among habitats. The latter result is indicated in the lack of a significant habitat (H) effect in the mixed-model analysis. There was a subtle age by provenance interaction (P * a) in the model, but this was minimal

Response variable	Most parsimonious mixed-effects model	Variance components		
		Percent explained by model	Percent associated with random effect (π)	Total variance
Height (cm)	$46.94 + 23.83 * P + 31.72 * H + 2.18 * a + 0.90*d + \pi + error$	62	3.0	1237
$Log_{10} (stems)^{a}$ $Log_{10} (root)^{a}$	$0.21 + 0.22 * P - 0.05 * H + 0.19 * H * P + \pi + error$ $-0.19 + 1.12 * P - 0.02 * P * a + 0.04 * a + \pi + error$	27 95	0.4 0.1	0.104 0.300

Table 3 Results of mixed-model regression analysis for stem height, number of stems and root diameter

^a Number of stems and root diameters (cm) were log₁₀-transformed prior to analysis

 π is the random effect of population nested within provenance, which has a mean of zero and an estimated variance shown in the table. The dummy variables in the fitted models presented above are evaluated as follows: P = [0 for CH; 1 for US] and H = [0 for mesic habitats; 1 for hydric habitats]. (See methods for a complete description of the approach and notation used in the analysis.)

in magnitude relative to the overall provenance effect (Table 3). The mixed-effects model explained 95% of the variance in root size, due primarily to the very strong provenance (*P*) effect.

PCA analysis

The PCA analysis examined correlated differences among the traits of height, root, age and stems with respect to plants growing in the different provenancehabitat combinations. The first PC axis (PC-1), which explained 51% of the variance in the data, can be interpreted as representing the general trend of size. The 3 size variables (height, root and stems) loaded positively on PC-1 with roughly equal weight (Fig. 3). There was a clear shift of the invasive plants in the direction of greater size on PC-1 (i.e., higher scores), as would be expected (Fig. 3). Invasive plants from hydric habitats were also somewhat more extreme in "size" than invasive plants from mesic habitats. The second PC axis (PC-2), which explained 22% of the variance, can be interpreted as being primarily an age axis, although the axis scores are also influenced by the joint effects of above ground size (i.e., *height* and *stems*) in the opposite direction from age. From the univariate analysis of age (Fig. 2), we would expect to see a general shift towards higher values on PC-2 by invasive plants in mesic habitat, relative to all the other plants (Fig. 3). However, this trend is apparently counteracted in part by a complex relationship between age and a shift in number of stems and overall height.

The third PC axis (PC-3) only explained 17% of the variance and represents a trade-off between stem

number and height, after adjusting for overall size (i.e., variance removed by PC-1). There was very little difference in the range of values on this axis separating native from invasive plants. Although the fourth PC axis (PC-4) only explained 10% of the overall variance, it clearly separated native from invasive plants, particularly when PC-4 is plotted against PC-1 (Fig. 3). PC-4 is primarily associated with changes in root diameter, independent of changes in overall size. As was seen in the univariate analyses of root diameter, there was a clear difference between native and invasive plants (cf., Fig. 2).

Discussion

Many invasive plant species growing in their introduced range exhibit increased vigour relative to plants of the same species growing in native habitat (c.f., Bossdorf et al. 2005). The results of our study are consistent with this general pattern. We found that plant height, number of stems produced, and root diameter were all greater in the invaded range under comparable moisture conditions, although the differences observed were most likely less than would normally be expected, due to drought conditions impacting Iowa during May through July of 2006 (National Climate Data Center 2007). In addition to the general size differences observed, there was also a clear shift in life-history strategy between invasive plants in Iowa and plants growing in native habitat in Switzerland. Although the overall change in size, as depicted by PC-1 (Fig. 3), could simply be a plastic response to different environmental conditions, the



Fig. 3 Results of the PCA analysis of *Lythrum salicaria* data. The individual figures contain convex hulls surrounding all the PCA scores corresponding to the plants for each particular

provenance-habitat combination (e.g., native-mesic; 30 data points per combination). Symbols drawn on the perimeter of each convex hull are the extreme points used to construct the hull

dramatic contrast in root size we found was independent of overall size differences and represents a dramatic shift in overall resource allocation patterns. Invasive *L. salicaria* plants are investing more resources in root production and are known to produce root crowns up to 0.5 m in diameter in some invasive populations (Thompson et al. 1987). Although this study, which was purely observational, cannot demonstrate that the change in root allocation represents an adaptive change, it is most likely associated with a shift in genetic makeup, perhaps in response to growth under more stressful mesic conditions. The source of the difference may be due in part to artificial selection, since invasion by *L. salicaria* in Iowa is generally associated with escape from naturalization of horticultural varieties originally planted by bee keepers (Pellett 1944).

Although we can clearly show differences in lifehistory strategy between plants from the native and invasive provenances, one of the key assumptions of our study is that the expansion of *L. salicaria* into mesic habitat in the invasive provenance represents a

secondary phase of invasion. According to the Dietz-Edwards hypothesis, the secondary phase of invasion should be accompanied by a shift in life-history strategy allowing successful establishment under more stressful conditions. One critical aspect of this argument in the context of our study is that more mesic habitats should represent more stressful growing conditions for L. salicaria and should be more resistant to invasion. There is good circumstantial evidence to support this contention. In our study we found that in the mesic sites the average height and number of stems of plants were lower than in the more hydric sites. A decrease in growth, such as this, would be expected under more stressful growing conditions. Increased allocation to root storage would also be expected under more stressful conditions (Chapin et al. 1993) and there is a trend in that direction, although it is not statistically significant given our small sample size.

When we considered allometric relationships among traits in the PC analysis, we found that the distribution of PC scores for invasive plants in the mesic sites were for the most part a subset of values observed in the hydric sites (Fig. 3). This would be expected for plants that are growing in more stressful habitats, as the range of values observed would be more constrained. The one exception to this occurs on the axis associated predominantly with plant age (PC-2). In this case, PC scores for plants in the mesic habitat of the invaded provenance had values lying outside the range of values observed for plants in the hydric habitat. This is attributable to plants attaining greater ages in the mesic habitat. When we look at the same comparisons for the mesic versus hydric sites in the native range, the distribution of PC scores does not vary much between the two habitats, leading to a higher degree of overlap in values (Fig. 3). This pattern is also consistent with the predictions of the Dietz-Edwards hypothesis, which would expect greater differentiation in the invaded range after the initiation of secondary invasion.

In addition to the circumstantial evidence found in our study, evidence from the literature also supports the claim that mesic habitats are more stressful for *L. salicaria*. Optimal growth for *L. salicaria*, as indicated by above ground biomass production, occurs when there is high nutrient availability under flooded conditions (Chun et al. 2007). In contrast, the poorest growing conditions correspond to situations of low nutrient availability under flooding, with growth under mesic conditions being not much better. The poorer conditions resulting under mesic conditions also appear to be, for the most part, independent of nutrient availability (Chun et al. 2007).

So, if mesic sites are more stressful and are the target of secondary invasion, do we in fact see a shift in lifehistory strategy as would be predicted by the Dietz-Edwards hypothesis? Although only observational, the combined evidence of generally smaller growth habit, greater root storage and increased longevity in mesic habitats of the invaded range would be consistent with changes predicted to occur under more stressful conditions and would be supportive of the Dietz-Edwards hypothesis. The subtle increase in longevity seen is perhaps the most compelling evidence, as the stress theory of aging predicts that longevity will increase in organisms as a secondary consequence of adapting to survive under more stressful conditions (Parsons 2002). We cannot claim that the differences we observed are evidence of an evolutionary change, as opposed to a purely plastic response, without conducting additional experimental studies. However, the experiment by Chun et al. (2007) described earlier has shown that there is a significant genetic component to differences in height, stem number, and root production between native and invasive L. salicaria grown under varying environmental conditions. Establishing that there is a genetic component for increased longevity would be, of course, more difficult to demonstrate.

Overall our findings are in general agreement with the hypothesis that secondary invasion by L. salicaria into mesic habitat is taking place in Iowa. If this process continues, L. salicaria may become an even more problematic species in the future, especially if it can continue to shift its life-history characteristics to occupy an even greater range of habitats and expand in those where it already occurs. It would be useful to extend our study to encompass a greater range of sites within the invaded and native ranges to determine how widespread the relationships we observed in Iowa and Switzerland are. Nonetheless, our results provide some of the first evidence in direct support of the predictions put forward by Dietz and Edwards (2006). It remains to be seen whether this is a general process in the etiology of invasion and, if so, what the general, underlying evolutionary mechanisms are. As such, it would be useful to explore these issues for other invasive species and other forms of secondary invasion. In general, developing a better understanding of life-history evolution during the process of invasion would benefit our overall understanding of the process of invasion in an evolutionary as well as an ecological context.

Acknowledgments The authors thank Young Jin Chun, and the Iowa State University Microscopy Lab for their help in the completion of this project. KM gratefully acknowledges support by the Velux Foundation and Iowa State University for his sabbatical at the ETH in Zürich, during which time this work was conducted. Field work was supported by the ETH Travel Fund. No support was provided by the United States National Science Foundation or United States Department of Agriculture.

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