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## Rapid growth and early flowering in an invasive plant, purple loosestrife (*Lythrum salicaria* L.) during an El Niño spring

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**Abstract** Phenological shifts may play a role in the success of invasive species, especially in association with climatic variability. We studied the response of a North American population of the invasive plant, *Lythrum salicaria* L., to changes in local climate associated with the El Niño/Southern Oscillation Event (ENSO) of 1997–1998. For *L. salicaria* plants at two wetland sites near North Bay, Ontario, Canada, we made weekly observations of flowering phenology and monthly measurements of aboveground biomass during the 1997 and 1998 growing seasons (April–October). Reproductive output was measured as cumulative length and biomass of inflorescences at the end of the growing season. Temperature and precipitation during the 1997 growing season were typical for the region and provided good baseline data for comparison to the full effects of the ENSO event in 1998, which increased spring temperatures and reduced precipitation in the study area. In response to these conditions, populations of *L. salicaria* began to flower 14 days earlier (Julian day =  $181 \pm 10$ ) in 1998 than in 1997 (Julian day =  $195 \pm 12$ ), and accumulated more aboveground biomass early in the growing season ( $P < 0.05$ ). However, by the end of the growing season, there were no significant differences between years in aboveground biomass or total inflorescence lengths, and senescence of plants occurred at similar times for both growing seasons. Advances in spring phenology during ENSO events offer several potential advantages to *L. salicaria*, and could

have a significant impact on biological control programs initiated for this species in North America.

**Keywords** El Niño/Southern Oscillation · Phenology · Invasive species · *Lythrum salicaria*

### Introduction

*Lythrum salicaria* L. (purple loosestrife) is a herbaceous perennial plant of Eurasian origin that has become distributed throughout the temperate wetlands of North America (Stuckey 1980; Thompson et al. 1987). Invasion of wetlands by *L. salicaria* displaces native plant species (Moore and Keddy 1989; Gabor et al. 1996; Mal et al. 1997), and alters ecosystem functions such as nutrient cycling (Templer et al. 1998; Otto et al. 1999) and organic matter decomposition (Bärlocher and Biddiscombe 1996; Emery and Perry 1996; Grout et al. 1997). The ecological consequences of invasion by *L. salicaria* have led to extensive study of its impact and management in North America (Blossey et al. 2001); however, the underlying factors that contribute to its success remain unresolved.

Resource allocation to growth over anti-herbivore defense in the absence of natural enemies (Blossey and Nötzold 1995), low leaf biomass construction costs relative to competing species (Nagel and Griffin 2001) and high phenotypic plasticity (Bastlová and Květ 2002) have all been proposed as explanations for the high competitive ability of *L. salicaria* in North America. The success of *L. salicaria* could also be related to advantageous phenological patterns, which contribute to competition avoidance, prolonged flowering and seed dispersal in some invasive species (Zotz et al. 2000; Meyer 1998).

In a common greenhouse experiment, Bastlová and Květ (2002) observed a 10-day delay in the flowering of alien (North American) compared to native (European) *L. salicaria* plants, which they attributed to an ecotypic variation in alien plants that increases allocation to vegetative growth over reproduction during the early part of the growing season. Rapid spring growth provides alien *L.*

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*salicaria* plants with access to light and space and a competitive advantage over other species; however, there is also evidence that delayed flowering reduces seed production in this species (O'Neil 1999). Thus, the success of alien *L. salicaria* plants must depend on a compromise in resource allocation between rapid spring growth and early flowering time, which are both supported by the mobilization of starch reserves stored in roots and crowns (Stamm Katovich et al. 1998). It follows that changes in environmental conditions that cause phenological shifts of alien *L. salicaria* plants could alter fitness by affecting this allocation compromise.

In temperate regions, flowering in perennial herbs often occurs in response to temperature (Rathcke and Lacey 1985). Periodic climatic perturbations such as the El Niño/Southern Oscillation (ENSO) event change temperature and precipitation characteristics and can have a strong effect on plant phenology (Walker et al. 1995; Beaubien and Freeland 2000). Whether or not populations of *L. salicaria* show phenological shifts during climatically anomalous growing seasons is an important question, because such shifts could represent a significant advantage to alien *L. salicaria* plants, by offsetting the delay in flowering associated with the strategy of rapid accumulation of biomass early in the season. Changes in the phenology of *L. salicaria* could also affect the success of insect biological control agents introduced to control *L. salicaria* in North America (Hight et al. 1995; Dech and Nosko 2002). Differential phenological responses of plants and insects during ENSO events could disrupt their synchronicity so that maximum impact of control objectives (e.g. spring feeding damage to meristematic tissues by *Galerucella* spp.) is not achieved. Our objective was to determine the phenological response (flowering time and biomass accumulation) of alien populations of *L. salicaria* in central Ontario, Canada, to the warm and dry spring conditions produced by the 1997–1998 ENSO event.

## Materials and methods

### Site description

The study area was located 1.8 km south of North Bay, Ontario, Canada (46°21'N, 79°26'W), and was part of a large complex of wetlands, interrupted by bedrock outcrops and a major highway. The local climate (Environment Canada 2003) is continental, with cold winters (January mean = −13.0 °C) and warm summers (July mean = 18.6 °C). The growing season extends from April to October, with a mean annual accumulation of 1,681 growing degree-days (above 5 °C). Mean annual precipitation is 1007.7 mm. Typically, growing season rainfall amounts to 653.6 mm.

### Sampling design

This study was conducted at two sites of differing topography and vegetation, separated by about 200 m on opposite sides of a major highway. Sites were chosen as part of a study on the establishment of leaf-feeding beetles (*Galerucella* spp.) introduced to control *L. salicaria* in central Ontario during 1995. The control agents had no

impact on *L. salicaria* during the study period (Dech 2000) and are not considered further here. At each site, transects (40 m) were established along five directions, radiating in a semicircular fashion from a single point near the roadside margin of the wetland. Along these transects, plots were established at four distance intervals (8.5, 15.5, 26.5, and 37.5 m) from the transect origin (one plot). Of the 21 possible plot locations provided by this design, 17 plots were established at site one, and 12 at site two, excluding inappropriate locations (e.g. bedrock outcrops, highway). Plots were 2 × 3 m rectangles divided into six 1 × 1 m sub-plots.

### Growth and phenology

Sample plants (individual shoot systems) were selected according to a stratified random design. Stratification was along distance intervals (0.0–37.5 m) from the roadside margin. Within each distance interval, sample plants were randomly chosen from 1 m<sup>2</sup> sub-plots. The maximum number of plants tagged for observation was increased from three per plot in 1997 to five per plot in 1998. The total number of tagged plants varied according to availability and loss of samples during the growing season in 1997 (site one  $n = 45$ , site two  $n = 38$ ) and 1998 (site one  $n = 69$ , site two  $n = 60$ ).

Weekly observations of floral phenology were made on tagged plants throughout each growing season (12 June–1 November 1997; 20 May–1 November 1998). Inflorescences having at least one flower with a fully developed corolla were considered to be in bloom. A measurement of the cumulative inflorescence length (total length of all flower spikes) for each plant was made on 30 August of each year. Harvests of aboveground biomass were conducted monthly (June, July, August) during 1997 (Julian days = 171, 202, 236) and 1998 (Julian days = 180, 204, 234). For each harvest, a total of 12 plants were collected from each distance interval from the pool of 1 × 1 m sub-plots designated for destructive measurements. All aboveground biomass was removed by cutting the stem at the base. Plants were then dried to a constant weight at 60 °C. The dry weight of total aboveground biomass, and that of inflorescences only, was determined to a precision of ± 0.01 g. Senescence (defined as full necrosis of all aboveground tissues) was recorded on tagged plants bi-weekly from September to November. Climate data (daily mean temperatures, precipitation, and growing degree-days accumulated above 5 °C) for each growing season (April–October) were obtained from Environment Canada (1999). Climatic means for the period of 1971–2000 were also obtained from Environment Canada (2003).

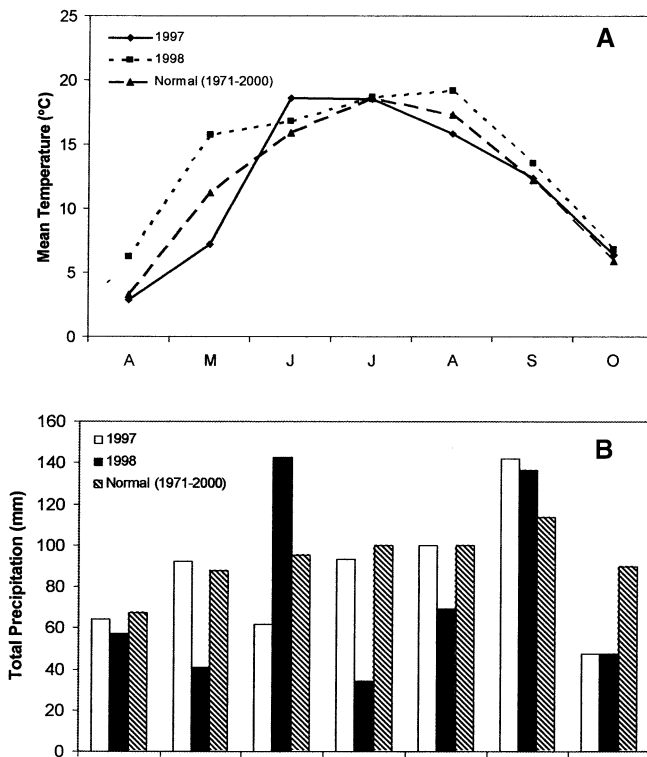
### Data analysis

Flowering phenology and growth data for *L. salicaria* at both study sites were not significantly different and were combined into one data set for all analyses. The mean day of first flowering, total inflorescence lengths and biomass, total aboveground biomass and senescence were compared between seasons using a one-way analysis of variance (ANOVA) (Zar 1999).

## Results

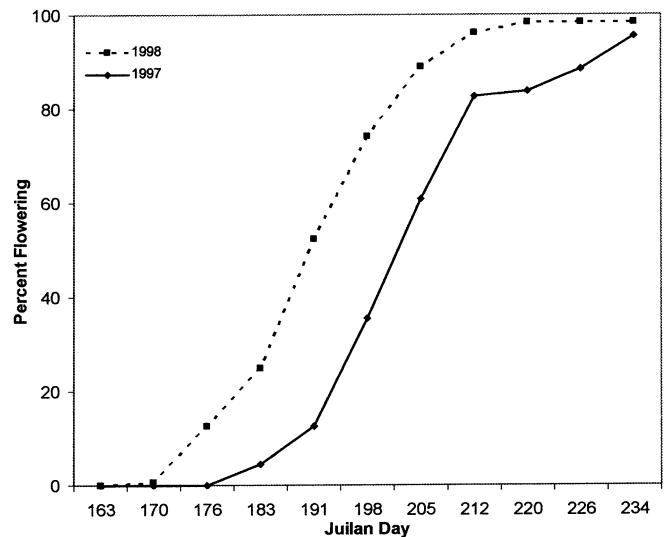
### Climatic variability

The climatic conditions for the 1997 growing season were similar to the means for the region from 1971–2000 (Fig. 1), and provide a good baseline for comparison to the 1998 ENSO departure. Generally, air temperatures in 1998 were higher than average, particularly in the early part of the growing season (Fig. 1). The mean air temperature for May 1998 was 15.7 °C compared to 7.2 °C for May 1997, and was well above the 1971–2000 mean



**Fig. 1A, B** Seasonal trends in temperature (A) and precipitation (B) for the 1997 and 1998 growing seasons and climatic means for the region (1971–2000) for North Bay, Ontario, Canada. Source: data for 1997 and 1998 (Environment Canada 1999), 1971–2000 means (Environment Canada 2003)

of 11.2 °C. Overall, the accumulation of growing degree days ( $\geq 5$  °C) from May to October was greater in 1998 (1946) than in 1997 (1622) or the 1971–2000 mean (1681). Precipitation also departed from average conditions in 1998 (Fig. 1). Generally, 1998 had a dry growing season, with an overall precipitation total of 528.2 mm, substantially less than the 1997 total of 600.5 mm and the 1971–2000 mean of 653.6 mm. The 1998 precipitation deficit was strongest in May, July and August (Fig. 1).



**Fig. 2** Percentage of individuals of the study population of *Lythrum salicaria* in bloom over two consecutive growing seasons (1997 and 1998) at North Bay, Ontario, Canada

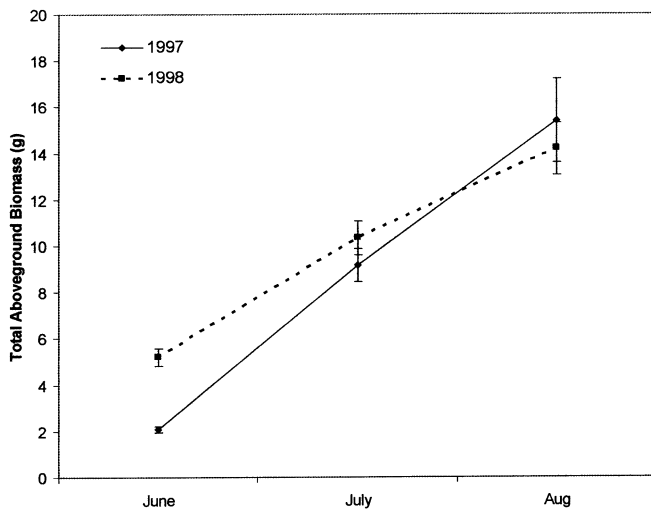
#### Flowering phenology

Earlier flowering in populations of *L. salicaria* in North Bay was associated with the atypically warm and dry conditions of the 1998 growing season (Fig. 2). During the more climatically typical growing season of 1997, flowers began to open in early July (Julian day = 183) and the population reached a total flowering frequency of 95.4% near the end of August (Julian day = 235). Following the 1998 ENSO spring, plants began to open flowers in mid June (Julian day = 170) and reached a total flowering frequency of 98.4% by mid August (Julian day = 220). The mean Julian day at which flowering began in 1998 was 14 days earlier than for 1997, which represents a statistically significant difference (Table 1). The accumulation of growing degree days was similar at the beginning (560 and 570) and the peak (1200 and 1250) of flowering activity for 1997 and 1998 respectively.

**Table 1** Interannual differences (mean  $\pm$  standard deviation) in first date of flowering, total inflorescence length, total above-ground biomass and senescence date in an alien population of *Lythrum salicaria* at North Bay, Ont, Canada, during the 1997–98 El Niño/Southern Oscillation event. Results of one way analysis of variance are given as total degrees of freedom (*df*), *F* statistic (*F*) and percentage variance explained by year (*Effect size*)

Variable	1997	1998	<i>df</i>	<i>F</i>	Effect size (%)
First flower (Julian day)	195 $\pm$ 12	181 $\pm$ 10	208	71.95**	25.80
Inflorescence length (cm)	98.00 $\pm$ 81.73	86.66 $\pm$ 78.18	208	1.02	0.50
August					
Inflorescence mass (g)					
June	0.00 $\pm$ 0.00	0.14 $\pm$ 0.28	199	22.19**	10.07
July	0.82 $\pm$ 1.12	1.46 $\pm$ 1.75	177	8.18*	4.44
August	3.95 $\pm$ 4.60	3.85 $\pm$ 3.92	138	0.02	0.01
Aboveground biomass (g)					
June	2.09 $\pm$ 1.38	5.20 $\pm$ 3.95	199	51.48**	20.64
July	9.14 $\pm$ 6.43	10.34 $\pm$ 7.08	177	1.39	0.78
August	15.50 $\pm$ 11.98	14.19 $\pm$ 11.05	137	0.34	0.24
Senescence (Julian day)	294 $\pm$ 13	290 $\pm$ 10	212	5.26*	2.44

Note: \*  $P < 0.05$ , \*\*  $P < 0.01$



**Fig. 3** (Mean  $\pm$  standard deviation of total aboveground biomass for *L. Salicaria* plants during two growing seasons (1997 and 1998) at North Bay, Ontario, Canada

### Growth responses

Growth in the study populations of *L. salicaria* was affected by the atypically warm and dry climatic conditions of 1998 only during the early part of the growing season. Aboveground biomass at the June harvest was significantly higher in 1998 than in 1997 (Table 1, Fig. 3). As part of this trend, the total inflorescence biomass for June, and to a lesser extent July, was higher in 1998 than 1997 (Table 1). However, by the end of the growing season, this difference was no longer evident as total aboveground biomass for July and August did not differ between years. Furthermore, the early start to flowering had no overall effect on inflorescence production during the 1998 growing season, as the means of the total inflorescence length and inflorescence biomass at the end of the growing seasons were similar between years (Table 1). A small decrease (4 days) in the mean Julian day of complete senescence from 1997 to 1998 was significant, but accounted for only 2% of the total variance in senescence times.

### Discussion

The El Niño/Southern Oscillation (ENSO) event is a reversal of oceanic and atmospheric circulation patterns over the equatorial Pacific Ocean, which shifts the mid-latitude jet stream and changes weather patterns throughout North America (Kousky and Bell 2000). The ENSO event that began in May of 1997 was one of the strongest on record (Changnon 2000), and produced very warm and dry conditions in central Ontario at the beginning of the 1998 growing season. The advance in flowering date and early rapid growth we observed in populations of the invasive wetland plant *L. salicaria* during the spring of 1998, compared to the more typical spring of 1997, sug-

gest that the phenology of this species is strongly affected by temperature. Furthermore, we made similar preliminary measurements of phenology and growth in 1996, another more climatically typical year, that support the notion that flowering times are relatively constant under average climatic conditions (Dech and Nosko unpublished data) and that the phenological shifts during 1998 were indeed a response to the changing climatic conditions.

The timing of spring flowering in many temperate species is temperature-dependent (Rathcke and Lacey 1985). Greenhouse experiments on *L. salicaria* demonstrated that growth and flowering were strongly inhibited at 8 °C compared to 18 °C (Shamsi and Whitehead 1974), which corresponds well to the interannual differences observed for May temperatures in this study. In alien populations of *L. salicaria*, springtime warming during ENSO events lifts the restrictions on growth and flowering time set by normal temperature regimes, and this may be a typical response in plants with temperature-based phenological cues. Indeed, early flowering (Beaubien and Freeland 2000) and enhanced vegetative growth (Walker et al. 1995) have been observed in other plant species as responses to the climatic effects of ENSO events. Furthermore, the advance of springtime phenological events in relation to increasing temperature is well established in many plant species (Bradley et al. 1999; Sparks and Menzel 2002). Early flowering in *L. salicaria* in response to warming during ENSO events suggests that this species could benefit from the projected warming of the global climate over the next century (IPCC 2001) and the subsequent potential for an increase in the frequency of ENSO conditions (Timmermann et al. 1999; Herbert and Dixon 2002).

Early flowering and rapid growth of *L. salicaria* during ENSO events could exacerbate the negative impacts of its invasion of North American wetlands. Pollination and seed set in sympatric co-flowering native species are reduced in the presence of *L. salicaria* (Grabas and Laverty 1999), and expanding the flowering time for *L. salicaria* could increase the extent and intensity of this effect. The competitive strategy of alien *L. salicaria* emphasizes early season vegetative development (Bastlová and Květ 2002). Starch reserves are mobilized from a common pool to support both vegetative and reproductive growth in *L. salicaria* (Stamm Katovich et al. 1998). Thus, increased allocation to vegetative biomass diverts resources from flowering, and delays flowering time. Ultimately, a delay in flowering reduces reproductive output (O'Neil 1999). During ENSO events, the cost of delayed flowering could be reduced or eliminated by minimizing the overlap in flowering time of pollen-limited *L. salicaria* plants with late-season competitors for pollinators such as *Solidago* spp. (O'Neil 1999), maximizing the post-flowering recovery period required to build up starch reserves to support next year's growth (Stamm Katovich et al. 1998) and decreasing the risk of frost damage during the maturation or dispersal of seeds (Rathcke and Lacey 1985). Such advantages have been implicated in the success of



invasive species such as *Bunias orientalis* L., a weed of central Europe that shows phenological displacement of maximum CO<sub>2</sub> assimilation and growth to avoid competition with native species (Zotz et al. 2000), and *Miconia calvenscens* DC, an invasive tree in Tahiti that flowers in cycles to maximize the production of seeds and recruitment of seedlings (Meyer 1998). Further research is required to confirm that reproduction and recruitment in *L. salicaria* do increase in response to ENSO events.

It is important to note that the overall growth of *L. salicaria* was unaffected by ENSO conditions. Edwards et al. (1995) found that populations of *L. salicaria* at drier sites showed reduced height and total biomass compared those at mesic sites, so it is possible that the lack of moisture associated with the ENSO events partially counteracts the advantages of rapid development. Furthermore, the biological control agents introduced to control *L. salicaria* in North America share close phenological ties with their host plants (Hight et al. 1995), and at our sites the small populations of leaf-feeding beetles (*Galerucella* spp.) showed increased activity during the 1998 season (Dech and Nosko 2002); however, there was no corresponding decrease in the growth and reproduction of *L. salicaria* (Dech 2000). Biological control agents could provide a negative feedback that neutralizes, or if populations are large enough, counteracts the advantages gained through phenological shifts in *L. salicaria* during ENSO events. Also, there may be significant positive effects carried over to the next spring, through increased accumulation of starch reserves in roots and crowns during a longer growing season (Stamm Katovich et al. 1998), which could explain the lack of a growth or reproduction effect we observed at the end of the 1998 growing season. The lack of a biologically significant difference in senescence times for *L. salicaria* between years further suggests that the recovery period for carbohydrate reserves was increased during 1998. The overall effects of the phenological shifts exhibited by *L. salicaria* during ENSO events are unclear; however, the potential impact of these changes on recruitment and control of this invasive species makes studies of these responses an important direction for future research.

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