Comparison of life history traits between invasive and native populations of purple loosestrife (*Lythrum salicaria*) using nonlinear mixed effects model

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**A B S T R A C T**

We compared growth patterns of invasive and native populations of purple loosestrife (*Lythrum salicaria*) while varying water and nutrient levels. We examined three life-history traits (height, number of branches, and the size of largest leaf) during the growth period adopting a nonlinear mixed effects model. Invasive populations were found to be slower in shoot elongation but grew to be taller than native populations. Invasive populations produced more branches than natives only in the high water, high nutrient treatment. Invasive populations had a similar increase in the size of the largest leaf compared to natives, but ultimately produced a greater size of largest leaf than natives. Invasive populations were found to display a greater vegetative expansion, but this was not strongly affected by our treatments.

**1. Introduction**

The introduction and spread of non-native species has become a global concern, as invasive species often compete for available resources, replace indigenous species, and ultimately may alter ecosystem function (D’Antonio and Vitousek, 1992; Mack et al., 2000; Lodge et al., 2006). Understanding their ecology is important to identify potential control points and effective management plans (Simberloff, 2003). In their new ranges, invasive populations are often assumed to exhibit higher survival, faster growth, and greater reproduction than native populations in their original range (Hinz and Schwarzlaender, 2004; Bossdorf et al., 2005). However, variability in the environmental conditions and habitat quality may also affect the success of invasive populations (Alpert et al., 2000). Empirical studies found that the growth of invasive vs. native populations is highly dependent on morphological and physiological traits and the biotic and abiotic conditions examined in the study (e.g. Willis and Blossey, 1999; Kaufman and Smouse, 2001; Leger and Rice, 2003; DeWalt et al., 2004). As successful invasion happens across a broad range of habitats, our understanding of the characteristics predisposing an invasive species will be improved through comprehensive biogeographical studies comparing multiple populations from diverse environmental ranges both in native and invasive ranges (Daehler, 2003; Bossdorf et al., 2005; Hierro et al., 2005).

In this paper, we measured vegetative life history traits of the perennial angiosperm purple loosestrife (*Lythrum salicaria* L.) under different water and nutrient conditions throughout the first growing season, and compared performance of invasive and native populations. Purple loosestrife is a well-known, noxious invader in North America, introduced from Europe in the beginning of 19th century (Stuckey, 1980). It has spread rapidly over many wetlands and marshes in the United States and neighboring Canada, often forming dense monospecific stands (Thompson et al., 1987). Differences in life history traits between invasive and native populations have been reported under field (Edwards et al., 1998) or in common garden conditions (Blossey and Nötzel, 1995; Bastlová and Květ, 2002; Bastlová et al., 2004; Chun et al., 2007). However, life history traits have been measured usually once at the end of the growing season. Tracing the changes in life history traits during the growth period under different environmental conditions may reveal more specific differences between invasive and native populations.

Nonlinear mixed models are a powerful tool for the analysis of experiments where some response variable is observed on multiple occasions, that is, during the whole growth period (Davidian and Giltinan, 1995). Mixed model is a general approach of accounting for the variability between individuals to estimate parameters for both random and fixed effects (Pinheiro and Bates, 1998). Each parameter in the model can be represented by a fixed effect that pertains to the levels of interest (e.g. groups), and a random effect...
that pertains to the differences between the value of the parameter fitted for each individual and the value of the parameter fitted for fixed effect (Davidian and Giltinan, 1995; Pinheiro and Bates, 2000). Potvin et al. (1990) developed ANOVAR (ANOVA with repeated measures) to test group differences of repeatedly measured physiological responses in a mixed model. However, as their method uses a linearized model, it lacks the ability of testing for the differences in biologically meaningful parameters between groups in a non-linear model (Peek et al., 2002).

Adopting a non-linear mixed model approach, we fitted three life history traits during the growth of purple loosestrife in a common garden in four combinations of water and nutrient availability. We compared the trait performance between invasive vs. native populations in each environmental treatment by assessing the effect of population on parameter estimation for fixed effects. Our study addresses the following questions: (1) Do invasive populations perform better than native populations through their growth? (2) How does environmental variation affect the differences in trait performance between invasive and native populations?

2. Methods

2.1. Population sampling

In the fall of 2002, we collected seeds from each of three native populations in Europe (Schollener See [52°59′N, 12°11′E]; Strodehne [52°45′N, 12°11′E]; and Meißen Dorfer Teiche [52°43′N, 9°50′E]), all in Germany, and three invasive populations in North America (Little South Storm Lake, Iowa [42°38′N, 95°13′W]; Shell Rock, Minnesota [43°32′N, 93°15′W]; and Fayetteville, New York [42°49′N, 76°49′W]). Populations were chosen to represent a range of nutrient and water conditions found naturally in the field. We randomly chose seeds from a bulk sample of a large number of plants within each population. Seeds were planted in Sunshine LC1 potting soil (Sun Gro Horticulture Canada, Seba Beach, Alberta, Canada) on May 20, 2004 to allow germination and initial growth for 20 days. Maternal effects were likely to be small because purple loosestrife seeds are minute (0.5–0.6 mg; Thompson et al., 1987).

On June 9, 2004, seedlings were individually transplanted into plastic pots (30 cm diameter × 25 cm depth). These pots contained the same potting soil used for germination and were placed in plastic wading pools (1.4 m diameter × 30 cm depth). We applied a split-plot design consisting of five complete blocks, with four wading pools within each block. Each wading pool in a block contained one of four environmental treatment combinations: (1) low water, low nutrient (WLN), (2) low water, high nutrient (WHN), (3) high water, low nutrient (WHN), and (4) high water, high nutrient (WHN). Two plants from each population were put in each wading pool in each block (12 plants per pool). The total number of experimental units for this experiment was five blocks × 4 treatment combinations = 20 units, with 6 populations × 2 plants = 12 observations per experimental unit. Pots in the high water treatments were kept at saturation, similar to the condition of lake and pond margins. Low water treatments are comparable to drier, upland conditions, where plants were watered every other day, letting the soil soak for a few hours, after which the soil was allowed to dry. In the low nutrient treatment no fertilizer was applied, whereas in the high nutrient treatment 100 g of slow-release 14:14:14 N:P:K Osmocote (The Scotts Company, Marysville, Ohio, USA) was applied once to a pot at the beginning of the experiment (N, 2481 mg/kg soil; P, 563 mg/kg soil; K, 1320 mg/kg soil). As a consequence, the low and high nutrient treatments were designed to be a reasonable approximation of low and high soil nutrient levels, respectively, which would be encountered under natural field conditions (cf. Bridgham et al., 1996; Thormann and Bayley, 1997; Bedford et al., 1999).

Day length during the experiment ranged from 13 h 18 min to 15 h 16 min, light availability was 11.09 ± 0.40 mmol photons m−2 s−1, and temperature ranged from 8.3 to 28.0°C.

We measured three life history traits for each experimental individual: (1) height, (2) number of branches, and (3) size of the largest leaf. To determine (3), we chose the largest leaf from each plant and calculated leaf area by multiplying the maximum length and width of the leaf. Traits were measured every week for six weeks of growth, and then finally measured after another 3 weeks when 92% of the plants initiated flowering (8, 15, 22, 29, 36, 43, 64 days). We also recorded the date of the onset of first flowering for each individual.

2.3. Fitting nonlinear models

All statistical analyses were conducted using the nlm package of R 2.11.0 (R Development Core Team, 2010). The program code for this study is provided in the Appendix. We first plotted the trait responses for invasive vs. native populations in each environmental treatment for an exploratory analyses (Figs. 1 and 3). Plant height and size of the largest leaf appeared to show sigmoid growth, while the number of branches followed exponential growth except for WLN (sigmoid growth). For sigmoid growth, we chose the logistic model (Ricklefs, 1967) which produced the lowest Bayesian information criterion (BIC) compared to other models (Gompertz, Michaelis–Menten, and Weibull; P < 0.0001 from paired t-tests).

\[
R_t = \frac{A}{1 + \exp[-(K(t-i))]} \tag{1}
\]

where \( R_t \) is the response variable (height, number of branches, and size of the largest leaf) at day \( t \); \( A \) is the asymptote (maximum size); \( K \) is the constant proportional to the overall growth rate; and \( I \) is the inflection point (i.e., the day at which \( R_t \) reaches \( A/2 \)). We developed a self-starting function to calculate initial values for parameters following Pinheiro and Bates (2000). The initial estimates of parameters were:

- **Height**
  \[
  \text{Height} = \frac{100.16}{1 + \exp[-(0.13)(t - (29.49))]} \tag{2}
  \]

- **Number of branched in WLN**
  \[
  \text{Number of branched in WLN} = \frac{20.68}{1 + \exp[-(0.21)(t - (21.63))]} \tag{3}
  \]

- **Size of the largest leaf**
  \[
  \text{Size of the largest leaf} = \frac{22.38}{1 + \exp[-(0.20)(t - (16.03))]} \tag{4}
  \]

The exponential model employed for the number of branches in WLN, WHN and WHN was:

\[
R_t = \exp(A + K \times t) \tag{2}
\]

where \( A \) is related to the initial response at \( t=0 \) and \( K \) is related to growth rate. The initial estimates of parameters were \( R_t = \exp(2.11) \times \exp(0.04) \times t \). We included latitude as a covariate in all models because the genetically-based difference in phenotypic performance between invasive and native populations may be also affected by phenotypic or genetic latitudinal clines (Colautti et al., 2009).
Fig. 1. Comparison of growth pattern in height between invasive and native genotypes in (a) low water, low nutrient (W_LNL); (b) low water, high nutrient (W_LNH); (c) high water, low nutrient (W_HNL); and (d) high water, high nutrient (W_HNH) treatments. Raw data were presented as boxplots and fitted growth curves as lines. Invasive genotypes: gray boxes and solid lines; native genotypes: white boxes and dashed lines.

2.4. Optimization of the initial model

We improved our models arrived at as described above to satisfy the basic assumptions of nonlinear model building (Davidian and Giltinan, 1995) that random effects are independent and normally distributed. We employed a diagonal matrix explaining the variance–covariance structure for the three random effects using “pdDiag” function in the nlme package of R. As our data include observations of unequal intervals, we adapted a continuous time autoregressive process of first order (“corCAR1” function) to the within-individual errors. The final model was diagnosed to verify that the standardized residuals meet the normality assumption. Finally, there should be no heteroscedasticity. Because the initial model showed increasing variance for within group errors (heteroscedasticity), we remedied this situation by modeling the variance of the within-individual errors using a variance function (i.e., a function that describes the variance of errors through covariates). This function expresses the variance as an arbitrary power of the expected values ($v_{ij}$) using “varPower” function.

$$\text{Var}(\varepsilon_{ij}) = \sigma^2 |v_{ij}|^{2\delta}$$

Fig. 2. Comparison of growth pattern in number of branches between invasive and native genotypes in the four treatments as in Fig. 1.
where $\delta$ is a vector of variance parameters. We grouped the entire data to eight combinations of treatment $\times$ population and determined the effects of groups on the parameter estimates of three fixed effects using maximum likelihood method.

3. Results

The estimates of the height asymptote ($A$) revealed that invasive populations grew significantly taller than native populations, except for the $W_{L} N_{H}$ (Table 1 and Fig. 1). The growth rate of native populations ($K$) was significantly higher than that of invasive populations in all treatments. In contrast, the inflection points of native populations ($I$) were significantly lower than invasive populations in all treatments, indicating that native populations deflect earlier from exponential increase. Together with this, we also observed that the days from planting to the onset of flowering in native populations ($37.0 \pm 0.29$) were fewer than in invasive populations ($50.7 \pm 0.82; P < 0.001$), indicating that native populations flower earlier than invasive populations.

In the three treatments ($W_{L} N_{L}$, $W_{L} N_{H}$, and $W_{H} N_{H}$) where plants showed an exponential increase in the number of branches, only in $W_{H} N_{H}$ invasive populations increased the number of branches faster than native populations ($P = 0.028$), although the initial growth was greater in native populations ($P = 0.033$; Table 1 and Fig. 2). In $W_{H} N_{L}$ (sigmoid growth), no difference in the final number of branches between native and invasive populations was found. However, native populations increased branches faster, with lower inflection point than invasive populations.

Our estimates of the asymptote in the size of largest leaf indicate that invasive populations had significantly greater size of the largest leaf than native populations in all treatments (Table 1 and Fig. 3), although no difference was found in the growth rate. The inflection point of native populations was significantly lower than invasive populations in two treatments ($W_{L} N_{L}$ and $W_{H} N_{H}$).

4. Discussion

The pattern in shoot elongation was consistent among all treatments: native populations grew faster than invasive populations, but reached lower asymptotes earlier than invasive populations (Table 1 and Fig. 1). In contrast, invasive populations grew more slowly, but reached higher asymptotes. This suggests that invasive populations have a greater ability to utilize available resources, except for $W_{L} N_{H}$ where the amount of available nutrient is limited by water.

An interesting point in shoot elongation pattern is that native populations reach the asymptote earlier than invasives. This may be coupled to a difference in flowering phenology between invasive and native populations, because we frequently observed that the flowering began at the terminal of main stem, when shoot elongation is finished (determinate growth; Larcher, 1995). This appears to happen earlier in native than invasive populations, because our results also indicated that native populations flower approximately 2 weeks before invasive populations. Consistently, Bastlová and Květ (2002) reported that invasive populations of purple loosestrife begin flowering approximately 10 days later than native populations. Thus, early-flowering native populations probably terminate shoot elongation earlier than invasive populations.

In contrast to a prolonged shoot elongation of invasive populations, this did not lead to higher branching than native populations (Table 1 and Fig. 2). Invasive populations increased branches faster than natives only in $W_{H} N_{H}$. The sigmoid growth in $W_{H} N_{L}$ showed contrasting patterns between invasive and native populations (Table 1 and Fig. 2), where native populations grew faster and utilized available resources earlier than invasive populations. However, it appears that both populations used up available resources and finally reached to a similar asymptote.

The size of largest leaf revealed another pattern of growth (Table 1 and Fig. 3). Both invasive and native populations grew at a similar rate, but invasive populations generally grew towards a higher asymptote than native populations. Invasive populations may be able to produce a greater size of the largest leaf for utilizing more light resources than natives. However, it does not necessarily mean that invasive populations produce larger leaves on average, or a larger total leaf area, as we did not measure leaf area index (LAI). In $W_{L} N_{L}$ and $W_{H} N_{H}$, native populations reached the inflection point earlier than invasives, limiting further growth.
Our results suggest that invasive populations generally utilize available resources more effectively to be taller and produce a greater size of largest leaf than native populations (Davis et al., 2000). However, this trend was evident for the number of branches only in the high water, high nutrient treatment, suggesting a strong water x nutrient interaction on the number of branches. In contrast, for height and the size of largest leaf, there appears to be a general difference between invasive and native populations, which does not depend on water or nutrient treatments. This would suggest that invasive species may be successful by utilizing excessive resources in disturbed habitats (Hobbs and Huenneke, 1992), but this can be observed in certain traits only, not in all traits. Therefore, the difference in growth patterns between invasive and native populations may vary depending on both traits and environments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.aquabot.2010.09.001.

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