

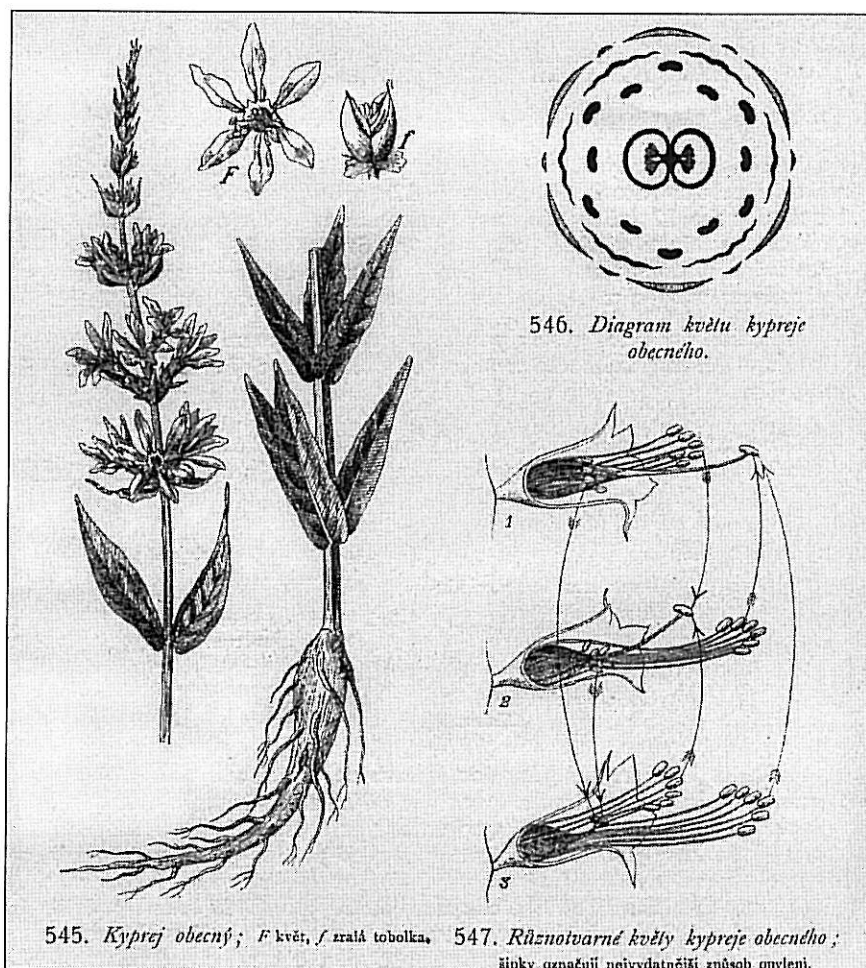
UNIVERSITY OF SOUTH BOHEMIA IN ČESKÉ BUDĚJOVICE  
FACULTY OF BIOLOGICAL SCIENCES

PhD thesis

**COMPARISON OF NATIVE AND INVASIVE  
*LYTHRUM SALICARIA* L. POPULATIONS**

AN EXPERIMENTAL APPROACH

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**Annotácia /Annotation**

Experiments with native and invasive populations of *Lythrum salicaria* L. were provided to describe differences in their basic life history and ecophysiological characteristics. Explanations of species invasive behaviour in conditions of its secondary area based on the experimental results are given. New hypotheses explaining differences between native and invasive *L. salicaria* plants are introduced.

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Prehlasujem, že som dizertačnú prácu vypracovala samostatne, na základe vlastných výsledkov a s použitím uvedenej literatúry.



Daša Bastlová

České Budějovice, 30. 9. 2001.

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## Zhrnutie (summary)

*Lythrum salicaria* L. (vrbica obyčajná, Lythraceae), je bylinný vytrvalý druh s pôvodným areálom rozšírenia pokrývajúcim takmer celú Euráziu. Tento druh bol pravdepodobne na začiatku 19. st. zavlečený s lodnou dopravou na východné pobrežie Severnej Ameriky, kde je z tohto obdobia roztrúsene dokumentovaný v sladkovodných častiach veľkých atlantických prístavov. Na konci 19. st. sa šíri spolu s vlnami európskych prisťahovalcov, ktorí ho používali ako významnú liečivú a medonosnú rastlinu, po severoamerickom kontinente smerom do vnútrozemia. K samovoľnému explozívne šíreniu druhu dochádza okolo r. 1930, kedy boli zaznamenané prvé monokultúrne populácie okolo rieky Sv. Vavrinca. Do roku 1985 bol výskyt *L. salicaria* zaznamenaný vo všetkých štátoch USA a provinciách Kanady medzi 37° s. š. a 50° s. š.

Jak v pôvodnom európskom, tak aj v sekundárnom severoamerickom areáli rastie *Lythrum salicaria* v širokom spektre rastlinných spoločenstiev, od relatívne suchých poloruderárnych až ruderalných stanovišť až po typicky mokradné stanovišťa s vyššou vodnou hladinou (kap. 2). Niektoré výsledky však naznačujú častejší výskyt invázných populácií na stanovištiach s vyššou vodnou hladinou v porovnaní s pôvodnými populáciami v strednej Európe. Na rozdiel od neinvázných rastlín, invázne rastliny sú schopné vytvárať pomerne husté až monokultúrne populácie na stanovištiach, ktoré sú veľmi podobné tým v primárnom areáli výskytu. Zdá sa, že vyššia kompetičná schopnosť invázných rastlín oproti neinváznym vyplýva z ich dvoch vlastností: 1) výška rastlín, rast koreňov a počet pupcov, ktoré tvoria základ nových stoniek pre ďalšiu sezónu je len veľmi málo ovplyvnený nízkym obsahom živín v pôde a trvalou saturáciou substrátu vodou (kap. 3). To umožňuje rastlinám nie len dobre získavať živiny na chudobných stanovištiach, ale navyše aj (úspešne) kompetovať o svetlo s podobne vysokými mokradnými rastlinnými druhmi, ktoré prevládajú na stanovištiach v sekundárnom areáli (napr. *Typha latifolia*). 2) Na vyšší obsah živín v substráte reagujú invázne rastliny výrazným nárastom mohutnosti primárnych vetiev. To v konečnom dôsledku aj výrazne zvyšuje celkovú generatívnu biomasu a tým aj reprodukčný potenciál invázných rastlín, pretože mohutnejších rast vetiev pozitívne ovplyvňuje tvorbu nových kvetenstiev a neskôr aj semien. Za lepšie kompetičné schopnosti však invázne rastliny „platia“ nižšou schopnosťou vytvárať kvetenstvo po strate rastového

vrcholu (napr. pri okuse), čo zrejme súvisí s dlhodobou absenciou herbivorného tlaku v sekundárnom areáli výskytu druhu.

Ani detailná rastová analýza nepotvrdila fyziologický základ rozdielov vo vzhľade (t. j. v množstve produkovanej rastlinnej hmoty) a následne aj kompetičných schopnostiach inváznych rastlín (kap. 4). Pretože relatívna rastová rýchlosť, rýchlosť fotosyntézy aj parametre fotosyntetickej krivky sa medzi inváznymi a neinváznymi rastlinami významne nelíšili, dá sa povedať, že kľúčovú úlohu vo vývoji a architektúre týchto rastlín hrajú pravdepodobne rozdiely v distribúcii asimilátov.

Všeobecne by sa rozdiely v alokácii asimilátov medzi inváznymi a neinváznymi rastlinami dali zhrnúť do dvoch rozdielnych stratégií. U inváznych rastlín je nápadná investícia rastlinnej hmoty do stonky, resp. rast do výšky a vývoj mohutného koreňového systému na začiatku sezóny. V ďalšom vývoji kroku rastie počet a mohutnosť laterálnych vetví, s čím súvisí aj výrazný rozvoj asimilačného aparátu. Dostatočne veľká listová plocha zabezpečuje dostatočné množstvo asimilátov na vytvorenie kvetenstva, ktoré sa však tvorí neskôr ako u neinváznych rastlín. Nevýhodou tejto stratégie je posun doby kvitnutia ku koncu sezóny, čím sa zvyšuje riziko nedozretia semien. Oproti tomu, vývoj neinváznych európskych rastlín je charakteristický rýchlou tvorbou laterálnych vetví a listov na úkor výškového rastu už od začiatku vegetatívnej sezóny, čo umožní vytvorenie kvetenstva v kratšom čase.

Rastliny pre štúdie porovnávajúce rozdiely medzi inváznymi a neinváznymi rastlinami *L. salicaria* boli väčšinou vybrané s ohľadom na podobnosť klimatických podmienok, a preto populácie pochádzali z pomerne malých geografických oblastí. Pretože oblasti s podobnými klimatickými podmienkami majú v Severnej Amerike južnejšiu zemepisnú šírku, dá sa očakávať, že rozdiely vo fotoperióde medzi primárnym a sekundárnym areálom budú hlavným selekčným faktorom pri vzniku týchto rozdielnych stratégií. To sa potvrdilo v pokuse, ktorý porovnával variabilitu a rozdiely v bionomických charakteristikách medzi rastlinami *L. salicaria* v rámci pôvodného areálu výskytu druhu (kap. 5). Rastliny z južných zemepisných šírok sa vyznačovali vyšším a mohutnejším vzrastom a posunom v dobe kvitnutia v porovnaní s rastlinami pochádzajúcimi zo severnejších zemepisných šírok. V tomto ohľade boli tieto rastliny podobné invázny rastlinám pochádzajúcim z centrálnej časti USA.

Ďalšie štúdie porovnávajúce pôvodné juhoeurópske rastliny vyznačujúce sa mohutným vzrastom s invázny rastlinami zo Severnej Ameriky by mali objasniť, či existujú rozdiely v stratégiách aj medzi týmito skupinami rastlín. Tieto štúdie, ktoré budú zahŕňať aj genetické analýzy inváznych a neinváznych rastlín sa pokúsia odpovedať na dve základné otázky: 1) sú

vlastnosti invázných rastlín výsledkom adaptívnej evolúcie na prevažujúce abiotické faktory (napr. dĺžka dňa alebo dĺžka vegetačnej sezóny), ktorá prebehla po zavlečení do nových podmienok, alebo 2) sú invázne rastliny „potomstvom“ pôvodných európskych populácií pochádzajúcich z južných častí pôvodného areálu?

**Chapter 1**  
**Introduction**

## Introduction

### Species description

*Lythrum salicaria* L. (Lythraceae) is a perennial herb 30-200cm tall with persistent woody rootstock. Squarish erect stems have evenly spaced nodes with two opposite or in whorl of three 3-10 cm long sessile, lanceolate to ovate leaves in each node (Mal et al. 1992, Thompson et al. 1987). Plants usually form branches in lower to mediate part of the stem, but the stem can be without the lateral branches too (pers. observation, Hegi et al. 1925). The length and number of lateral branches is very variable and it depends on habitat conditions (probably amount of nutrients in substrate, competition) (personal observation). Leaves are glabrous to pubescent on the stem and branches or sub-tomentose in the inflorescence. In June to August, plants create a dense terminal spike of purple inflorescences up to 1m long. In the first year, plants form only one main stem, which dies at the end of growing season. In older plants, annual herbaceous stems, each with terminal spike of flowers rise from the rootstock to make the wide-topped crown (Thompson et al. 1987). *L. salicaria* is facultatively mycorrhizal (Stevens and Peterson 1996) and there is also evidence that a minority of established plants can remain dormant above-ground for a year and then resume growth in the next growing season in North America (Thompson et al. 1987). The species is heterostylous with three distinct arrangements of pistils and stamens. The flowers are categorized according to stylar morphs as short-, medium- and long-styled (Mal et al. 1992).

### Distribution and habitats in its native range

In its native range, *L. salicaria* grows in almost all Europe with the exception of the most northern parts of Scotland, Scandinavia, Russia, and high mountains areas (Wangerin and Schröter 1937). The northern limit is around 57° N in the British Islands, where is common in Ireland, UK and often found in Scotland. It is absent on Faerer Islands and Island. In Scandinavia, it occurs up to around 64° N in Norway, with the most northern limit in Kautokeino (69° 30') (Blytt in Wangerin and Schröter 1937) and up to 67° N in Finland. The northern limit continues in the European part of Russia around 65° N. In Asian part of Russia, the northern border of occurrence lies at 61° N. At around 55° N and 97 ° E the limit turns back to west through Altai. The southern limit in China is at 24-25° N. The species is absent in Mongolia and northern part of Indian subcontinent (Tibet, Ladach). In northern India and

Kashmir, *L. salicaria* grows scattered similarly as in Afghanistan and Persia where the southern occurrence is known around 33° N. In southern Europe, *L. salicaria* is common in all countries except Balearic Islands and Crete. In Africa, it is known from northwest Morocco, Algeria and Tunis.

*L. salicaria* has a wide ecological range in Europe. It persists in a wide variety of environmental conditions; in littoral vegetation of fishponds or streams (Hejný 1960), rock-pools (Hæggström and Skytén 1987), mud-flats raising after lowering of water level (Toivonen and Bäck 1989), fen meadows or woodlands, swamp basins on mineral substratum or open woody margins (Wheeler 1980a). In England, Pearsall (1918) reported *L. salicaria* as a frequent species in a wide variety of sites: in open carrs with very rich vegetation and fluctuating water levels, moist woody water margins and also drier habitats on stable gravel with water level 10-15 cm below the soil surface during the summer. Wheeler (1980a, b) reported occurrence of *L. salicaria* in 14 of 22 tall sedges and reed communities in England and Wales. He listed many syntaxonomic units of rich-fen vegetation, usually sedge and fen meadow plant communities, where *L. salicaria* occurred in such alliances as Phragmition (communis), Magnocaricion, Caricion davallianae, Junco-Molinion and in alliances of carrs (wet shrub communities) such as Salicion cinereae and Alnion glutinosae (mire forests) on nutrient-rich substrates. In the Czech Republic, *L. salicaria* is listed as one of diagnostic plant species of Magnocaricion alliance, association Caricetum ripario-acutiformis (Hejný 1960, Dubyna et. al. 1993) together with other plant species such as *Lysimachia vulgaris*, *Sium latifolium*, *Oenanthe aquatica* or *Glyceria fluitans*. Usually it is described as a component of early successional vegetation on slightly disturbed or open sites with periodical fluctuations of water level (Hejný 1960). Toivonen and Bäck (1989) found *L. salicaria* commonly in pioneer stands also in Finland. They described changes in lake vegetation after eutrophication and lowering of water level during 38 years' period. In 1947, *L. salicaria* grew together with other commonly occurring species in the relatively narrow belt at the water edge with *Carex pseudocyperus* as a main species. In 1975, after heavy eutrophication and lowering of water table, *L. salicaria* became the most frequent species in mixed heliophyte vegetation in pioneer stands on mud flats. Ten years later, the stand was dominated by *Typha latifolia* in mean water level and *Typha angustifolia* at deeper water. Frequency of *L. salicaria* occurrence declined rapidly and the species grew, together with other heliophytes, in a small mixed stand at the margins of reedbeds or in open places with pioneer vegetation (Toivonen and Nybom 1989).

### Spread, distribution and habitats in its invasive range

Originally an Eurasian wetland plant species, *Lythrum salicaria* was introduced to the east shore of North America at the beginning of 19<sup>th</sup> century (Stuckey 1980, Thompson et al. 1987). Its further distribution history in North America is well documented (Stuckey 1980, Thompson et al. 1987) and is probably connected with its importance as a honeybee (e. g. Hayes 1979, Pellett 1977) and herb and with increased ship traffic and construction of channels at the end of 19<sup>th</sup> century (for references see Thompson et al. 1987). Around 1930, the first monocultural populations and rapid expansion of this species westward were observed (Stuckey 1980). By 1985, occurrence of *L. salicaria* was documented in all states of USA and southern provinces of Canada between the 37 and 50 north parallels (Edwards et al. 1995) with the most frequent occurrence around the St. Lawrence River.

In its secondary range, occurrence of *L. salicaria* is well documented mainly in North America (Stuckey 1980), where this species occurs at the highest frequency in northeastern part of the USA and southeastern part of Canada. In northeastern and north-central USA and adjacent provinces of Canada, alluvial floodplains are described as its optimal habitats (Thompson et al. 1987). In South America, it was reported from Rio Negro (Argentina). In Australia, the range of occurrence lies between 23 and 42 south parallels and 137 and 153 east meridians; southeast and east Tasmania and the provinces of Victoria, New South Wales and Queensland in south Australia (Wangerin and Schröter 1937).

Similarly as in Europe, in North America *L. salicaria* occurs in littoral vegetation of freshwater marshes, open stream margins (for review see Thompson et al. 1987), but its presence was also recorded in sedge meadows (Larson 1989), road sides (Isabelle et al. 1987) or, in contrast to European habitats, often in wetlands with high water level (40 cm or more) (Rawinski and Malecki 1984, Bastlová-Hanzélyová 2001). Larson (1989) mentions the occurrence of *L. salicaria* in a Wisconsin sedge meadow with standing or slightly fluctuating water table, growing together with 46 other plant species; *Scirpus cyperinus* (L.) Kunth, *Juncus* sp., *Hypericum canadense* L., and *Panicum* sp. were the most abundant. The list of co-occurring species also includes eight woody species. Thompson et al. (1987) list 29 associated wetland species at 45 sites across the United States and southern Canada. Some of the associates in North American wetlands are similar to those in Europe. Among the listed species, *Typha latifolia* was the most frequent in Northeast United States and *Phalaris arundinacea* in Northwest United States. Different *Carex* and *Scirpus* species were the next



common co-occurring plants in all studied areas. Edwards et al. (1998) described in more detail three North American and three central European sites with the presence of *L. salicaria* and found that climatic conditions are similar in both studied areas. But precipitation and average temperature in particular year seems to affect strongly plant growth characteristics. At the studied sites, the shoot density was significantly greater in most USA populations, but shoot height and biomass were similar in both invasive and native populations growing in similar habitats in years with similar precipitation regimes.

### **Control of *Lythrum salicaria* invasion**

In the United States, there has been considerable research on the spread and possible control methods involving physical, chemical, and biological control of *L. salicaria* impact on native flora and fauna. The impact of this species on native flora and fauna is not clear yet and there are still a lot of uncertainties about its negative influence on a species (for review see Anderson 1995, Hager and McCoy 1998) or ecosystem level (Emery and Perry 1996, Gabor et al. 1996, Hager and McCoy 1998). To eradicate *L. salicaria* in North America a lot of methods were tested. Physical control, such as mowing, flooding or burning appears to be of limited usefulness (Malecki and Rawinski 1985, Wilcox et al. 1987). The date of cutting plays an important role in the reduction of the number of shoots and does not result in permanent control. Flooding to a depth 0-50cm for two years had little effect on the plants' stature and reproductive characteristics. Use of herbicides seems to be more efficient in control of *L. salicaria* spread (Malecki and Rawinski, 1985, Welling and Becker 1993, Balogh 1993). But it is complicated because of negative impact on native and often threatened flora and as well as environmental contamination due to the need for repeated treatment. Studies on the seed bank dynamics of purple loosestrife have shown that for its effective control, a control program has to operate for a longer time. One-time treatments had only a temporary effect due to new plants being recruited from the seed bank (recorded 410 000 seeds per m<sup>2</sup> in the top 5cm of soil) and due to resprouting from roots (Welling and Becker, 1990).

Plant competition experiments as one of the possible control methods were only partly successful and their results highly differed with the competing plant species used in the experiment. *Echinochloa frumentacia* (Japanese millet) and *Polygonum lapathifolium* (nodding smartweed) grew well and out-competed *L. salicaria* (Rawinski 1982). On the other hand, *Echinochloa walteri* (Walter's millet), *Cyperus ferganescens* (chufa) (Balogh 1993) and *Phalaris arundinacea* (reed canarygrass) (Malecki and Rawinski 1985) were unsuccessful in out-competing purple loosestrife. The control using plant competitors is questionable because



many of the plant species, which successfully compete with *L. salicaria*, are often also non-native. Risk of new introduction of potentially invasive species is high in this kind of control. Using a native species in competition experiments would be more convenient. One of potentially successful species could be *Typha x glauca*. Rawinski and Malecki (1984) described competition between *L. salicaria* and *Typha x glauca* at the Montezuma National Wildlife Refuge. Both shoot density and the competitive ability of *L. salicaria* increased with decreasing water levels. However, on a permanently flooded site (water level always > 40 cm), the number of *L. salicaria* shoots decreased from 143 per m<sup>2</sup> in 1978 to 11 per m<sup>2</sup> in 1980, probably as a result of competition with *Typha x glauca*. High water level could also be a reason of *L. salicaria* shoots number.

In the last ten years, great attention has been paid to the biological control of *L. salicaria* in North America and Canada. There are few definitions of biological control, but one considering biological control from both applied and ecological perspective is that of DeBach in Garcia et al. (1988). He defined it as "the action of parasites, predators or pathogens in maintaining another organism's population density at a lower average than would occur in their absence". In Europe, 120 species of phytophagous insects were found to be associated with *L. salicaria* and 14 of them are restricted to *Lythrum* spp. only (Batra et al. 1986). Out of these insects, 13 were selected as potential agents for classical biological control (Batra et al. 1986). In 1992, two folivorous insects (*Galerucella californiensis* and *Galerucella pusilla* Coleoptera: Chrysomelidae) and one root weevil (*Hyllobius transversovittatus* Coleoptera: Curculionidae) were approved for release as purple loosestrife control agents after laboratory tests in Europe and North America (Hight et al. 1995), although as many as 59 species of phytophagous insects were collected on *L. salicaria* plants in the northeastern USA (Hight 1990). The three released species have successfully established in new conditions and even started to reproduce (Hight et al. 1995). To my best knowledge, there is a lack of studies evaluating the impact of released insects on invasive *L. salicaria* populations in the USA or Canada.

### **Ecophysiology**

The most comprehensive work describing eco-physiology of *L. salicaria* was done by Shamsi and Whitehead about 25 years ago (Shamsi and Whitehead 1974a, b, Shamsi 1974, Shamsi 1976, Shamsi and Whitehead 1977 a, b). Their studies involving basic life requirements and influence of a set of experimental conditions (nutrients, temperature, light, pH, competition, etc.) are universally cited in publications concerning this species. In their

studies, *L. salicaria* appears as a highly plastic species. The highest percentage of seeds germinated between 15 and 20 °C (tested range 10°C - 30 °C). In darkness, germination starts at 20 °C and increases rapidly to a maximum at 30 °C (Shamsi and Whitehead 1974a). Sand and clay as a media reduced and delayed germination by about 5 or 10 days, respectively, in comparison with germination on filter paper. Both daylength and mineral nutrition had no significant effect on germination. One of the factors which plays an important role in further development and growth of *L. salicaria* plants is light (Shamsi and Whitehead 1974b). At the beginning of the plant development, the total plant mass production is similar in plants growing at full natural light and at 70 % of full light in a greenhouse. As the experiment continued, the plants in the shaded treatment increased their leaf area and produced less dry mass and fewer lateral branches. Also, these plants flowered later and dry weight of their fruits and seeds was lower than in plants from full sun. Lower dry weight of seeds was due to smaller number of seeds per fruit since the dry weight per seed was similar at all light intensities. Distribution of dry weight between roots, stem and leaves was only moderately influenced by light intensity – roots formed a high proportion relatively to stems and their proportion remained the same, while the proportion of leaves increased slightly during ontogeny. The variation in daylength had a dramatic effect on growth of *L. salicaria* plants. Plants in short-day treatment (9 h of light) were small with reduced stem, low number of internodes and low number of branches, which were initiated but not elongated, and small leaves. The proportion of roots was very high in these plants. In long-day treatments (13, 14, 15 and 16 h of light), the plants had erect stems with large internodes and opposite hairy leaves. Together with elongation of main stem, a rapid growth of lateral shoots was observed. Daylength of 13 h seems to be critical for this species. At this daylength, elongation of the main stem and growth of lateral branches were strongly enhanced. Total dry weight increased about 50 times in comparison with short-day plants and flowering occurred within few weeks. Similarly to differences in daylength, *L. salicaria* responds to differences in nutrient supply. Shamsi and Whitehead (1977a) grew *L. salicaria* plants in Long Ashton nutrient solution (N:P:K 140:41:78) at full strength (140ppm of N) and five dilutions (S/10, S/50, S/100, S/200 and S/300). The tested plants responded to each successive dilution by an increase in root/shoot ratio; this proportionate increase in the roots or decrease in shoots was at the expense of dry weight of the stem rather than leaves. The proportion of leaves remained similar at all dilutions at final harvest. With decreasing nutrient concentration the plant dry weight and number of lateral branches decreased progressively together with reduction of flowering and fruiting.

No significant effect of high water level on growth and biomass production of *L. salicaria* was reported from either field (Edwards et al. 1995) or greenhouse experiments (Stevens et al. 1997). Edwards et al. (1995) reported that fluctuating water level rather than flooding acts as an important environmental factor stressing *L. salicaria* plants. Decreasing water availability reduced stem height (Edwards et al. 1995) or total plant height (Stevens and Peterson 1996). Stevens et al. (1997) studied morphological and anatomical responses of *L. salicaria* to three water levels – low, intermediate and high. They found no significant effect of water level on shoot, root and total plant fresh or dry matter production within 8 weeks of experiment duration. Only total stem diameter and porosity and root water content were higher in submersed portions of flooded stems, in both the flooded and the intermediate treatment. Increase in stem porosity and diameter was caused by the presence of aerenchyma in flooded plant parts.

### **Differences between native and invasive plants**

Edwards (1996) studied differences between native and invasive populations of *L. salicaria* in both field and experimental conditions. *L. salicaria* grows under similar environmental conditions ranging from nutrient rich saturated soils to nutrient poor soils with fluctuating water level in both North America and Central Europe. Invasive plants growing in nutrient rich habitats have greater shoot stature, fertility (number of flowering shoots per plot), fecundity (number of seeds per capsule) and growth rates than plants growing in nutrient poor and intermediate habitats. When populations from both native and invasive ranges were compared, life history and population dynamics were similar between native and non-native *L. salicaria* populations growing in nutrient-poor and nutrient-intermediate field conditions; significant between-population differences were found only in nutrient-rich, productive habitats (Edwards et al. 1998).

Garden experiments with selected native European and non-native North American populations of *L. salicaria* showed that the non-native populations usually grew taller and flowered later than the native populations (Blossey and Nötzold 1995, Edwards 1996). These differences persist regardless of the growing environment, as shown in cross-continental transplant experiments (Willis and Blossey 1999). Non-indigenous genotypes grew taller and produced more root, shoot and fruit mass than plants from the native range in both North American (Ithaca) and European (Silwood Park, UK) conditions. Nevertheless, the variability in measured characteristics was high within each plant origin category and differences between native and invasive genotypes were not significant (Willis and Blossey 1999,

Blossey and Kamil 1996). Edwards (1996) and Bastlová and Květ (unpublished manuscript) showed that population and plant characteristics in *L. salicaria* change with environmental conditions. Different environmental conditions in variety of habitats where *L. salicaria* occurs results in high degree of variability in biomass production and allocation within both native and non-native populations and may cause that some of native genotypes are similar to the invasive ones. Edwards et al. (unpublished manuscript) tested differences in one USA and two central European populations in a common garden experiment. The USA population differed significantly from one of the European population in terms of flowering phenology, biomass allocation patterns (roots, shoot and inflorescence dry weight) and allometric relationships (root/shoot ratio, leaf weight ratio), but not from the other native population. USA population, if differed from the European populations, were taller and allocated significantly more dry mass to root structures indicating their higher competitive ability. On the other hand, native European populations allocated more dry mass to reproductive structures. Similarly as in field conditions, these differences between native and non-native plants were apparent only under higher nutrient levels conditions.

### **Reasons of *L. salicaria* invasion: Hypotheses**

Currently, numerous opinions exist concerning why a plant species is a successful competitor or invader (e. g., Gaudet and Keddy 1988a,b, di Castri et al. eds. 1990, Pyšek et al. eds. 1995, Brock et al. eds. 1997, Starfinger et al. eds. 1998). One of the few generalities of competitively successful plant species is that they tend to allocate more biomass to growth, and less to reproduction or defense, than less competitive species (Crawley 1987, Gaudet and Keddy 1988 b, Blossey and Notzöld 1995, Grime 1974). Blossey and Notzöld (1995) came with the Evolution of Increased Competitive Ability (EICA) hypothesis, based on two theories relating to resource allocation: (1) optimal defense hypothesis (Coley et al. 1985 in Blossey and Notzöld 1995), and (2) environmental constraint hypothesis (Bryant et al. 1988 in Blossey and Notzöld 1995). Their hypothesis explains higher competitive ability and more vigorous growth of invasive plant species in their secondary distribution ranges by changes in allocation patterns. They hypothesize that in the absence of herbivores and other natural control agents, new and more competitive genotypes are selected, showing reduced resource allocation to herbivore defence and improved allocation to vegetative structures. They supported their hypothesis by experimental results with native and non-native genotypes of *L. salicaria*. More rapid vegetative growth and weaker resistance against herbivores were confirmed in non-native North American and Australia genotypes, although vegetative growth

of some native genotypes was similar to that of non-native ones (Blossey and Kamil 1996). Authors discuss this fact as: "...European populations showing increased vegetative growth in our experiments are, possibly, recently established. In these populations, herbivores have not yet completed the selective removal of less-well-defended genotypes." The second prediction of the EICA hypothesis is that specialized herbivores will show improved performance on non-native genotypes. Authors also tested survival and larval weight of two herbivores (leaf-feeder *Galerucella pusilla*, Coleoptera: Chrysomelidae and root-feeder *Hylobius transversovittatus*, Coleoptera: Curculionidae) fed with native and non-native *L. salicaria* plants. Of the two herbivores, only one had significantly higher survival and larval weight on non-native plants. More recent study (Willis et. al 1999) quantifies secondary plant metabolites in native and non-native *L. salicaria* plants. This species is rich in phenolic compounds and its use as a drug was often been cited (e. g., Rauha et al. 2001, Thompson et al. 1987). The leaf phenolic content was significantly higher in native than in non-native genotypes (total phenolic content in leaves 0.48% in native in comparison to 0.33% in non-native plants), but herbivore bioassay revealed no significant intra-specific variation in herbivore resistance between these genotypes. Also, the developmental rate, adult mass and adult size of neither of the two tested herbivores (specialist *Galerucella pusilla* and polyphagous *Spodoptera exigua*, Lepidoptera: Noctuidae) were not significantly affected by origin of host plant population. Also Edwards (unpublished manuscript) subjected native and non-native populations of *L. salicaria* to natural levels of foliar insect herbivores in a field conditions in central Europe. He found no significant differences in herbivore resistance (measured as percent leaf area lost) between the native and non-native plants of *L. salicaria*. The second prediction of EICA hypothesis was thus not fully confirmed.

EICA hypothesis does not deal with the fact, that herbivory need not necessarily affect negatively plant growth. The well known and best documented effects of herbivory are a reduction of plant mass, seed production (either number or weight, or both), and delay or reduction of flowering in host plants (for review see Belsky 1986). But plants that are damaged by herbivory, especially when they lost the growth apex, may produce more total biomass and/or seeds than undamaged plants (Irwin and Aarssen 1996, Venecz and Aarssen 1998). Shoot apex removal may release lateral meristems from apical dominance and thus may overcompensate losses by herbivory either in the year of damage or in the next year. The ability of plants to (over)compensate herbivory losses can depend on species or environmental conditions. Venecz and Aarssen (1998) tested the effect of shoot apex removal on growth of *L. salicaria* plants. Dry mass of the flowering spikes, the mean seed number per fruit and the



total number of seeds per plant were significantly reduced in pre-flower clipped plants in comparison with unclipped control plants. These seeds showed a lower percent germination. Although clipping reduced plant height and delayed flowering in *L. salicaria* plants, the authors reported increased branching associated with release of lateral meristems from apical dominance. Nevertheless, increased branching did not compensate losses of dry weight caused by clipping. In the year following the treatment, the number of flowering spikes was similar in both clipped and unclipped (control) plants. The number of fruits per plant was slightly higher (but not statistically significantly) in plants that had received pre-flower clipping treatment in previous year.

A more vigorous growth and higher competitive ability of invasive *L. salicaria* plants may have also other reasons than these explained in EICA hypothesis.

1) The non-native plants may have undergone an adaptive evolution to the prevailing abiotic environmental conditions in a new geographical range, e.g. daylength or length of the growing season (Ray and Alexander 1966, Weber and Schmid, 1998). This hypothesis is also supported by two following facts. Firstly, similar climatic conditions occur at more southern latitude in invasive range than in native ones (Edwards et al. 1998), and thus differences in daylength arising from this fact may be important in plant selection and development. Additionally, *L. salicaria* is reported as sensitive to photoperiod and its development (flowering time) and dry weight partitioning may be strongly affected by length of the dark period (Shamsi and Whitehead 1974b). Secondly, the species was introduced to North America at the beginning of 19<sup>th</sup> century and its invasive spread begun a hundred years later, at the beginning of 20<sup>th</sup> century (Thompson et al. 1987). Time for natural selection in non-native (North American) populations of *L. salicaria* was thus sufficiently long to breed a new genotypes with a different dry weight allocation pattern in comparison with native plants (Peacock and McMillan 1968, Abrahamson and Gadgil 1973, Shamsi 1974, Waite and Hutching 1982).

2) The non-native plants may originate from populations introduced from countries situated at low latitudes (e.g., southern Europe). In literature, there is a numerous examples, that plants originating from low latitudes often possess more vigorous growth than their conspecifics from more northern latitudes (e. g., Ray and Alexander 1966, Weber and Schmid, 1998).

3) Present non-native *Lythrum salicaria* plants could be a vigorous hybrid between introduced European plants and some other native American species of *Lythrum* genus (e. g. *Lythrum alatum*) (Edwards unpublished manuscript, Abbott 1992).

4) As *Lythrum salicaria* is often planted as ornamental plant (per. observation) and was an important plant species in honey production (Thompson 1987), American plants may have been knowingly selected by beekeepers and gardeners to obtain plants that grow taller and flower later in the season, when other sources of honey in flowers are restricted or insufficient.

Studies comparing ecological, physiological, developmental and genetic characteristics of both native and invasive *L. salicaria* plants could help to confirm or reject these hypotheses.

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## Chapter 2

**Comparative study of native and invasive populations of *Lythrum salicaria* L.: population characteristics, site and community relationships.**

## COMPARATIVE STUDY OF NATIVE AND INVASIVE POPULATIONS OF *LYTHRUM SALICARIA* L.: POPULATION CHARACTERISTICS, SITE AND COMMUNITY RELATIONSHIPS

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### Abstract

*Lythrum salicaria* L., a herbaceous perennial native to Europe and Asia, is recognized as an aggressive invasive species of North American wetlands. In this paper, 26 invasive and 32 native populations of *L. salicaria* were compared in terms of their growing habitats (native populations in Třeboň Biosphere Reserve – South Bohemia, Czech Republic and invasive populations in Indiana Dunes National Lakeshore – Indiana, USA). Population characteristics (shoot density and average height of plants) and site characteristics (water level, irradiance) were quantified in native and invasive locations. Additionally, phytosociological relevés were taken to evaluate the frequency of co-occurring species in the primary and secondary regions.

*Lythrum salicaria* occurs in a wide variety of habitat conditions in both native and invaded areas, from very dry locations along railroads to deep water in lakes or ponds. Native sites in the Czech Republic had higher species diversity than invasive sites in the USA. Forty vascular plant species were found growing with *L. salicaria* in selected American sites, while there were 129 in the selected Czech sites. Shoot density as well as percent cover of *L. salicaria* was significantly greater in the American invasive populations than in the European ones. Invasive plants were significantly taller than native plants.

### Introduction

Alien plants, which have colonized and become established in new geographical areas, are usually taller and have a greater amount of biomass than plants of the same species growing in their native range (e.g. Mooney and Drake 1986; Pyšek *et al.* 1995; Williamson 1996; Starfinger *et al.* 1998). By growing taller, the alien plants can become the dominant species in the new habitat, shading out the native plants (Mooney and Drake 1986; Lodge 1993; Williamson 1996). In this way, the alien plants show a more competitive behavior, which is lacking in their native counterparts.

A large environmental tolerance is a general characteristic of many successful invasive plant species (Baker 1965; Bazzaz 1986; Roy 1990), allowing these species to establish and reproduce successfully in different habitats. One purpose of studies with invasive species is to



determine how their growth and vigour are affected when growing under different environmental conditions (Ashton and Mitchell 1989). Another is to determine why these species succeed in new geographic areas by comparing invasive populations of plants of the same species growing in their native areas (Harper 1965; Sukopp and Starfinger 1995).

The comparison of a species' ecology in its native and invasive ranges is a valuable tool in explaining the success of the species as an invader of new geographic regions (Sukopp and Starfinger 1995). However, there are only a few published examples of comparative ecological studies (Sukopp and Starfinger 1995; Starfinger 1997; Edwards *et al.* 1999). In this paper, *Lythrum salicaria* L., an invasive species of North American wetlands, was studied in terms of the conditions of its primary and secondary regions of occurrence.

The objective of this study is to show how the ecological characteristics of native and invasive populations of *L. salicaria* differ, by describing the variability of growing habitats and environmental conditions.

## **Methods**

### *Studied species*

*Lythrum salicaria* is a perennial herb 0.3-2.7 m tall (Hegi 1925; Mal *et al.* 1992) with many herbaceous stems rising from a persistent perennial tap root. Annual, erect squarish stems have evenly-spaced nodes with a dense terminal spike-like purple inflorescence. Leaves are 3-10 cm long, lanceolate to ovate, and opposite or in whorls of three (Mal *et al.* 1992). Flowers of *L. salicaria* exhibit tristylly, where individual plants bear short-, mid- or long-styled flowers. The fruit is an oblong-ovoid capsule with up to 130 seeds (Mal *et al.* 1992).

This species is native to Eurasia, with its most prevalent distribution in moist or wet habitats of central and southern Europe and central Siberia (Shamsi and Whitehead 1974). Introduced to North America at the end of 18<sup>th</sup> century, *L. salicaria* became an invasive weed in the 1930s (Thompson *et al.* 1987). Presently, it is an aggressive invader of temperate wetlands of North America, occurring between the 37<sup>th</sup> and 50<sup>th</sup> parallels (Edwards *et al.* 1995).

### *Data collection*

Two areas were selected for a comparative study of native and invasive populations: 1) Třeboň Basin Biosphere Reserve (Europe, Czech Republic) and 2) Indiana Dunes National Lakeshore (USA). Basic characteristics of both areas are in Table 1.

For this study, 32 populations of *L. salicaria* were selected in the Třeboň Basin Biosphere Reserve and 29 populations in Indiana Dunes National Lakeshore. Permanent plots of 10



meters square size were established in habitats covering the variability of sites and plant communities where *L. salicaria* populations occur in their primary natural (Czech Republic) and secondary (USA) habitats.

*Table 1.* Basic characteristics of studied areas.

	<b>Mean annual temperature</b>	<b>Mean annual rainfall</b>	<b>Geographical location</b>
<b>Indiana Dunes National Lakeshore (USA)</b>	9.6 °C	800 mm	42° N; 87° W
<b>Třeboň Basin Biosphere Reserve (CZ)</b>	7.5 °C	600-650 mm	49° N; 15° E

Two phytosociological relevés were taken in each permanent plot to characterize the plant community. Plant communities in permanent plots were relatively homogenous thus 1-meter square relevés covered sufficiently the variability in plant density and diversity in respective habitat. In permanent plots where the plant community was heterogeneous and the number and percent cover of co-occurring species were highly variable, the number of phytosociological relevés was increased to three. All species occurring in the phytosociological relevés were identified and their percent cover assessed. In order to characterize site conditions, irradiance (at a relative scale; from 1=full sun to 0=full shade) and water level depth at time of flowering were assessed. Population density was determined by counting the total number of shoots in each permanent plot. Fifteen randomly selected plants were measured for height (from the soil surface to the growth apex).

#### *Data analyses*

Species composition of native and invasive sites was analyzed with Detrended Correspondence Analysis (DCA). The relationship of species composition of native and invasive sites to environmental characteristics was evaluated by Canonical Correspondence Analysis (CCA). Both analyses were made using the software CANOCO for Windows (ter Braak and Šmilauer 1998). Significance was tested by the distribution-free Monte Carlo permutation test (MCPT). In the MCPT, the distribution of the test statistics under the null hypothesis is generated by random permutations.

The number of shoots, percent cover, water level, irradiance and height of plants in native and invasive populations were analyzed by generalized linear models (GLM) (McCullagh and Nelder 1989). The S-PLUS software package (Anonymous 1995a, b) was used.

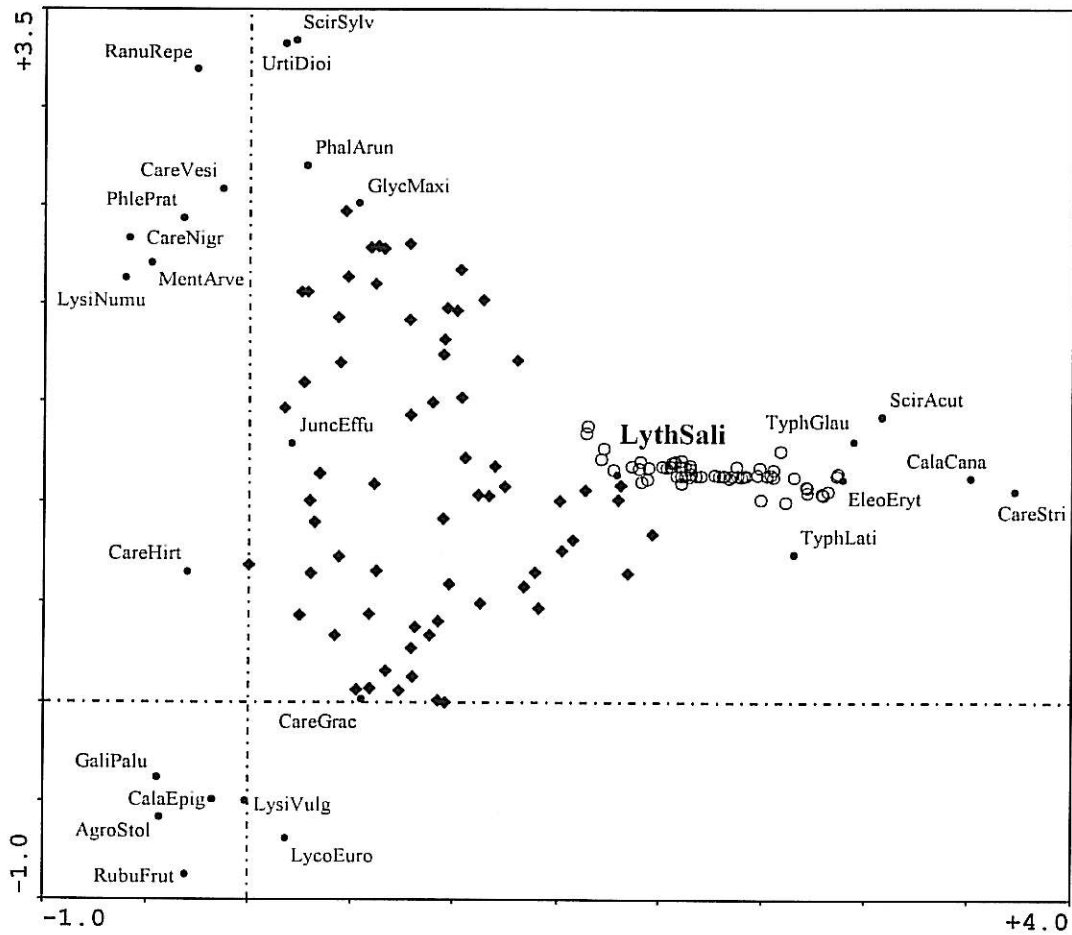
Nomenclature follows Rothmaler *et al.* (1994) and BONAP/MIP (Botanical Checklist of North America).

## Results

Detrended Correspondence Analysis (DCA) results show apparent differences between native European and invasive American sites (Fig. 1). First DCA axis (explains 7.1% of variability in species data) reflects gradient from Czech (left side of the graph) to American (right side of the graph) sites. Second DCA axis (explains 4.8% of variability in species data) reflects variability in species composition of particular sites, which was not explained by the first DCA axis and shows much wider variability among the Czech sites in comparison to the American ones. American sites are also less diverse, in terms of the species richness of plant communities, than European sites. Forty vascular plant species were found growing with *L. salicaria* in selected American sites, while there were 129 in corresponding area in the selected Czech sites. The five most frequent species found in the natural and invaded plant communities are shown in Table 2.

**Table 2.** The most frequent plant species associated with *Lythrum salicaria* in native and invasive ranges of occurrence. Percent frequency of occurrence was counted as number of phytosociological relevés in which the species was found/ total number of phytosociological relevés (N).

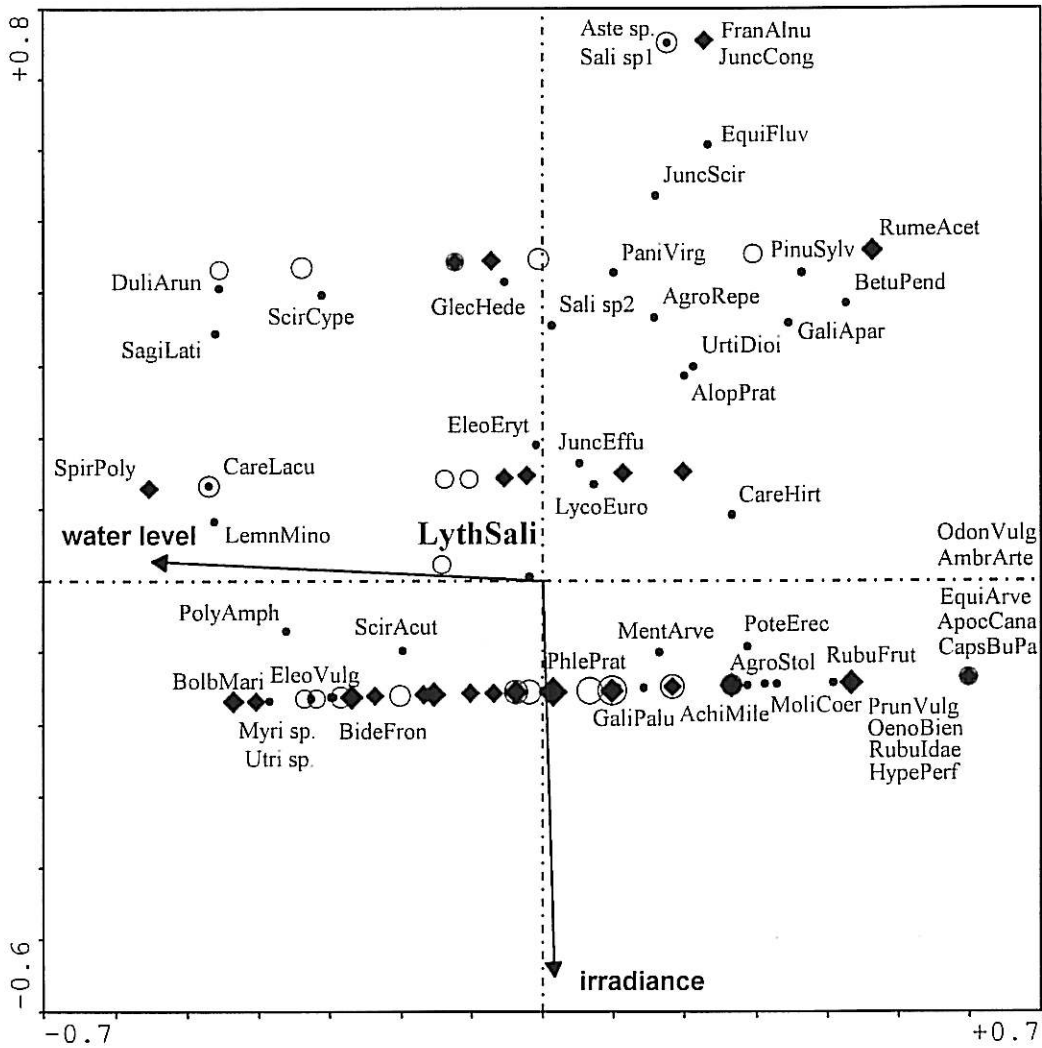
	<b>Třeboň Basin Biosphere Reserve (CZ) (N=66)</b>		<b>Indiana Dunes National Lakeshore (USA) (N=62)</b>	
Total number of plant species	129		40	
The most frequent species	<i>Calamagrostis epigejos</i>	21%	<i>Calamagrostis canescens</i>	37%
	<i>Juncus effusus</i>	21%	<i>Typha latifolia</i>	23%
	<i>Ranunculus repens</i>	21%	<i>Eleocharis erythropoda</i>	21%
	<i>Glyceria maxima</i>	20%	<i>Carex stricta</i>	18%
	<i>Galium palustre</i>	18%	<i>Scirpus acutus</i>	15%



**Fig. 1.** Detrended Correspondence Analysis (DCA) illustrates differences in species composition between European (full diamonds) and American sites (empty circles). Plant species are marked with full circles and abbreviation set up of the first four letters of genus and first four letters of the species name. (For abbreviations and full species names see Appendix 1)

Results of CCA show differences in distribution of European and American habitats with *L. salicaria* along two environmental gradients (Fig. 2). Both the effect of water level ( $F=2.826$ ,  $P=0.001$ ) and water level and irradiance together ( $F=2.577$ ,  $P=0.001$ ) were highly significant (MCPT, 1000 permutations). GLM found no significant differences between the Czech and American sites in relation to water and/or irradiance gradients, although the invasive sites had on average slightly higher water level. *L. salicaria* grows mostly in habitats with full sun, but it may be present in a variety of habitats and plant communities in both native and invasive areas. These communities range from typically wetland plant communities (left-hand side of the graph), through wet meadow communities (lower part in the center of the graph) to the ruderal communities (lower right hand part of the graph). The occurrence of *L. salicaria* was

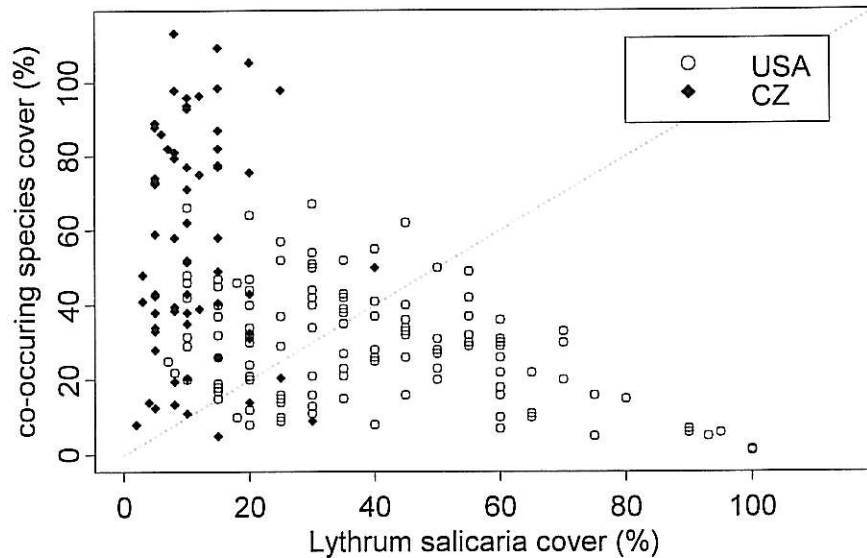
recorded also in plant communities with woody species (upper right-hand corner of the graph) in both native and invasive areas.



**Fig. 2.** Results of Canonical Correspondence Analysis (CCA) ordination. Biplot shows the relationship of site (either invasive or native) and environmental variables (water level and irradiance). Percentage of variability in species data explained by the CCA axis is 2.2% for 1<sup>st</sup> axis and 1.8% for 2<sup>nd</sup> axis. (For differentiation of sites and plant species see legend in Figure 1. The size of site symbols reflects the number of relevés at the same point in the ordination diagram ranging from one (the smallest symbols) to six (the largest symbol)) (For abbreviations and full species names see Appendix 2)

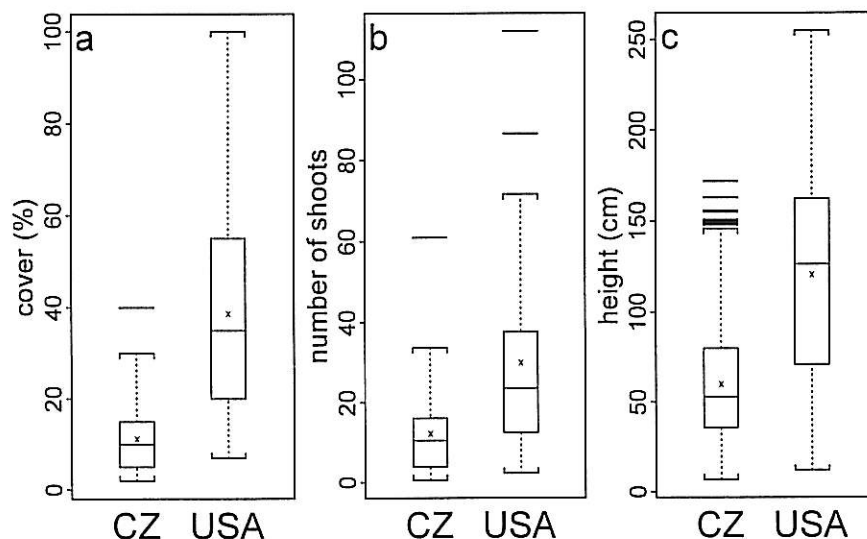
Percent cover of *L. salicaria* was significantly lower ( $P < 0.001$ ) in European than in American plant communities (Fig. 3, 4a). The average percent cover of *L. salicaria* was  $11 \pm 1$  (mean  $\pm$  standard error of mean) at European sites. Only 4 of 66 European phytosociological relevés (2 of the 32 populations) had higher percent cover of *L. salicaria* than other associated species. Percent cover of *L. salicaria* was  $32 \pm 2$  (mean  $\pm$  standard error of mean) at the American sites

and ranged much more than at the Czech sites. In majority of invasive habitats *L. salicaria* was the dominant species of plant community.



**Fig. 3.** Relationship between percent cover of *Lythrum salicaria* and total percent cover of associated species in native European and invasive American sites. Total percent cover of co-occurring species was calculated as sum of particular species covers. This resulted in few values greater than 100% due to overlapping in plant communities. Dotted line shows equal percent cover of *L. salicaria* and co-occurring species.

*Lythrum salicaria* cover and ratio showing a species dominance (cover of *L. salicaria*/co-occurring species cover) didn't show apparent variability for Czech sites along the water gradient, but higher values for both characteristics were found in relatively high water levels (between -10 and +20cm) at American sites.



**Fig. 4.** Box and Whisker plots showing: a) percent cover, b) population density (number of shoots per 1m<sup>2</sup>) and c) plant height of *L. salicaria* in native (CZ) and invasive (USA) populations. Graphs show the upper and lower quartile (box size), mean values (x), median (black stripe inside the box), upper and lower extreme - nearest values not beyond a standard span (1.5x inter quartile range) from the quartiles (whiskers) and outliers (black lines beyond whiskers) (Hoaglin et al. 1983).

Shoot density (per 1 square meter) was significantly greater in the American invasive populations than in the European ones ( $P < 0.001$ ) (Fig. 4b). Mean total shoot number was  $29.9 \pm 5.3$  in American invasive and  $12.2 \pm 2.2$  in European native populations.

Invasive plants were significantly taller than native plants, with a mean height of  $121 \pm 3$  cm in invasive American populations, compared to  $60 \pm 1$  cm in the European Czech populations ( $P < 0.001$ ) (Fig. 4c).

## Discussion

*Lythrum salicaria* is considered as a typical wetland species in both native and invasive areas of occurrence (Hegi 1925; Wangerin and Schröter 1937; Hejný 1960; Thompson 1987), but there are some similarities and differences between the native and invasive populations and habitats.

Based on our study provided on two restricted geographical areas within the native and invasive range of *L. salicaria* occurrence, it seems that the most apparent difference between sites and/or habitats of native and invasive populations is in their species composition. The differences between the native and invasive sites showed in DCA are mainly, but not only due to differences in plant species between the North American and Central European flora, because there was also a lot of identical associated species in both locations. Significantly higher co-occurring species diversity in the native sites may reflect higher variability of occupied habitats in Central Europe. It seems, that native European sites are distributed along both measured environmental gradients and that invasive North American sites occurred more often (but not statistically significant) in habitats with higher water level. Some of the frequent co-occurring plant species found in North America (e.g. *Typha latifolia*, *Scirpus acutus*, *Eleocharis erythropoda*) also indicate slightly higher water level in invasive habitats. Larger area allowing better generalization and more detailed description of variability and differences between the native and invasive populations is necessary to be included in ongoing comparative study.

Thompson *et al.* (1987) lists 29 associated wetland species at forty-five sites across the United States and southern Canada. Typically wetland species *Typha latifolia* L., *Phalaris arundinacea* L., *Carex sp. pl.*, and *Scirpus sp. pl.* were as the most frequent among. Larson (1989) mentions the occurrence of *L. salicaria* in a Wisconsin sedge meadow with standing or slightly fluctuating water table, growing with 46 other plant species; *Scirpus cyperinus* (L.) Kunth, *Juncus sp.*, *Hypericum canadense* L., and *Panicum sp.* were the most abundant.



Although *L. salicaria* is referred mostly from wetland habitats in the North America, it is probably not able to tolerate habitats with permanently high water level. Rawinski and Malecki (1984) described competition between *L. salicaria* and *Typha x glauca* at the Montezuma National Wildlife Refuge. Both shoot density and the competitive ability of *L. salicaria* increased with decreasing water levels. In a permanently flooded site (water level always > 40 cm), the number of *L. salicaria* shoots decreased from 143 per square meter in 1978 to 11 per square meter in 1980. Authors attributed rapid decline in *L. salicaria* shoots density to the competition with *Typha x glauca*.

In contrast to the common opinion that *L. salicaria* is a frequent species of littoral vegetation in central Europe, no significant general trend to littoral habitats was found in our study. In the Třeboň Basin Biosphere Reserve, *L. salicaria* was associated slightly more often with ruderal habitats, which are typical of a high frequency of disturbance and lower competition. In these stands, plant populations were denser than in non-disturbed stands or stable plant communities. High shoot density and small shoot stature are characteristics of pioneer plant species, which colonize new established stands, such as the edges of agricultural land or bare edges of ponds or lakes (after declining of water level) (Toivonen and Bäck 1989; Hægström and Skytén 1987). In our study, the densest populations (up to 60 shoots per 1 square meter) in Czech sites were found in similar stands: the bare edges of fish ponds after a declining water level during winter.

In England, Pearsall (1918) reported occasional occurrence of *L. salicaria* in marsh vegetation. On the other hand, frequently is reported in open carrs with very rich vegetation and fluctuating water level, moist woody water margins and drier habitats of stable gravel with water level 10-15 cm below the soil surface during the summer. In our study, *L. salicaria* was found in habitats similar to those described by Pearsall (1918), but in contrast, we never found *L. salicaria* in habitats with a dense canopy of trees, with limited light intensity.

Wheeler (1980 a, b) and Toivonen (1989 a) listed *L. salicaria* as a characteristic or associated species of many syntaxonomic units of rich-fen vegetation, usually sedge and fen meadow communities, in England and southern Finland, respectively. Some typical species of rich-fen vegetation units (e. g. *Lycopus europaeus* L., *Lysimachia vulgaris* L., *Juncus effusus* L., *Lysimachia nummularia* L.) were found as frequent associates in the Třeboň Basin Biosphere Reserve.

Our study supported a opinion, that invasive plants grow taller and form populations with higher shoot density than in populations of the same species growing in its native range. Some exceptions were found in populations growing in habitats with a lower intensity of light. As a

result of competition for light with other plants (e. g. *Urtica dioica* L., *Rubus* sp., different graminoides), *L. salicaria* grew taller (up to 170 cm), but never overgrew the surrounding vegetation. In addition, population densities in shaded habitats were smaller than in open areas.

### Conclusions

The results of comparative study of *L. salicaria* native and invasive populations can be summarized as follows:

1. Generally, invasive populations of *L. salicaria* in Indiana Dunes National Lakeshore grow in similar habitats as the native populations in the Třeboň Basin Biosphere Reserves, but it seems that dense invasive North American populations occur more often in habitats with higher water level.
2. Native European and invasive American sites of *L. salicaria* are significantly different in term of species richness; American sites are less diverse than European sites.
3. Invasive populations are denser ( $29.9 \pm 5.3$  shoots per square meter) and plants grow taller on average ( $121 \pm 3$  cm) than native populations (average population density  $122 \pm 22$  shoots per square meter and average plant height  $60 \pm 1$  cm).

### Acknowledgments

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## Appendix 1

### Abbreviations and full species names used in Figure 1:

- AgroStol *Agrostis stolonifera* L.  
CalaCane *Calamagrostis canescens* (Weber)Roth  
CalaEpig *Calamagrostis epigejos* (L.)Roth  
CareGrac *Carex gracilis* Curtis  
CareHirt *Carex hirta* L.  
CareNigr *Carex nigra* (L.)Reichard  
CareStri *Carex stricta* Lam.  
CareVesi *Carex vesicaria* L.  
EleoEryt *Eleocharis erythropoda* Steud.  
GaliPalu *Galium palustre* L.  
GlycMaxi *Glyceria maxima* (Hartman)Holmberg  
JuncEffu *Juncus effusus* L.  
LycoEuro *Lycopus europaeus* L.  
LysiNumu *Lysimachia nummularia* L.  
LysiVulg *Lysimachia vulgaris* L.  
LythSali *Lythrum salicaria* L.  
MentArve *Mentha arvensis* L.  
PhalArun *Phalaris arundinacea* L.  
PhlePrat *Phleum pratense* L.  
RanuRepe *Ranunculus repens* L.  
RubuFrut *Rubus fruticosus* agg.  
ScirAcut *Scirpus acutus* Muhl. ex. Bigelow  
ScirSylv *Scirpus sylvaticus* L.  
TyphGlau *Typha x glauca* Godr.  
TyphLati *Typha latifolia* L.  
UrtiDioi *Urtica dioica* L.

## Apendix 2

### Abbreviations and full species names used in Figure 2:

- AchiMile *Achillea millefolium* L.  
AgroStol *Agrostis stolonifera* L.  
AlopPrat *Alopecurus pratensis* L.  
AmbrArte *Ambrosia artemisiifolia* L.  
ApocCana *Apocynum cannabinum* L.  
Aste sp. *Aster* sp.  
BetuPend *Betula pendula* Roth  
BideFron *Bidens frondosa* L.  
BolbMari *Bolboschoenus maritimus* (L.)Palla  
CapsBuPa *Capsella bursa-pastoris* (L.)Med.  
CareHirt *Carex hirta* L.  
CareLacu *Carex lacustris* Willd.  
DuliArun *Dulichium arundinaceum* (L.)Britton  
EleoEryt *Eleocharis erythropoda* Steud.  
EleoVulg *Eleocharis palustris subsp. vulgaris* S.M.Walters  
EquiArve *Equisetum arvense* L.  
EquiFluv *Equisetum fluviatile* L.em.Ehrh.  
FranAlnu *Frangula alnus* Mill.  
GaliApar *Galium aparine* L.  
GaliPalu *Galium palustre* L.  
GlecHede *Glechoma hederacea* L.  
HypePerf *Hypericum perforatum* L.  
JuncCong *Juncus conglomerates* L.em.Leers  
JuncEffu *Juncus effusus* L.  
JuncScir *Juncus scirpoides* Lam.  
LemnMino *Lemna minor* L.  
LycoEuro *Lycopus europaeus* L.  
LythSali *Lythrum salicaria* L.  
MentArve *Mentha arvensis* L.  
MoliCoer *Molinia caerulea* (L.)Moench  
Myri sp. *Myriophyllum* sp.

OdonVulg *Odontites vulgaris* Moench.  
OenoBien *Oenothera biennis* L.  
PaniVirg *Panicum virgatum* L.  
PhlePrat *Phleum pratense* L.  
PinuSylv *Pinus sylvestris* L.  
PolyAmph *Polygonum amphibium* L.  
PoteErect *Potentilla erecta* (L.)Räuschel  
PrunVulg *Prunella vulgaris* L.  
RubuFrut *Rubus fruticosus* agg.  
RubuIdae *Rubus idaeus* L.  
RumeAcet *Rumex acetosella* L.  
Sali sp. *Salix* sp.  
ScirAcut *Scirpus acutus* Muhl. ex. Bigelow  
ScirCype *Scirpus cyperinus* (L.)Kunth  
SpirPoly *Spirodela polyrhiza* (L.)Schleiden  
UrtiDioi *Urtica dioica* L.  
Utri sp. *Utricularia* sp.

### **Chapter 3**

## **Effects of nutrient and water supply and decapitation on growth of native and invasive plants of *Lythrum salicaria* L.**



## **Effects of nutrient and water supply and decapitation on growth of native and invasive plants of *Lythrum salicaria* L.**

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### **Abstract**

Purple loosestrife (*Lythrum salicaria* L.), an originally Eurasian plant species, has successfully invaded North American wetlands, where invasive plants grow taller and show higher competitive ability in comparison with native plants. Influence of nutrient supply (four nutrient levels), permanent and fluctuating water level and decapitation on growth of native and invasive population of *L. salicaria* were tested. The invasive plants grew taller, had a significantly higher vegetative shoot as well as root dry weight, produced more new root buds and primary lateral branches and flowered two to three weeks later than the native plants under intermediate nutrient supply. Under absence of nutrients or at nutrient concentration of 4 g.dm<sup>-3</sup>, no significant differences were found between the native and the invasive plants. In both kind of plants, increased nutrient supply affected reproductive traits by increasing the number and vigour of flowering lateral branches, but this response is stronger in invasive plants. Water supply did not affect any of the growth characteristics, except for the higher number of new root buds formed in native decapitated plants at 1 g.dm<sup>-3</sup> nutrient concentration in fluctuating water level. Decapitation affected negatively both the native and the invasive plants, by reducing their dry matter production and by delaying their flowering in the year of decapitation. The invasive plants responded to decapitation stronger than the native plants in reproductive dry weight production under intermediate nutrient concentrations. Decapitation slightly increased the number of new root buds, what indicates a high potential for regeneration of shoots in both the native and invasive plants.

*Additional key words:* plant invasions, dry weight partitioning, non-native plants

### **Introduction**

Purple loosestrife (*Lythrum salicaria* L., Lythraceae) is an originally Eurasian plant species commonly occurring in moist to wet open or slightly shaded habitats. It has successfully invaded numerous wetlands in North America, with the most aggressive spreading in the northeastern to mid-western USA and in southeastern Canada. In both Eurasia and North America, purple loosestrife is present in a wide range of plant community types, from

wetlands dominated by common reed (*Phragmites australis*) to edges of bottomland soft- or hardwood forests (Bastlová-Hanzélyová 2001). While purple loosestrife only exceptionally becomes dominant in Eurasian plant communities, it often becomes an important constituent or dominant species in North American plant communities invaded by it.

Invasive plants of *L. salicaria* often grow taller and produce more biomass than native plants (Willis and Blossey 1999, Edwards *et al.* 1998). This more vigorous growth of invasive plants seems to be the reason for higher competitive ability and frequent dominance of *L. salicaria* in North American wetlands. Shamsi (1976) demonstrated that *L. salicaria* plants are highly plastic and able to tolerate shade, low pH and nutrient-poor and relatively dry habitats. Addition of fertilizer or water rapidly increased dry weight of the *L. salicaria* plants and greatly improved their ability to compete with *Juncus* plants in Shamsi's (1976) experimental plots. More detailed studies (Shamsi and Whitehead 1977, Edwards *et al.* 1998, D. Bastlová, unpublished manuscript) showed, that the supply of available nutrients influences not only biomass production, but may also change allometric ratios and architecture of *L. salicaria* plants. As shown by Körner (1991), differences in allometry can be very important for final biomass production in plants.

One of the hypotheses about the reasons of more vigorous growth of invasive plants of the same species in new geographical areas is the Evolution of Increased Competitive Ability (EICA) hypothesis (Blossey and Notzöld 1995). According to it, the absence of natural control agents (herbivores, diseases) in a new range of occurrence allows plants of the same species to allocate more biomass to vegetative growth instead of production of secondary chemical compounds. On the other hand, Irwin and Aarssen (1996) and Venecz and Aarssen (1998) showed that plants which are damaged by herbivory, especially when they have lost their growth tip, may produce more total biomass and/or seeds than undamaged plants. Release of lateral meristems from apical dominance may overcompensate losses by herbivory either in the year of damage or in the next year. Irwin and Aarssen (1996) predicted that overcompensation generally should be most common under conditions of intermediate soil fertility.

The wide variety of environmental conditions in both native (Eurasia) and invasive (North America) habitats of *L. salicaria* corresponds to a combination of nutrient and water gradients. These two factors seem to determine the plant growth (in terms of dry matter production and allometric ratios), their competitive ability and architecture (in terms of the strength of apical dominance) (Irwin and Aarssen 1996, Edwards *et al.* 1998). In both areas, some kinds of herbivory are connected with shoot apex removal, e.g. by deer or ducks.

The objective of this study was to determine: (1) how is the growth of selected native and invasive plants influenced by nutrient and water supply, (2) how are both the native and invasive plants able to compensate the loss of shoot apex, and (3) how is their compensatory growth influenced by nutrient and water supply.

## **Material and Methods**

**Species description:** *Lythrum salicaria* L. (Lythraceae) is a perennial herb 30-200cm tall with persistent woody rootstock. Squarish erect stems have evenly spaced nodes with two opposite or in whorl of three 3-10 cm long sessile, lanceolate to ovate leaves in each node (Mal *et al.* 1992). The stem can be without the primary lateral branches but plants usually form branches in lower to mediate part of the stem (Hegi *et al.* 1925). In June to August, plants create a dense terminal spike of purple inflorescences up to 1m long. In the first year, plants form only one main stem, which die at the end of growing season. At the end of growing season, plants create buds forming the basis for next growing season shoots (new root buds) at the top of woody rootstock. In older plants, annual herbaceous shoots each with terminal spike of inflorescences rise from buds on the rootstock to make a wide-topped crown (Thompson *et al.* 1987).

**Experimental design and plants handling:** For the experiment, seeds of *L. salicaria* populations originating from climatically similar conditions in both native and invasive range of species occurrence were used. USA locality is located at the southern tip of Lake Michigan (41° 50' N, 87° 00' W), in center of north-south range of species invasive occurrence in North America (for detailed description see Edwards *et al.* 1995). The Czech site is located in southwestern part of České Budějovice town (49° 00' N, 14° 28' E). The seeds of native plants for the experiment were collected along the drainage stream with fluctuating water level, where *L. salicaria* grew at slightly disturbed sites.

The seeds of both the native and the invasive populations were sown on garden soil contained in plastic saucers (each population in a separate saucer) at the beginning of April 1997. Young plants with one pair of true leaves were selected for uniformity of size one and half month later (on May 18, 1997) transplanted into 5 l pots (24 cm tall) filled with sand, one plant per pot. Totally 256 pots with transplanted plants were placed in 16 containers (10 cm deep) with water in a greenhouse. Each container contained 16 plants - eight native and eight invasive.

One week later, these 16 containers were assigned to 16 treatments – four nutrient concentrations in combination with two water levels in combination with two decapitation treatments.

For addition of nutrients, commercial fertilizer Floran (N:P:K 14:20:20 + microelements, Druchema, Praha, Czech Republic) was used. Once a week, containers were filled with fertilizer solution of the respective concentration (see below). In the meantime, water was added according to the water treatment. Water level treatments consisted of either permanent or fluctuating water level. In the first treatment, water level was maintained at the top of the containers (+10 cm), -14cm below the soil surface respectively. In the other treatment, water level in the containers fluctuated with the range of 0 to + 10 cm, -14 to -24cm below the soil surface respectively. In this treatment, the containers were first filled with water up to the top, and then the water level was allowed to sink to 0 cm; then the containers were filled up to the top again. For the decapitation treatment, four plants of invasive and four of native populations were randomly selected in each container on June 18, 1997. The average number of internodes was five to six (10-12 leaves) at this time. The shoot apex was cut above the third node measured from the basis of plant. The rest of the plants remained intact. The 16 treatments thus were: no nutrients ( $0 \text{ g.dm}^{-3}$ ),  $0.25 \text{ g.dm}^{-3}$  of nutrients,  $1 \text{ g.dm}^{-3}$  of nutrients and  $4 \text{ g.dm}^{-3}$  of nutrients, each with either permanent (+10cm) or fluctuating water level and with either decapitated or intact plants. Each of 16 treatments consisted of two replicates.

The onset of flowering was recorded successively at weekly intervals during the corresponding period of the growing season in all plants. A plant was recorded as flowering when the first flower buds opened. The experiment was finished at the end of August when the first leaves on the plants fell off. The plant height was recorded for all plants. In non-decapitated plants, the numbers of primary lateral branches and flowering primary lateral branches and the numbers of internodes below the inflorescence, if present, were additionally counted. Afterwards, sand was washed out of the plant roots. On the roots, the number of new root buds forming the basis for next growing season's shoots was counted. The aboveground plant parts were divided into vegetative ones, i. e. main stem and lateral branches, both with leaves, but without inflorescences, and reproductive parts, i.e., inflorescence on both main stem and lateral branches. All samples were then oven-dried at  $72 \text{ }^\circ\text{C}$  for 24 hours and weighed to the accuracy of 0.01 g. Root to shoot (R/S) ratio was defined as dry weight of roots/dry weight of aboveground plant mass. Reproductive effort (RE) was estimated as the ratio of dry weight of reproductive parts to total plant dry weight (Abrahamson and Gadgil 1973).

**Statistical analysis.** Differences in dry matter production between native and invasive plants were analyzed by generalized linear models (GLM) (McCullagh and Nelder 1989) using the S-PLUS software package (Statistical Sciences 1995 a, b). Significance levels in all multiple comparisons were adjusted using Bonferroni correction (Holm 1979).

## Results

### Response to differences in water supply

Water supply did not affect significantly ( $P > 0.05$ ) any of the growth characteristics, except for the number of new root buds formed in native decapitated plants. Fluctuating water level influenced positively the number of new root buds in decapitated native plants at 1  $\text{g}\cdot\text{dm}^{-3}$  nutrient level (Fig. 1) in comparison to the same nutrient treatments in permanent water level. In decapitated invasive plants, the numbers of new root buds were similar at both fluctuating and permanent water levels in respective nutrient concentration treatments. Within 0, 0.25 and 1  $\text{g}\cdot\text{dm}^{-3}$  nutrient concentration treatments, the invasive plants formed more new root buds than the native plants in both fluctuating and permanent water level. The only exception was the similar number of new root buds formed by both the native and the invasive plants at fluctuating water at 1  $\text{g}\cdot\text{dm}^{-3}$  of nutrients.

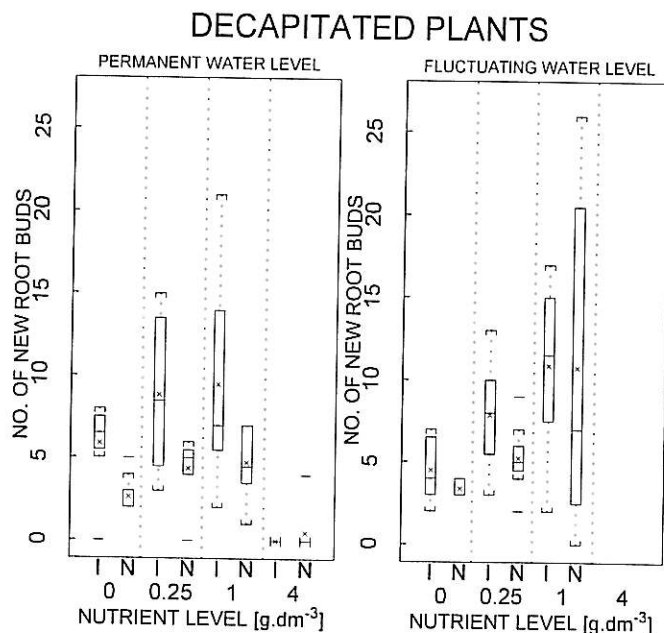


Fig. 1. Box and Whisker plot of the number of new root buds formed by decapitated native (N) and invasive (I) plants growing at permanent or fluctuating water level. The other growth characteristics were not significantly affected ( $P < 0.05$ ) by water supply and therefore are not presented. Graphs show the upper and lower quartile (box size), mean values (x), median (black stripe inside the box), upper and lower extreme - nearest values not beyond a standard span (1.5x inter quartile range) from the quartiles (whiskers) and outliers (black lines beyond whiskers) (Hoaglin *et al.* 1983).



Response to nutrient supply in intact plants

Nutrient supply affected significantly all measured plant growth characteristics in both the native and the invasive plants ( $P < 0.001$ ) (Fig. 2., Tab. 1)

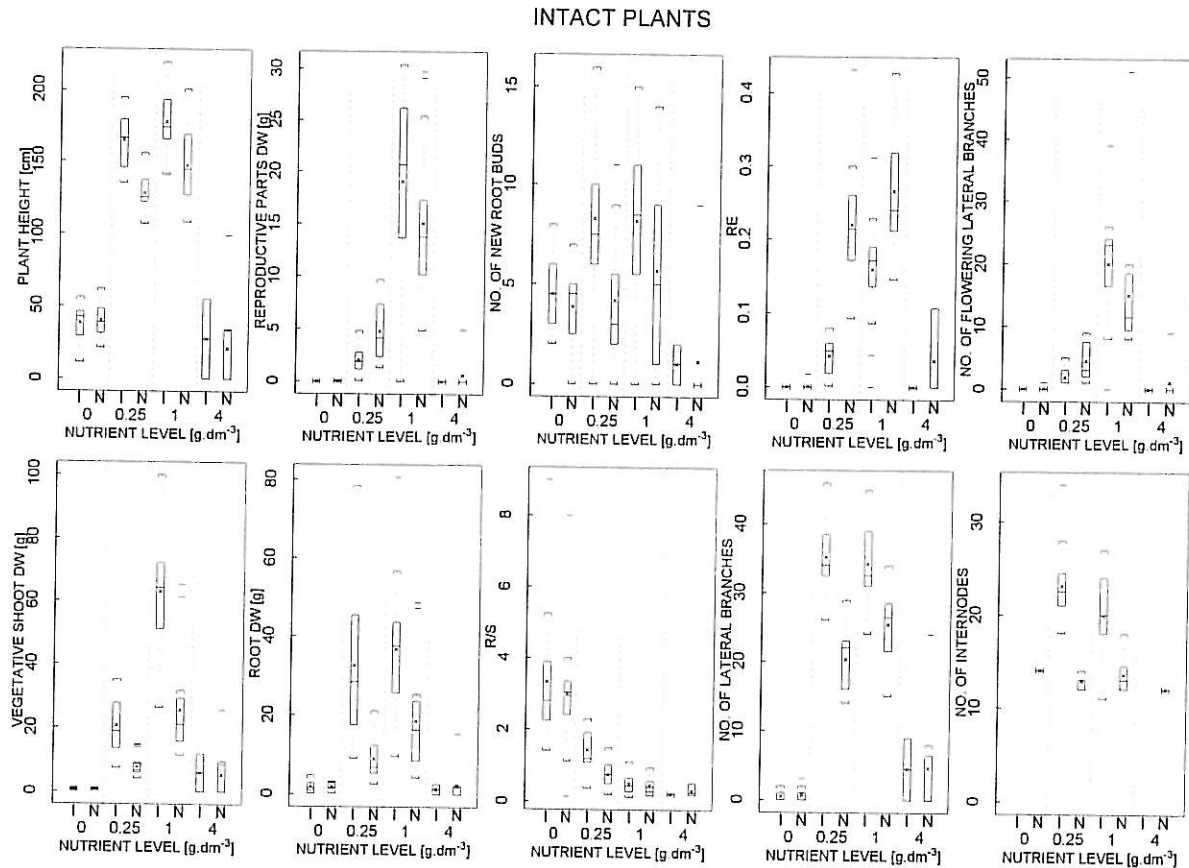


Fig. 2. Box and Whisker plots of measured growth characteristics in intact native (N) and invasive (I) plants at different nutrient supply. (For explanation of the graphs see Fig. 1.)

Without added nutrients ( $0 \text{ g.dm}^{-3}$ ), no difference was found between the native and the invasive plants. These plants were the shortest ones and had the lowest vegetative shoot and root dry weight, formed only few primary lateral branches (2.3 on average) and did not flower (with one exception) until the end of experiment. Root to shoot ratio was highest in these plants (3.7 on average) and was similar in both the native and the invasive plants.

Plants supplied with  $0.25$  and  $1 \text{ g.dm}^{-3}$  of nutrients had similar height, root dry weight, number of primary lateral branches, internodes and new root buds formed, and started to flower at much the same time. On the other hand, reproductive dry weight, vegetative shoot dry weight, R/S ratio and the number of flowering primary lateral branches showed higher values at the  $1 \text{ g.dm}^{-3}$  nutrient concentration in both the native and the invasive plants. The

most apparent increase between 0.25 and 1 g.dm<sup>-3</sup> nutrient treatments was recorded in reproductive dry weight in both the native and the invasive plants. In the invasive plants, the reproductive dry weight of plants growing at 0.25 g.dm<sup>-3</sup> was only 11% of reproductive dry weight of plants growing at nutrient concentration 1 g.dm<sup>-3</sup>. In the native plants, the plants growing at 0.25 g.dm<sup>-3</sup> produced 32 % of the reproductive dry weight in comparison with plants from 1 g.dm<sup>-3</sup> nutrient supply. Within both nutrient levels, the invasive plants grew taller, had a significantly higher vegetative shoot as well as root dry weight, produced more new root buds and primary lateral branches and flowered two to three weeks later than the corresponding native plants. On the contrary, reproductive effort (RE) was smaller in the invasive plants than in the native plants at both nutrient levels while the dry weight of their reproductive parts was lower at the 0.25 g.dm<sup>-3</sup> and higher at 1 g.dm<sup>-3</sup> nutrient concentration.

Table 1. Weeks from transplantation of plants to start of flowering ± SE in the native and the invasive plants of *Lythrum salicaria* at different nutrient supply. Water supply did not influence flowering in either native or invasive plants and its impact is not presented. No data are presented for intact invasive plants because of their high mortality during the experiment.

		nutrient concentration [g.dm <sup>-3</sup> ]			
		0	0.25	1	4
<b>native plants</b>	intact	16.6 ± 1.8	9.1 ± 0.9	9.5 ± 0.8	9.3 ± 0.6
	decapitated	not flowered	11.0 ± 0.6	11.9 ± 2.7	12.0 ± 3.5
<b>invasive plants</b>	intact	not flowered	12.6 ± 1.2	11.6 ± 1.7	-
	decapitated	not flowered	15.6 ± 1.8	14.6 ± 2.2	13.0 ± 5.7

At 4 g.dm<sup>-3</sup>, both the native and the invasive plants were short with very low both reproductive and vegetative shoot as well as root dry weight. Also, the numbers of internodes, primary lateral branches and new root buds were low. These plants flowered the latest of all plants cultivated in the experiment and exhibited the lowest reproductive effort and R/S ratio. No differences in growth characteristics were found between the native and the invasive plants within the 4 g.dm<sup>-3</sup> nutrient level. A great number of both the native and the invasive plants died in this treatment during the experiment. Five weeks after transplantation, necrosis appeared on distal ends of the plants' leaves. Death of the affected plants usually followed.

#### *Response to nutrient supply in decapitated plants*

Both the native and the invasive plants formed new shoots after decapitation. But the height of these shoots was only about 70 % of the intact plants shoots in two intermediate nutrient



treatments in both the native and the invasive plants. In some cases, the plant height decreased even more: in the native plants at 0 g.dm<sup>-3</sup> the plant height decreased to 45 % of intact plants height and in the invasive plants at 4 g.dm<sup>-3</sup> to 16 % of intact plants. Similar influence of decapitation was observed also in vegetative dry matter production in both the native and the invasive plants. Relatively less affected was the vegetative dry weight production in the invasive plants at 0 g.dm<sup>-3</sup>. In these plants, the vegetative dry weight decreased to only 95% of intact plants vegetative dry weight. Reproductive dry weight was affected the strongest of all plant characteristics. In the invasive plants, the dry weight of inflorescences in plants growing at 0.25 g.dm<sup>-3</sup> and 1g.dm<sup>-3</sup> decreased to 24 % and 21 %, respectively, in comparison with intact plants subjected to the same nutrient supply. In native plants, the reproductive dry weight decreased to 48 % and 37%, respectively after decapitation. Root dry weight, R/S ratio and the number of new root buds formed were not significantly affected by decapitation (P>0.05). Decapitation also delayed the flowering time in both the native and the invasive plants. In the 4 g.dm<sup>-3</sup> nutrient level treatment, decapitated plants of the invasive population suffered higher mortality than the native plants.

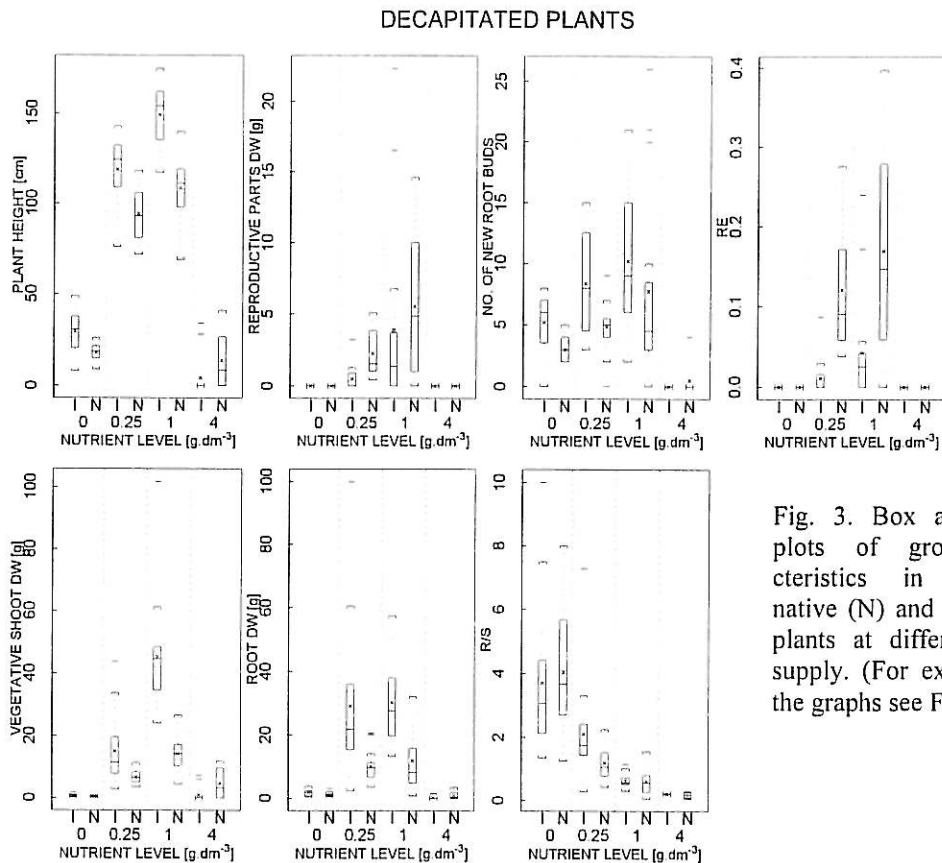


Fig. 3. Box and Whisker plots of growth characteristics in decapitated native (N) and invasive (I) plants at different nutrient supply. (For explanation of the graphs see Fig. 1.)

The differences between nutrient concentration treatments and between the native and the invasive decapitated plants within the treatments followed those in non-decapitated plants (Fig. 3, Tab. 1).

Plants grown at 0 and 4 g.dm<sup>-3</sup> were shorter and had lower vegetative and reproductive shoot as well as root dry weight than plants at the 0.25 g.dm<sup>-3</sup> and 1 g.dm<sup>-3</sup> nutrient concentrations. Decapitated plants grown at 0 g.dm<sup>-3</sup> had the highest R/S ratio and did not flower until the end of the experiment. Plants in the 4 g.dm<sup>-3</sup> nutrient concentration treatment flowered later and showed a smaller reproductive effort than plants in the other two nutrient treatments. Both native and invasive plants growing at 1 g.dm<sup>-3</sup> were the tallest, had the highest both reproductive and vegetative shoot dry weight, and formed the highest number of new root buds. In the 0.25 g.dm<sup>-3</sup> and 1 g.dm<sup>-3</sup> nutrient levels, the invasive plants had higher values than the native ones of all recorded growth characteristics, except for the dry weight of reproductive parts and RE.

## **Discussion**

Although all plants in the experiment were of the same species, and the seeds of the studied populations originated from geographical areas with similar average annual rainfall and temperature (Edwards *et al.* 1998), apparent differences were recorded in the plants' responses to nutrient supply and to decapitation. Overall, intact invasive plants tended to grow taller and more vigorously, producing more both above and belowground dry weight under a wide range of experimental conditions. Additionally, the invasive plants produced more new root buds than the native plants at both permanent and fluctuating water level, thus indicating a higher growth potential for the next growing season.

### *Influence of water supply*

Similar as in the present experiment, also Stevens *et al.* (1997) reported no significant influence of high water level on the dry weight of either shoots or roots, or that of whole plants in *L. salicaria*. Total fresh/dry weight ratio, stem diameter and stem porosity were the only characteristics influenced by water level in their experiment. Changes in these characteristics were connected with aerenchyma production in the flooded plants, what did not happen in our experiment because of relatively low water level in permanent water level treatment. As *L. salicaria* is a wetland plant species (Hejný 1960), negative influence of

fluctuating water level connected with occasionally dry soil conditions could be also expected. Nevertheless, the results of the present experiment showed that neither permanent nor fluctuating water levels stressed *L. salicaria* plants. Additionally, a positive response was observed in one case what indicates that under specific conditions (fluctuating water level and slightly higher nutrient concentration), decapitated native plants can increase the number of their shoots in the subsequent growing season.

#### *Growth of intact plants*

The results of this experimental study are partly in agreement with those of earlier studies reporting on a taller stature and higher aboveground net production in invasive plants of *L. salicaria* in comparison with native ones (Blossey and Kamil 1996, Edwards *et al.* 1998). Such differences were found in two intermediate nutrient levels; with lack of nutrients, or at their extremely high concentration, differences between the native and the invasive plants disappear. In two intermediate nutrient levels, vegetative dry weight increased more with increasing nutrient level in the invasive plants than it did in the native plants. Simultaneously, neither plant height nor the number of primary lateral branches increased in invasive plants. Apparent increase in vegetative dry weight in the invasive plants may be thus attributed to the increase in thickness of the main stem and more vigorous growth of lateral branches at higher nutrient supply ( $1 \text{ g.dm}^{-3}$ ). Additionally, similar root dry weight in two intermediate nutrient treatments shows that root growth was relatively less affected by lower nutrient concentration in the invasive than in the native plants. This is indicative of a higher belowground competitive ability of these plants at poor nutrient supply.

This study has confirmed the previously reported differences in the timing of flowering between the native and the invasive plants of *L. salicaria* (Blossey and Kamil 1996, Edwards *et al.* 1998). Shamsi and Whitehead (1977) considered daylength as the most important factor for flower induction in *Lythrum salicaria*. Developmental differences thus resulting from selection with respect to photoperiodic response (Oneil 1999, Weber and Schmid 1998, Peacock and McMillan 1968), or to other ecological factors, are probably genetically based (Hickman 1975, 1977, Waite and Hutching 1982). Edwards *et al.* (1995, 1999) stressed the similarity of climatic conditions (temperature, rainfall) in both areas of origin of the *L. salicaria* seeds used also in the present experiment. In this context and with respect to the differences in latitude between the original Central European and North American sites, the importance of daylength is prominent.

Reproductive dry weight was affected by nutrient supply in both the native and the invasive

plants, but the invasive plants responded more strongly to increased nutrient supply than the native plants. While in the native plants reproductive dry weight increased three times between the treatments 0.25 and 1 g.dm<sup>-3</sup>, almost ten times higher reproductive dry weight was recorded in the invasive plants at 1 g.dm<sup>-3</sup> than at 0.25 g.dm<sup>-3</sup>. Increase in reproductive dry weight corresponded to an increase in the number of flowering lateral branches without any apparent increase in the total number of lateral branches. Correlation between nutrient supply, vigour of lateral branches and inflorescence size on these branches seems to be stronger in the invasive plants than in the native ones.

In some plant species, more vigorous growth resulted in a higher reproductive effort (Waite and Hutching 1982). In the present study, higher reproductive effort in the native plants may be influenced by later flowering of the invasive plants. At the time all the native plants had finished their flowering and started to produce capsules, the invasive plants were still flowering.

#### *Plant responses to decapitation*

Decapitation of plants served as a simulation of losses by herbivory and as a test of the ability of both the native and the invasive plants to compensate these losses. No overcompensation was observed in the present experiment, although positive reaction of the native plants to fluctuating water level at nutrient concentration 1 g.dm<sup>-3</sup> could indicate overcompensation in these plants in the subsequent year. Results of our experiment showed that both the water and nutrient supply as well as plant origin plays an important role in the ability to regenerate after decapitation. The invasive plants responded to decapitation more dramatically than the native plants in reproductive dry weight production under intermediate nutrient concentrations. On the other hand, under absence of nutrients added, the reduction of plant height, vegetative shoot and root dry weight was less outstanding in the invasive than in the native plants. In other growth characteristics and nutrient concentration treatments, the reaction to decapitation did not differ between the native and the invasive plants, except for the higher mortality of decapitated invasive plants at the highest nutrient level.

Although no significant difference in the number of new root buds and root dry weight was recorded between decapitated and intact plants (except for decapitated native plants at fluctuating water level at 1 g.dm<sup>-3</sup>), their slightly higher values recorded at most of the nutrient treatments in decapitated in comparison with intact plants indicate that both the native and the invasive plants have a high potential to compensate their losses and regenerate shoots in the year following damage to their apical meristems, (mostly) by herbivores. This potential

for regeneration is similar at a wide variety of experimental conditions in the invasive plants, but is limited to some of them in the native plants. While the invasive plants formed similar numbers of new root buds in both 0.25 g.dm<sup>-3</sup> and 1 g.dm<sup>-3</sup> nutrient treatments in permanent and fluctuating water level treatments, apparent positive response of the native plants to increasing nutrient supply was observed at fluctuating water level at 1 g.dm<sup>-3</sup> nutrient level only. We can thus assume that nutrient shortage and permanent water level would influence the number of shoots in the subsequent year more negatively in the decapitated native plants than in the decapitated invasive plants.

Although our results are restricted to one native and one invasive populations of *L. salicaria* and more data would better allow generalization, we can conclude our results as follows: higher competitive ability of invasive *L. salicaria* plants could ensure from their higher tolerance to less favorable environmental conditions and from very strong reaction to increasing nutrient concentrations. The shoot height, root dry weight and number of new root buds giving rise to next growing season's shoots were only slightly affected by low levels of nutrient supply or by permanent water level. Increasing nutrient supply affects the vigour of lateral branches, and subsequently, by increasing the number of flowering branches significantly increased the reproductive potential of these plants. No overcompensation was observed in either native or invasive plants, although the ability to produce inflorescences after the loss of shoot apex seems to be higher in native plants.

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## Chapter 4

**Differences in dry weight partitioning and flowering phenology between native and non-native plants of purple loosestrife (*Lythrum salicaria* L.): an experimental study.**

**Differences in dry weight partitioning and flowering phenology between native and non-native plants of purple loosestrife (*Lythrum salicaria* L.): an experimental study.**

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**Abstract**

Invasive plants of *Lythrum salicaria* (purple loosestrife), a species native to Eurasia, exhibit different ecological strategies to indigenous plants by growing more vigorously. In our study, we tested the hypothesis that more vigorous growth of invasive plants of *Lythrum salicaria* is a result of differences in dry weight partitioning between the native and the non-native plants. Plants of three native Central European and three non-native North American populations of *L. salicaria* were cultivated in the greenhouse. All plants were exposed to the same solar irradiance, temperature and nutrient supply. Differences in total dry weight and height of the plants, dry weight of their roots, stems, leaves and reproductive parts, dry weight and the numbers of all primary lateral branches and number of internodes and onset of flowering between native and non-native plants were tested. Relative growth rate, reproductive effort and leaf weight ratio were calculated from obtained characteristics. The dependence of net photosynthesis on photon flux density in both native and non-native plants of *L. salicaria* was measured. Plants of the non-native populations grew significantly taller than the native plants and produced, on average, twice as much dry weight of stems, leaves and primary lateral branches as plants of native populations. The native and non-native plants exhibited different dry weight partitioning patterns, connected with differences in flowering phenology. Non-native plants exhibited a morphological strategy facilitating their successful competition in plant communities. The differences in growth pattern between native and non-native plants are probably genetically based.

*Key words:* biological invasion, dry matter allocation, growth strategy, growth analysis, plasticity

## **Introduction**

*Lythrum salicaria* L. is a herbaceous perennial species native to Eurasia. This species was introduced to the east shore of North America at the beginning of 19<sup>th</sup> century and has spread westward since the end of 19<sup>th</sup> century (Thompson, Stuckey & Thompson 1987). Nowadays, it causes serious ecological and economic problems in wetland communities in many regions of Canada and the United States (Thompson, Stuckey & Thompson 1987) by forming dense dominant stands.

Some earlier papers (e.g. Blossey & Kamil 1996; Edwards 1996; Edwards, Květ & Adams 1998) indicate differences in ecological strategies between native and non-native plants of *L. salicaria*. Blossey & Kamil (1996) found, in a garden herbivory experiment, taller stature and lower reproductive effort in non-native populations of *L. salicaria* from America and Australia in comparison with native European populations. Edwards (1996) used the terms C-strategist for non-native plants and R-strategist for native ones in his field studies comparing the biomass production and reproductive effort in native and non-native populations in North America and Central Europe. He described more vigorous stature and higher aboveground biomass production, in North American non-native populations in comparison with native European populations from South Bohemia, Czech Republic.

According to the EICA (Evolution of Increased Competitive Ability) hypothesis (Blossey & Notzöld 1995), the lack of natural herbivory agents allows more vigorous and successful growth of non-native plants in new geographical areas. Absence of herbivory allows non-native plants to allocate more biomass to vegetative structures instead of defensive chemicals produced by native plants in their original area of distribution. This feature results in higher competitive ability of non-native plants and their successful spreading in new (secondary) geographical areas. Although Willis, Thomas & Lawton (1999) found a significantly higher content of phenolics in leaves of native genotypes of *L. salicaria*, their herbivore bioassay revealed no significant intra-specific variation in herbivore resistance between native and non-native plants. In another experimental study (K. R. Edwards, unpublished manuscript), no significant preference was found to either native or invasive *L. salicaria* genotypes by herbivores in the primary area. The EICA hypothesis was thus not confirmed as an explanation of the taller stature and higher biomass production of non-native *L. salicaria* plants.

Another reason for higher biomass production of invasive plants could be a positive influence of environmental factors (e.g. higher nutrient status in soil, higher temperatures) on plant growth in the new geographical area. Edwards, Květ & Adams (1999) and Bastlová-Hanzélyová (2001) compared the climatic and edaphic conditions and site and community relationships in invasive area of distribution in midwest USA, where aggressive behaviour of *L. salicaria* has been described and in its native area in South Bohemia. No relevant difference was found between either stand or climatic conditions, except for slightly higher occurrence of invasive plants on sites with a high water table in the USA than in central Europe.

Daylength plays a key role in plant development, often acting through changes in dry weight partitioning (e.g. Aung & Austin 1971; Mooney 1972; King 1991; Pigliucci & Schlichting 1995). Weber & Schmid (1998) showed differences in dry matter allocation in 24 populations of two *Solidago* species connected with shift in phenology of the plants. The populations originated from different latitudes and thus from sites with different daylength regimes. Many similar studies have shown the plasticity and variation in growth responses (including changes in dry weight partitioning) of *L. salicaria* plants to different photoperiod regimes (e.g. Ray & Alexander 1966; Kigel & Koller 1970; Aung & Austin 1971; Pigliucci & Schlichting 1995, 1996).

Dry weight partitioning is a major determinant of overall dry matter production in plants (Körner & Menendez-Riedl 1989; Körner 1991). Körner (1991) demonstrated, that plants with the same CO<sub>2</sub> assimilation rate can differ enormously in their net biomass production due only to differences in dry weight partitioning ratios or plant characteristics like leaf weight ratio or specific leaf area.

Similar climatic conditions occur at more southern latitude in the secondary range of occurrence than in the primary ones (Edwards *et al.* 1998), it is therefore highly probable that differences in photoperiod regimes between these two areas will play an important role in the development and growth (including biomass allocation pattern) of *L. salicaria* plants. In this paper, we test the hypothesis that the more vigorous growth of invasive plants is due to differences in dry weight partitioning between native and non-native plants of *Lythrum salicaria*.

## Materials and Methods

The seeds of *L. salicaria* plants from three different sites in the Czech Republic (locations Branna, Mlaka and Vlkov) and from three sites in the USA (locations Long Lake, Ogden Dunes and Tolleston Dunes) were used for this experimental study. All the Czech sites are situated in the Třeboň Basin Biosphere Reserve (around Třeboň town 49°N, 15°E, South Bohemia, Czech Republic). The USA locations are part of the Indiana Dunes National Lakeshore (42°N, 87°W, Indiana, USA). Both areas have similar climatic and edaphic conditions (Edwards, Květ & Adams 1999). The sites for seed collection were selected to cover the variability of conditions (nutrients and water), under which *L. salicaria* plants grow either in native or invasive areas. The three selected native sites represent: 1) Mlaka - eutrophicated village pond, where *L. salicaria* grew in water about 30 cm deep, 2) Branna - abandoned extracted drained peat bog, and 3) Vlkov - abandoned sand pit with fluctuating water level. The three non-native sites, selected in respect to similarity with the native ones, represent: 1) Long Lake - a shoreline site with deep water and organic soil, 2) Ogden Dunes - site intermediate in nutrients and soil water content, and 3) Tolleston Dunes - abandoned sand pit with fluctuating water level. The collected samples were dried at room temperature and the seeds were then shaken out from the capsules, cleaned and kept dry in plastic vials stored in the refrigerator at 4°C during the winter.

A greenhouse experiment was carried out at the University of Wisconsin, Madison, USA (43° 04'N 89° 24' W). At the end of April, the seeds of all six populations of *L. salicaria* were sown on soil contained in plastic saucers (each population in one saucer). Young plants with one pair of true leaves were selected for uniformity of size and transplanted into 4 l pots filled with a mixture of sand (2/3) and field soil (1/3) - one plant per pot, on June 3, 1998. The pots were kept permanently moist in the greenhouse. The greenhouse conditions were not regulated, except for air ventilation during summer. The plants were fertilized once weekly with a nutrient solution (commercial fertilizer Peterson Professional diluted to the nitrogen concentration of 200 mg.l<sup>-1</sup> N (N:P:K weight ratio in fertilizer 1:1:1)). Each plant obtained the same amount of nutrient solution.

Six randomly selected plants of each population were sampled at ten-day intervals starting from July 2. The experiment was finished at the end of August, when the first leaves started to fall off. In order to describe the growth of both native and non-native plants, the shoot height, number of internodes below the inflorescence, and the total number of primary

lateral branches (growing directly from the main stem) were recorded for each plant sampled. Afterwards, the plants were divided into roots, stems and lateral branches (without leaves and inflorescences), leaves and reproductive parts (inflorescence on main shoot + inflorescences on lateral shoots + flower-bearing part of stem). These samples were then dried in the oven at 72 °C for 24 hours. The dried samples were weighed to the accuracy of 0.001 g.

The onset of flowering was recorded successively at daily intervals during the growing season. A plant was recorded as flowering when the first flower buds opened.

Leaf area was recorded once in the growing season. In each population studied, the leaves of six selected plants (those used in growth analysis) were scanned (scanner Astra 2000, Umax, resolution 600dpi) and their area and afterwards dry weight were determined. The leaf area values obtained were used for calculating the specific leaf area (leaf area/leaf dry weight) and leaf area ratio (leaf area/total plant dry weight). Leaf weight ratio (leaf/total plant dry weight) was calculated successively during the whole growing period. (Květ *et al.* 1971; Hunt 1982).

Reproductive effort (RE) was determined as the ratio of dry weight of reproductive parts of a plant to total plant dry weight (Abrahamson & Gadgil 1973). Relative growth rate (RGR) was calculated from the obtained morphological plant characteristics using the equation:

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{T_2 - T_1} \quad (\text{Květ } et al. \text{ 1971; Hunt 1978})$$

The rate of net photosynthetic CO<sub>2</sub> uptake was measured once in the growing season. Four plants of each population were randomly selected. On each plant, the ninth pair of leaves below the inflorescence was marked and used for the measurements. This pair of leaves is sufficiently large for a measurement and is not influenced by shade of other plant leaves. Dependence of CO<sub>2</sub> assimilation rate on PhAR irradiance was measured with a portable IRGA instrumentation LI-6200 (LI-COR, Inc., Lincoln, Nebraska, USA). The response of CO<sub>2</sub> assimilation rate per unit leaf area to the gradients of photon flux density of 1.5, 10, 50, 100, 200, 500, 1000, 1500 and 1740 μmol m<sup>-2</sup> s<sup>-1</sup> was recorded for each selected plant.

The resulting curves showing time changes of the recorded characteristics were smoothed by a robust scatterplot smoother (function lowess with  $f = 2/3$  (fraction of data smoothed at each point) which uses locally linear fits) using the S-PLUS software package (Statistical Sciences 1995a,b). Curves for subsequent tests were fitted using generalized linear models (GLM) (McCullagh and Nelder 1989) using the S-PLUS software package. Differences between curves for native and non-native plants were considered as significant if



an addition of interaction between origin and time significantly improved GLM model of dependence of particular *L. salicaria* growth characteristics on time. Differences in curves within native and non-native populations were considered as significant if an addition of interaction between population and time significantly improved previously mentioned GLM model of dependence of particular *L. salicaria* growth characteristics on time and interaction between origin and time. GLM was used also for hierarchical analysis showing differences and partitioning of variation for final sampling between plants of native and non-native origins and within non-native and native populations and to analyse differences in dry weight partitioning between native and non-native plants. Significance of particular models was tested using F-test (Zar 1984; Sokal & Rohlf 1995). Significance levels in all multiple comparisons were adjusted using Bonferroni correction (Holm 1979).

Models for RGR, LWR and RE were fitted without observations after curves break (last sampling interval omitted for RGR and two last sampling dates omitted for LWR and RE) caused by unusual plant development in the greenhouse at the end of the growing season (for details see results). Models for RGR and LWR didn't include differences between populations within origin because of insufficient number of "observations" for model formation for these calculated characteristics.

## **Results**

### PLANT DRY WEIGHT

Significant differences ( $P < 0,05$ ) were found in both time courses and most of the measured plant characteristics between native and non-native plants (Table 1). The between populations differences within the either native or invasive group of plants were found in number of internodes and dry weight of reproductive parts.

Non-native plants were significantly ( $P < 0,001$ ) taller, had more internodes and lateral branches and greater total plant dry weight, as well as that of leaves, roots, branches and shoots, than the native plants, starting from the first weeks of cultivation (Fig. 1a-h).

Dry weight of reproductive parts was significantly different ( $P < 0,001$ ) between the native and non-native plants at the end of the experiment. During the growing season, dry weight of reproductive parts was greater in the native plants during the first 60-70 days of cultivation (Fig. 1i). The non-native plants had greater dry weight of reproductive parts starting from the 70<sup>th</sup> day of experiment and this difference increased until the end of the experiment.



**Table 1.** Differences in time courses and final values (tested at the end of the experiment) of plant growth characteristics tested between the native and non-native plants (influence of origin) and between populations within the origin. (dw = dry weight, NS = not significant, \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001)

plant characteristic	time courses			end of the experiment		
	df	F	P	F	P	explained variability
<b>height</b>						
origin	1	14,74	***	19,16	***	34%
population within the origin	4	0,93	NS	1,81	NS	13%
<b>total plant dw</b>						
origin	1	16,19	***	39,08	***	52%
population within the origin	4	0,49	NS	0,61	NS	3%
<b>no. of internodes</b>						
origin	1	185,89	***	120,48	***	75%
population within the origin	4	8,81	***	3,86	*	10%
<b>leaf dw</b>						
origin	1	31,44	***	25,55	***	43%
population within the origin	4	0,44	NS	0,84	NS	6%
<b>dw of lateral branches</b>						
origin	1	14,62	***	37,45	***	48%
population within the origin	4	0,46	NS	1,31	NS	7%
<b>shoot dw</b>						
origin	1	57,32	***	58,63	***	63%
population within the origin	4	1,31	NS	1,16	NS	5%
<b>no. of lateral branches</b>						
origin	1	36,71	***	10,28	**	27%
population within the origin	4	4,58	**	0,79	NS	8%
<b>root dw</b>						
origin	1	6,96	**	23,17	***	37%
population within the origin	4	0,85	NS	1,72	NS	11%
<b>dw of reproductive parts</b>						
origin	1	0,13	NS	14,36	***	25%
population within the origin	4	0,33	NS	3,44	*	24%
<b>RGR</b>						
origin	1	4,17	NS	10,01	*	71%
population within the origin	4	0,24	NS	-	-	-
<b>LWR</b>						
origin	1	6,16	*	54,21	**	93%
population within the origin	4	0,12	NS	-	-	-
<b>RE</b>						
origin	1	213,45	***	170,78	***	79%
population within the origin	4	2,93	*	3,72	*	7%

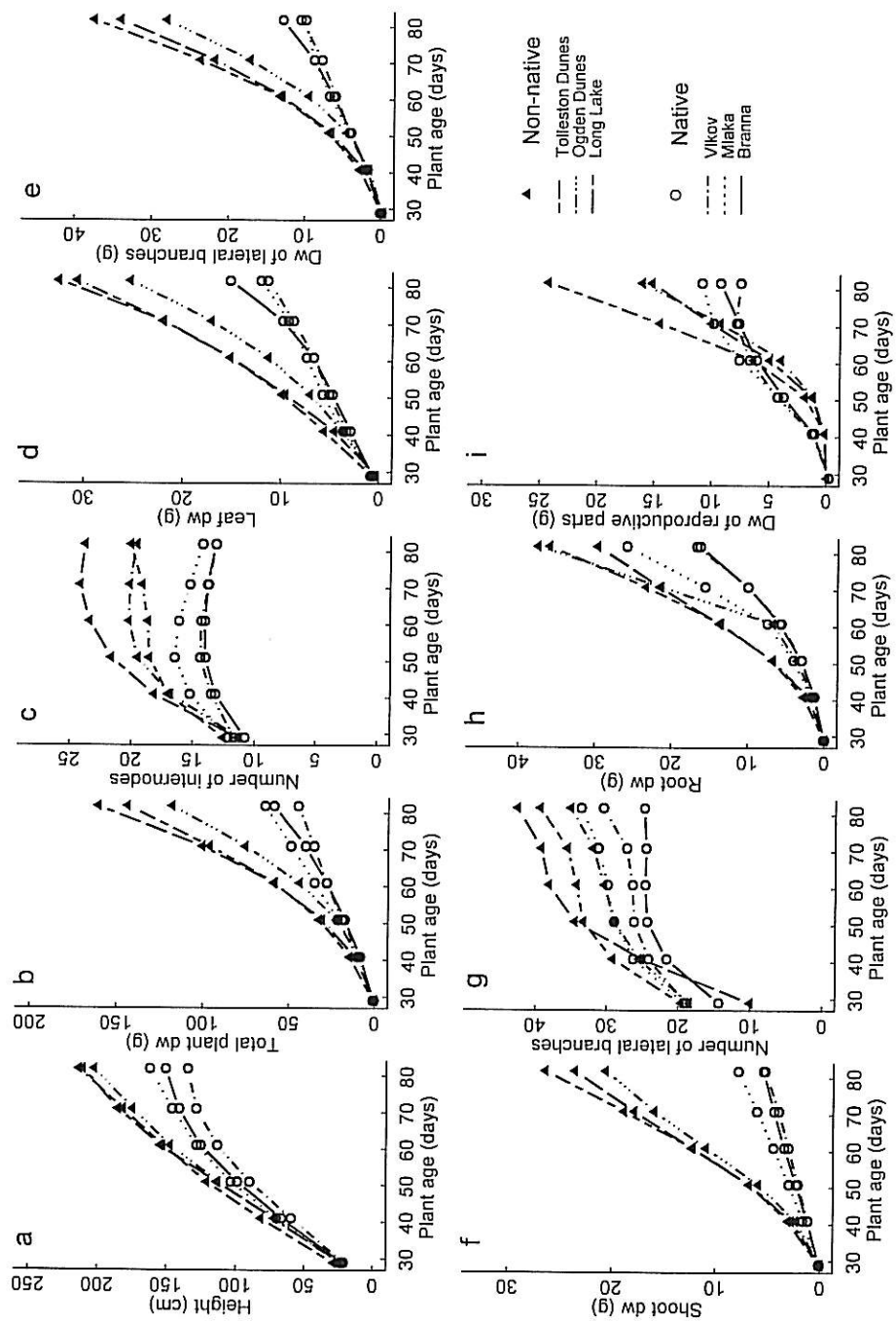


Figure 1. Time courses of basic life history plant characteristics in native and non-native plants of *Lythrum salicaria*. The characteristics were measured at ten-day intervals starting from July 1. Differences between the curves are summarized in tab 1. (dw = dry weight).

CALCULATED GROWTH CHARACTERISTICS

Time courses of relative growth rate (RGR) (Fig. 2a, Tab 1.) were similar in both native and non-native plants. A significant difference ( $P < 0,05$ ) was found between the 61<sup>st</sup> and 71<sup>st</sup> day of the experiment (before the curve break), when the non-native plants had a higher RGR. RGR decreased with time less steeply in the non-native populations of *L. salicaria* than in the native ones. In all populations RGR increased slightly at the end of the experiment probably as a results of new lateral branches emergence. The same is apparent also on time courses showing LWR. Emergence of new lateral branches at the end of the growing season is rather unusual in this species and is caused probably by stopping of capsules and seeds development and renewal of growth in the greenhouse conditions.

In the middle of August, the non-native plants had a significantly larger leaf area and smaller specific leaf area (SLA). Leaf area ratio (LAR) was similar in the native and the non-native plants (Tab.2).

**Table 2.** Leaf area, specific leaf area and leaf area ratio in native and non-native plants of *Lythrum salicaria*, on August 13. Average values (n=18) and standard errors of mean are shown for both native and non-native plants. (NS non significant, \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ )

	Leaf area (cm <sup>2</sup> )	Specific leaf area (cm <sup>2</sup> . g <sup>-1</sup> )	Leaf area ratio (cm <sup>2</sup> . g <sup>-1</sup> )
	***	**	NS
Native plants	3149 ± 256	385 ± 32	80 ± 5
Non-native plants	5301 ± 283	283 ± 19	68 ± 6

Leaf weight ratio (LWR) was lower in non-native plants than in the native ones at the start of the experiment, but became higher in the middle. At the end of the experiment, LWR was similar in both the native and the non-native plants (Fig. 2b).

Reproductive effort (RE) was significantly greater ( $P < 0,001$ ) in the native plants for most of the time of cultivation (Fig. 2c), but was similar at the end of the experiment. Native plants reached the highest values of RE within 60 days of cultivation, but afterwards RE was decreasing. In the non-native plants, RE kept increasing until the end of the experiment, and reached the highest values at its end.

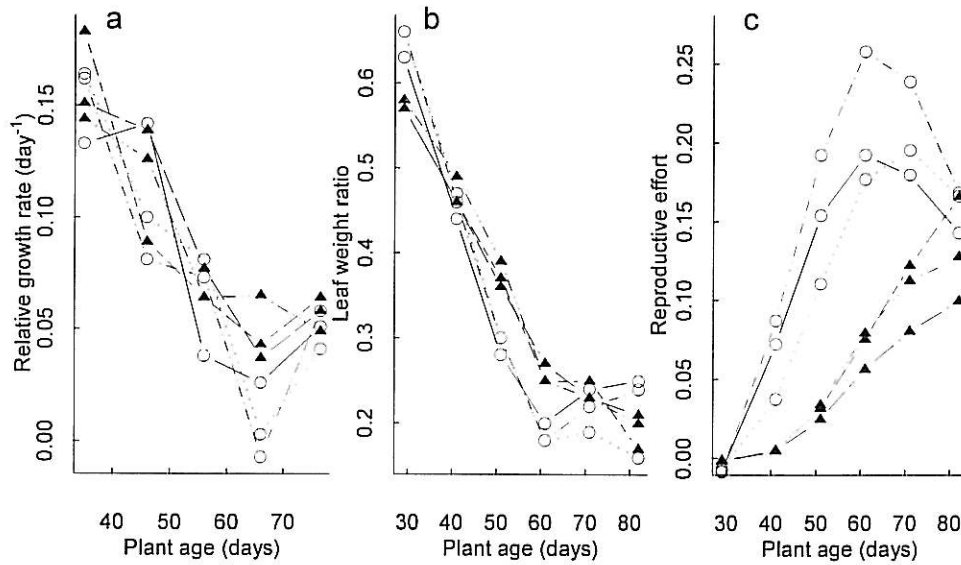


Figure 2. Time courses of calculated plant growth characteristics for native and non-native plants of *Lythrum salicaria*. For details see text, for legend see Fig. 1.

#### PHOTOSYNTHESIS

No significant differences were found for the dependence of net photosynthesis per unit leaf area on photon flux density in both native and non-native plants of *L. salicaria* (Fig. 3).

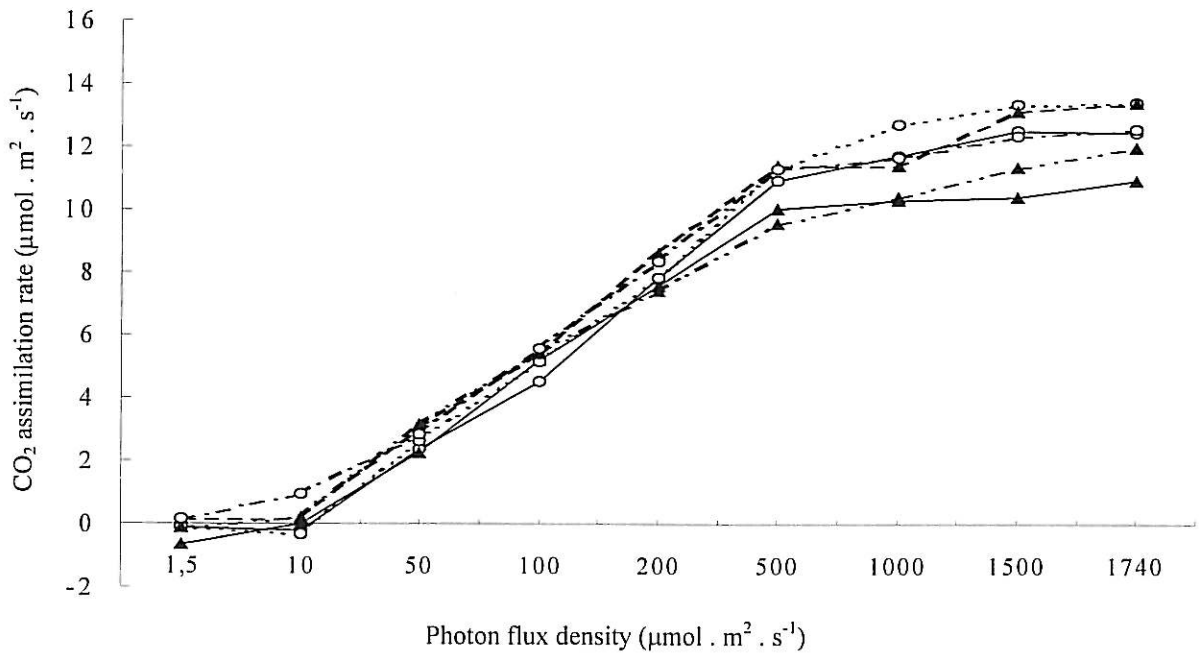


Fig. 3. Dependence of net photosynthesis of native and non-native plants of *Lythrum salicaria* on PhAR. The values for each population were obtained as averages of four measurements (each on a separate plant). (For legend see Fig. 1)

DRY WEIGHT PARTITIONING

Native and non-native plants exhibited different patterns of dry weight partitioning to different plant parts (Fig. 4). In the non-native plants, a significantly greater proportion of total dry weight ( $P < 0,001$ ) was allocated to the shoots than in the native plants throughout the growing season. At the beginning of the growing season, native plants allocated more biomass to the leaves ( $P < 0,001$ ) and reproductive parts ( $P < 0,001$ ) and less to the roots ( $P < 0,01$ ) than the non-native plants. An apparent delay was observed in the formation of inflorescences in the non-native plants against native ones. The percentage of total dry weight allocated to the lateral branches was similar in both native and non-native plants.

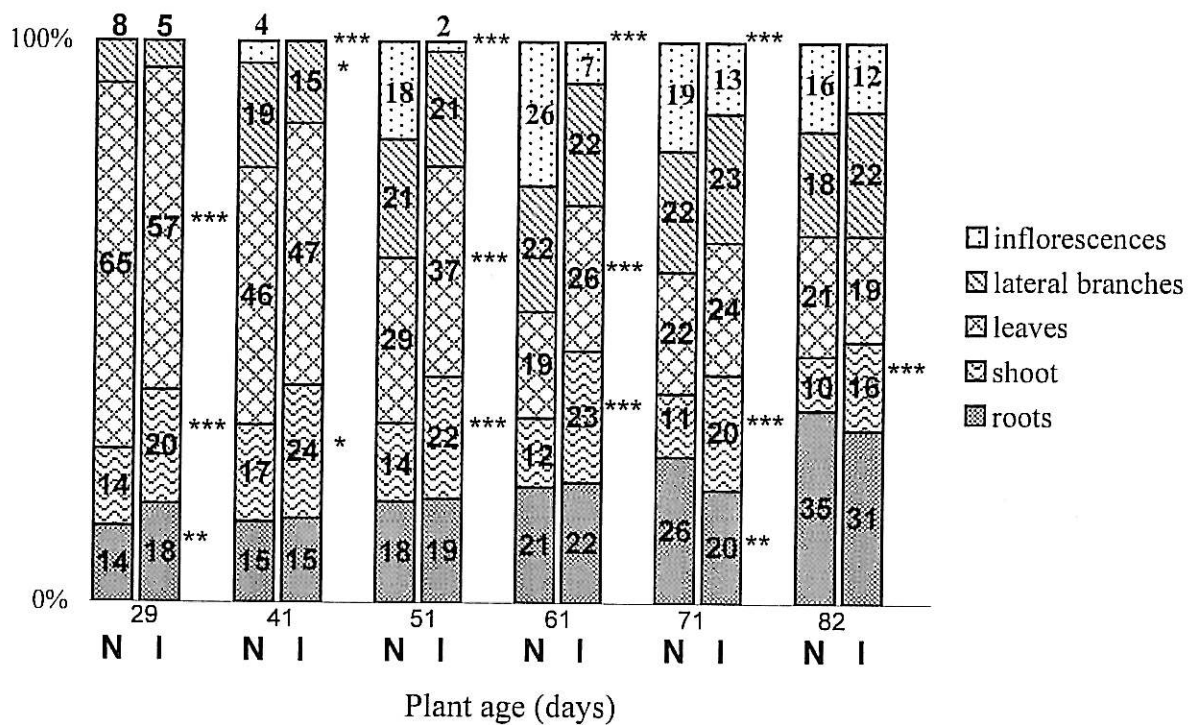


Figure 4. Comparison of average dry weight partitioning in the native (N) and non-native (I) plants of *Lythrum salicaria*. Numbers in columns show the mean percentages of total plant dry weight allocated to the respective plant parts. Asterisks along the columns indicate significant differences between corresponding plant parts in native and invasive populations (\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

FLOWERING PHENOLOGY

Native plants started to flower ten days on average earlier than the non-native ones (Fig. 5). The first plants of the native populations started to flower in the middle of July, after 43 days, and 100% of these plants were flowering 11 days later. Plants of the non-native populations started to flower after 52 days, and reached 100% flowering after another 17 days. Within the

native populations, the greatest difference in the onset of flowering was five days; it was four days within the non-native populations in which flowering started at a slower rate.

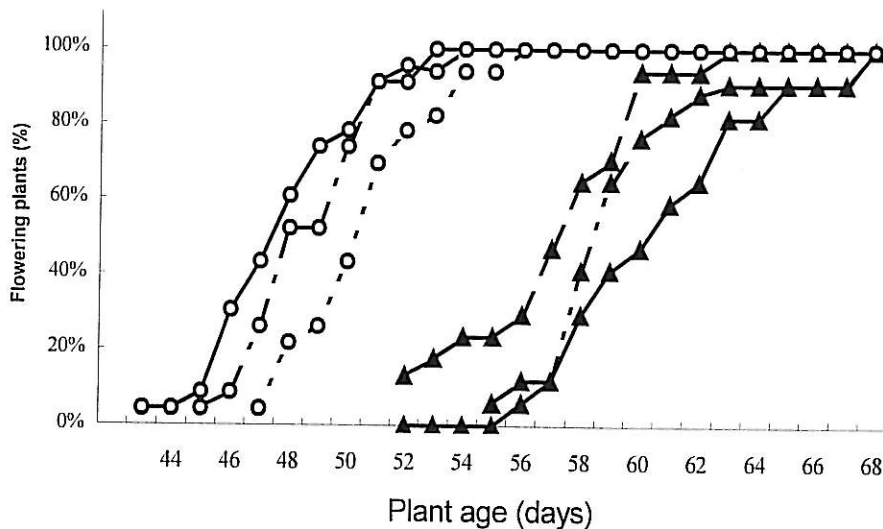


Figure 5. Flowering phenology of native and non-native plants. (For legend see Fig.1)

## Discussion

Although structural plant characteristics are „among the most species-specific features of plants” (Körner 1991), this experimental study shows that plants of the same species apparently originating from two distant geographical regions can differ significantly in their life history characteristics and morphological strategies.

The results of this experimental study are in agreement with those of earlier studies reporting on a taller stature and higher aboveground net production in non-native plants of *L. salicaria* in comparison with native ones (Blossey & Kamil 1996; Edwards, Květ & Adams 1998). Additionally, the measurements of photosynthesis and detailed growth analysis show that the more vigorous stature of non-native plants is not a result of differences at net photosynthesis level, but is due to differences in dry weight partitioning and thus in the growth strategy between native and non-native populations of *L. salicaria*. This study also confirmed the plasticity of *L. salicaria* as indicated in the earlier study by Shamsi (1974). Three native and three non-native populations were selected to represent different habitats in which *L. salicaria* can live in both primary and secondary areas of distribution. Significant between-population differences in some plant characteristics within the sets of both native and

non-native plants are probably due differences in environmental conditions in habitats where the seeds were collected.

As indicated by the greater dry weight allocation to the stems, the non-native plants possess a stronger apical dominance (Tamas 1995). A firm and fast growing stem allows non-native plants quickly to overgrow the surrounding vegetation and thus better compete for solar irradiance from the start of growing season (Hickman 1975; Menges 1987; Gaudet & Keddy 1988a, b). Taller stem also facilitates pollen exchange and seed dispersal later in the growing season (Levin & Kerster 1972). In the further development, both the number and dry weight of primary lateral branches increase, they start to form a „life space” around the main stem. This strategy allows the non-native *L. salicaria* populations to suppress native species populations in a plant community. Increasing number and dry weight of primary lateral branches increase also the dry weight of leaves. *L. salicaria* produces inflorescences not only on main stem, but also on lateral branches. Larger leaf area supported by development of new lateral branches is reflected in higher production of inflorescences in the non-native plants as compared with the native ones at later stages of the plants' development. The only disadvantage of delayed flowering is the risk of late seed ripening at the time of early autumn frosts.

Smaller leaf area ratio in non-native plants and non-significant differences in net photosynthesis and relative growth rate between native and non-native plants, lead to the assumption of a higher net assimilation rate (dry matter production per unit leaf area) in the non-native plants (Květ *et al.* 1971). This assumption was not confirmed in our experimental study. No significant differences in net assimilation rate were found between the native and non-native plants. Higher dry matter production in the non-native plants was probably due to their larger total leaf area on the taller and more branched stems.

More vigorous growth of non-native plants would manifests itself in their greater reproductive effort (Waite & Hutching 1982). In our study, reproductive effort of the non-native plants was less than in the native ones, but this result cannot be considered as conclusive. While the native plants attained their maximum RE after 61 days of cultivation and RE was then decreasing, RE of the non-native plants was increasing throughout the whole experiment. Additionally, dry weight of reproductive parts was greater in the non-native plants than in the native ones at the end of experiment. Declining RE of the native plants towards the end of the growing season was probably due to the absence of pollinators in the greenhouse. Seed formation was reduced or stopped, and the native plants shed off dry generative parts. This did not occur in the non-native plants, which flowered later. At the time



the experiment was terminated, the non-native plants were still flowering and no decline in inflorescence dry weight was apparent. RE of the non-native plants would thus probably have reached its maximum after the end of the experiment.

The growth strategy of the native plants is different from the non-native ones. Higher dry weight allocation to the leaves and lateral branches at the beginning of their development allows early formation of generative structures and subsequently seeds. This gives these plants a competitive advantage in early successional stages (Gross 1983) and, in a short growing season. On the other hand, the formation of generative parts slows down the relative growth rate. The native plants are unable to compete with others for space in a dense plant community at the beginning of the growing season. Also, their great reproductive effort may result in a strong depletion of their carbohydrate reserves (Waite & Hutching 1982; Chapin III, Schulze & Money 1990). Apparent increase in RGR and LWR at the end of growing season is a consequence of the emergence of new tertiary lateral branches after the flowering period.

Differences in these two growth strategies are reflected in the occurrence of *L. salicaria* in plant communities in Central Europe as compared with midwestern US. *L. salicaria* grows in a wide variety of habitats in Central Europe, but its occurrence is mostly associated with that of shorter plant species or with some kind of site disturbance. *L. salicaria* occurs only rarely in tall littoral vegetation in Central Europe (Bastlová-Hanzélyová 2001). On the other hand, in midwestern US, *L. salicaria* successfully competes with tall plant species (e. g., *Phragmites australis*, *Typha latifolia*, *Typha x glauca*) in littoral plant communities (Bastlová-Hanzélyová 2001; Mal, Lovett-Doust & Lovett-Doust 1997) and occurs more frequently in shrub communities or at forest edges (Bastlová-Hanzélyová 2001).

As *L. salicaria* plants of all six populations (three non-native and three native ones) were studied under the same experimental conditions, it can be assumed that the recorded differences in dry matter production, flowering phenology and dry weight allocation between the native and non-native populations are genetically based (Hickman 1975, 1977; Waite & Hutching 1982) and are probably a result of some kind of selection and local adaptation (Oneil 1999; Peacock & McMillan 1968). Weber & Schmid (1998) described differences in morphological and life-history characteristics between populations of two *Solidago* species originating from different latitudes across the Europe. Plants of populations originating from northern localities flowered earlier and reached a smaller size at maturity than plants from southern localities. The same applies to plants of *Phragmites australis* from different latitudes in Europe, which were cultivated at a site in the middle of the North-South gradient (Véber &

Dykyjová 1978). This variability in phenology and life-history characteristics was genetically based and strongly correlated with physiological requirements for floral initiation in the plants. One of these requirements is the length of the dark period (Ray & Alexander 1966, Oneil 1999). Ray & Alexander (1966) found a strong photoperiodic adaptation to latitude in *Xanthium strumarium* (critical night length 7.5 to 10 h). The plants from southern latitudes possessed the longer critical night lengths. In view of similar climatic conditions in both areas from which the *L. salicaria* seeds in this experiment originated (Edwards, Květ & Adams 1999), differences in latitude and, consequently, in daylength could have acted as the main factor of adaptive selection in this species. If the non-native plants originated from more northern latitudes in Eurasia than those of the sites of their secondary occurrence in Northern America, they may have undergone an adaptive evolution (Ray & Alexander 1966; Weber & Schmid 1998; Peacock & McMillan 1968). Indirect support for this hypothesis is the fact that this species was introduced to North America probably from northern and/or western Europe at the beginning of 19<sup>th</sup> century, while its invasive spread started about one hundred years later, at the beginning of 20<sup>th</sup> century (Thompson, Stuckey & Thompson 1987). Nevertheless, a hitherto unproven alternative hypothesis could be that of a possible later import of *L. salicaria* seeds from southern Europe. This import may have induced the delayed but subsequently rapid spread of *L. salicaria*.

This paper deals with the well-known fact that invasive populations of *L. salicaria* become more vigorous than the native populations. On the basis of my experiment with native and non-native plants of *L. salicaria*, it is possible to conclude that more vigorous stature and subsequently higher competitive ability of the non-native plants is essentially due to differences in dry weight allocation pattern. These differences are connected with differences in phenology and can affect the competitive ability of the native and non-native invasive plants.

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**Chapter 5**

**Phenotypic variability in native populations of  
*Lythrum salicaria* L.: between- and within-  
population differences.**



## **Phenotypic variability in native populations of *Lythrum salicaria* L.: between- and within-population differences.**

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### **Abstract**

The study deals with the variability and changes in life history characteristics in native populations of *L. salicaria* across the native geographical gradient. Plants from 15 populations originating from Sweden, Poland, Slovenia and Israel were cultivated in a garden tub experiment. The plant height, total plant mass and their components (dry weight of shoots, roots, lateral branches, leaves and inflorescence) as well as other life history characteristics (basal stem diameter, number of lateral branches and internodes etc.) were investigated at the end of the first growing season.

The greatest proportion of total variability in plant height, above-ground and shoot dry weight, dry weight of lateral branches, leaves and inflorescences, as well as basal diameter, leaf area, specific leaf area, flowering time and number of primary lateral branches between the populations can be explained by differences in latitude of geographical location from which the populations originated. On the contrary, variability in number of roots and number of internodes and partly in root dry weight is higher between and within the populations than between the geographical locations. Most of the life history characteristics, except for number of roots, flowering time and number of internodes were significant dependent on the latitude of geographical location indicating an existence of natural gradient in *L. salicaria* phenotypic variability in its native range.

Keywords: flowering time, latitudinal differences, invasion

### **Introduction**

Purple loosestrife (*Lythrum salicaria* L.), an originally Eurasian plant species, has successfully invaded North American wetlands, where invasive plants grow taller and show higher competitive ability in comparison with native plants (for references see Thompson et al. 1987). Experiments with native European and non-native North American populations of *L. salicaria* showed that the non-native populations usually grew taller and flowered later than the native populations (Edwards 1996, Bastlová-Hanzélyová 2001, Bastlová submitted manuscript). Evolution of Increased Competitive ability (EICA) hypothesis (Blossey and Notzöld 1995) explains higher competitive ability and more vigorous growth of invasive plant species in their secondary distribution ranges by changes in allocation patterns. Based on this hypothesis, in the absence of herbivores and other natural control agents, new and more competitive genotypes are selected, showing reduced resource allocation to herbivore defense

and improved allocation to vegetative structures. But many studies show differences in growth pattern between ecotypes or even populations also within the native ranges (e. g. Sowell and Spomer 1986). Shift in allocation pattern is very often connected to where the populations fall along environmental gradients (Weber and Schmid 1998, Peacock and McMillan 1968) and reflects an adaptation to natural variation in environmental conditions along the geographical gradients.

Plants for comparative studies with native and invasive populations of *L. salicaria* were selected usually with respect to similarity of climatic conditions (average annual temperature and rainfall) and thus native and non-native originated mostly from restricted geographical areas. Nevertheless, when comparing native and non-native populations of *L. salicaria* originating from wider geographical areas (Blossey and Kamil 1996, Willis and Blossey 1999) some native populations were more similar in vegetative growth and reproduction to invasive ones. These native genotypes with increased vegetative growth and thus higher competitive ability (Gaudet and Keddy 1988 a, b) may create a base for the invasive populations (Mooney and Drake 1986, di Castri et al. 1990).

This study addresses two questions: 1) what is the magnitude of variability in life history characteristics in native populations of *L. salicaria*, 2) how plant growth characteristics change across the native geographical gradient?

## **Material and Methods**

Plant material used in this study was collected from populations across Europe in 1998-1999. The seeds of individual plants, in total from 32 *Lythrum salicaria* populations were collected at 11 locations across the native area of occurrence; seeds from each plant were placed in a separate bag and sent together with description of the habitat conditions of respective locations (co-occurring plant species, hydrological regime, soil type) to the Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic. The sampled seeds were labeled and stored dry in refrigerator at 4° C. The latitude of the locations where the seeds were collected ranges from 60° to 30° N. The obtained material thus covers almost the entire latitudinal range of *L. salicaria* occurrence and wide variability of habitat conditions in Europe and Israel. In this seeds' collection, six geographical locations (Sweden, Spain, Poland, Slovenia, Hungary and Israel) were represented by more than three populations; one or two populations represented the others only. From these six locations, four (Sweden, Poland, Slovenia and Israel) were selected for the experiment with respect to their positions

along the north-south geographical gradient (Table 1) to cover as wide as possible north-south range of this species occurrence in its native area of distribution. From each country (except Slovenia), four populations were used in experiment. The seeds of one population from Slovenia did not germinate thus I used three populations only. From each population, seeds of four individual parental plants were used in the experiment. In the final, offspring of totally 60 parental plants originating from 15 populations and four countries across the Europe create an experimental design. The set of 60 pots with these plants was considered as one replicate, the experimental design consisted from four replicates.

**Table 1.** Countries and localities with their geographical coordinates and habitats of *L. salicaria* populations where seeds were collected.

country	locality/population	geographical coordinates	habitat notes
Sweden	Lake Rastsjon	60° 01' N 17° 08' E	terrestrial part of the lake shore
	Lake Hammardammen	60° 02' N 17° 08' E	shore habitats occasionally flooded
	Lake Slagsmyren	60° 01' N 17° 09' E	nearshore stand in water
	Dannemora	60° 01' N 17° 08' E	nearshore stand in water
Poland	Sniardwy	53° 07' N 21° 08' E	wet lakeshore
	Mikolajskie	53° 06' N 21° 03' E	wet meadow
	Mikolajskie/Talty	53° 06' N 21° 03' E	wet lakeshore
	Mikolajskie/Gardynskie	53° 07' N 21° 05' E	wet meadow
Slovenia	Drenov Grič	46° 07' N 14° 27' E	drainage ditch with fluctuating water
	Mengeš	46° 09' N 14° 33' E	small stream with water 10-20cm
	Ljubljana moor	46° 01' N 14° 30' E	gleyed soil, periodically inundated
Israel	Alexander stream	30° 03' N 34° 07' E	no data available
	Yarkon stream	30° 03' N 34° 07' E	no data available
	Poleg stream	30° 03' N 34° 07' E	no data available
	Taninim stream	30° 03' N 34° 07' E	no data available

A common garden tub experiment was carried out at the Institute of Botany, Academy of Sciences of the Czech Republic, Třeboň, Czech Republic (49° N 14° 47' E, 430 m a. s. l). The seeds were sown on garden soil contained in plastic saucers, seeds of each individual parental plant in a separate saucer on June 6, 2000. To germinate the seeds, all saucers were placed in a greenhouse and watered every two days. Young plants with two pairs of true leaves were selected for uniformity of size and transplanted into 2.5 l plastic pots filled with a mixture of

sand and fertilizer (a slowly diluting granulate fertilizer, Osmocote Plus, concentration 6 g.l<sup>-1</sup> of soil) – three plants per pot, on June 27, 2000. The pots were placed into plastic tubs (150 x 230 x 50 cm) filled with water up to 10 cm (about one half of pot height). One week later, all plants were selected for uniformity and thinned to only one plant in each pot. At its end, the experiment consisted of four tubs (each tub as one replicate); with a set of 60 pots in each tub (offspring of 60 parental plants from 15 populations originating from four different geographical locations), with one plant per pot.

The plants from Poland and Slovenia were sampled successively at the same phenological stage, when 70% of their inflorescences were in bloom. At the beginning of September, the leaves of plants from Sweden started to fall off. In order to avoid early frost damage to the plants and losses by falling leaves, the experiment was finished in mid-September, although plants of both Sweden and Israel populations did not yet flower at that time. In order to describe the growth characteristics of the plants, the shoot height, number of internodes below the inflorescence (in flowering plants only), total number of primary lateral branches (growing directly from the main stem), basal stem diameter and number of thick (more than 0.5cm in diameter) roots longer than 2.5 cm were recorded for each plant sampled. Afterwards, the plants were divided into roots, stems and lateral branches (without leaves and inflorescences), leaves and reproductive parts (inflorescences on main shoot and on lateral shoots + flower-bearing parts of the stems). These samples were then dried in the oven at 72 °C for 24 hours. The dried samples were weighed to the accuracy of 0.001 g. The onset of flowering was recorded successively at daily intervals during the corresponding period of the growing season. A plant was recorded as flowering when the first flower buds opened.

For determination of leaf area, all leaves from the longest primary lateral branch were scanned (scanner Astra 2000, Umax, resolution 600dpi) and afterwards their dry weight was determined. From the obtained values and from dry weight of whole plant leaves, the total leaf area was determined for each plant. The leaf area and dry weight values of the measured leaf sub-samples were used for calculating the specific leaf area (leaf area/leaf dry weight) (Květ et al. 1971, Hunt 1982).

Dependence of plant growth characteristics on latitude of original geographical location were fitted by generalized linear models (GLM)(McCullagh and Nelder 1989) using S-plus software package (Statistical Sciences 1995a,b). GLM was used also for hierarchical analyses showing partitioning of variation among geographical locations, among populations within particular geographical location (between populations) and among parental plants within

particular populations (within population). Significance of GLM was tested using F-test (Zar 1984, Sokal and Rohlf 1995).

## **Results**

Based on the results of hierarchical analysis (Table 2), plant growth characteristics could be divided into two main groups. In the first group, the greatest proportion of total variability between the plants can be explained by differences in geographical location from which the plants originated. Plant height, above-ground and shoot dry weight, dry weight of lateral branches, leaves and inflorescences, as well as basal diameter, leaf area, specific leaf area and number of primary lateral branches belong to this first group. Much smaller proportion of variability in these plant characteristics can be attributed to within and between population differences.

In the second group of plant characteristics, the variability between and within the populations is higher than the variability across the geographical gradient. The second group lists number of roots and number of internodes and partly root dry weight.

Differences in all assessed plant growth characteristics, except for the number of roots, number of internodes and time of flowering, were significantly dependent on the latitude of geographical location from which the plants originated (Table 2, Fig. 1). The plant height, total aboveground plant mass as well as its components (dry weight of main stem, lateral branches, leaves, inflorescences and roots), basal stem diameter, number of primary lateral branches and leaf area decreased with increasing latitude of the populations' geographical locations. On the other hand, specific leaf area increased with increasing latitude.

Flowering time and number of internodes have to be considered separately. These two characteristics were assessed in Slovenia and Poland populations only, because plants of Sweden and Israeli populations did not flowered until the end of experiment. In these two characteristics, low percentage of explained variability between the geographical locations as well as insignificant results of regression analysis is probably due to reduced number of tested geographical locations.

**Table 2.** Partitioning of the variation among geographical location, between populations within one geographical location (between population) and between parental plants originating from one population (within populations). The last column shows significances of regression analysis with plant growth characteristics as dependent and latitude as explanatory variable. (\*\*\*)  $P < 0.001$ , (\*\*)  $P < 0.01$ , (\*)  $P < 0.05$ )

	df	F	P	explained variability	significance of regression
<b>plant height</b>					***
geographical location	3	906,30	***	91%	
between population	11	5,34	***	2%	
within population	45	1,48	*	2%	
<b>above-ground dry weight</b>					***
geographical location	3	363,04	***	79%	
between population	11	5,67	***	4%	
within population	45	1,81	**	6%	
<b>shoot dry weight</b>					***
geographical location	3	503,74	***	83%	
between population	11	3,41	***	2%	
within population	45	1,50	*	4%	
<b>dry weight of lateral branches</b>					***
geographical location	3	193,83	***	65%	
between population	11	4,81	***	6%	
within population	45	2,02	***	10%	
<b>dry weight of leaves</b>					***
geographical location	3	298,57	***	76%	
between population	11	4,84	***	4%	
within population	45	1,79	**	7%	
<b>dry weight of inflorescences</b>					***
geographical location	3	229,60	***	67%	
between population	11	7,93	***	8%	
within population	45	1,50	*	7%	
<b>dry weight of roots</b>					***
geographical location	3	27,85	***	21%	
between population	11	4,98	***	14%	
within population	45	2,14	***	24%	
<b>number of primary lateral branches</b>					***
geographical location	3	143,52	***	64%	
between population	11	0,90	NS	1%	
within population	45	1,53	*	10%	
<b>number of roots</b>					NS
geographical location	3	5,67	**	6%	
between population	11	3,94	***	15%	
within population	45	1,42	NS	22%	
<b>basal diameter</b>					***
geographical location	3	82,04	***	49%	
between population	11	4,40	***	10%	
within population	45	1,14	NS	10%	
<b>number of internodes</b>					NS
geographical location	1	0,35	NS	0%	
between population	5	3,96	**	24%	
within population	19	1,07	NS	25%	
<b>flowering time</b>					NS
geographical location	1	19,88	***	22%	
between population	5	2,94	*	16%	
within population	19	0,67	NS	14%	
<b>leaf area</b>					***
geographical location	3	179,52	***	69%	
between population	11	3,03	**	4%	
within population	44	1,60	*	9%	
<b>specific leaf area (SLA)</b>					***
geographical location	3	93,27	***	55%	
between population	11	1,87	*	4%	
within population	44	1,70	*	15%	



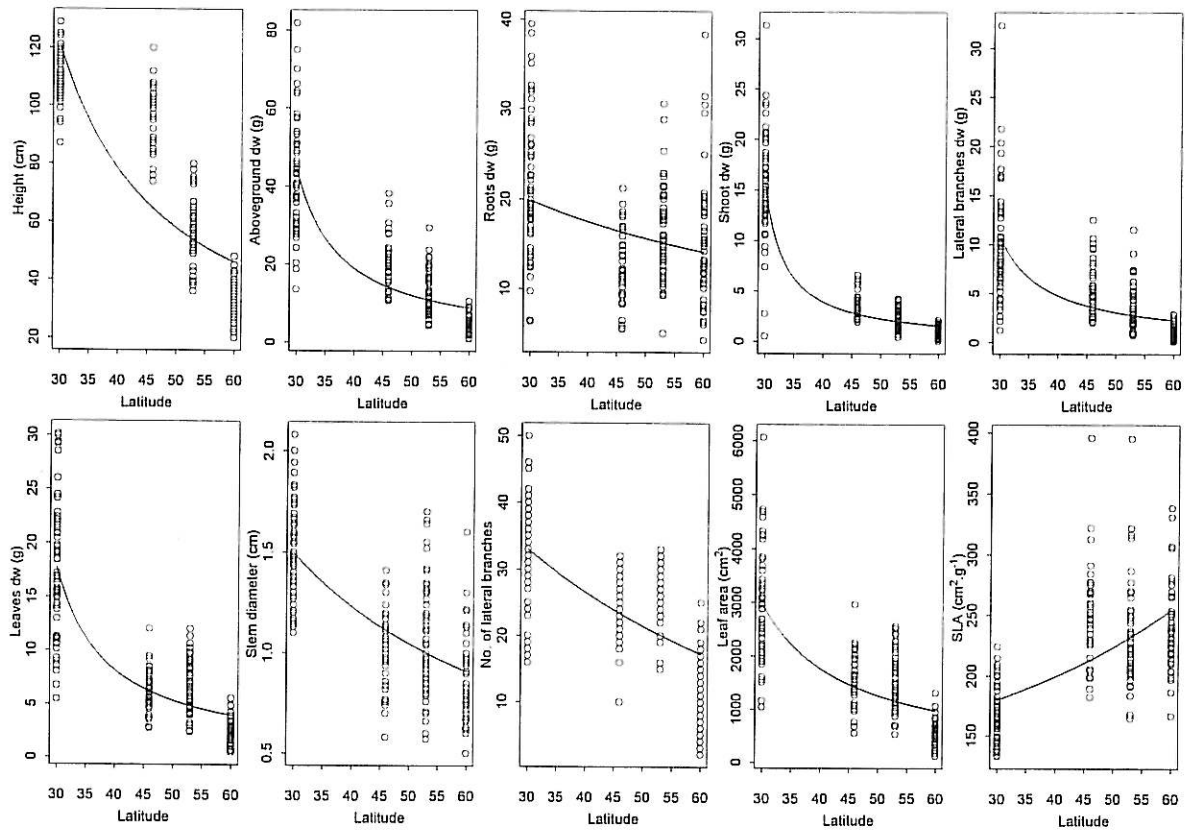


Fig. 1. Dependence of the plant growth characteristics on the latitude of geographical location from which the population originated. Lines represent regression curves fitted using GLM ( $P < 0.001$  in all cases). (dw=dry weight)

## Discussion

This study with 15 populations of *L. salicaria* originating from four different geographical locations situated across the native north-south gradient confirmed high phenotypic plasticity of this species (Shamsi and Whitehead 1974a,b, 1977a,b). Most of the life history characteristics vary with latitude of the geographical location and indicate a genetic variability (Hickman 1975, 1977, Waite and Hutching 1982) and long term adaptation across the natural gradient in the native range of *L. salicaria*. Higher variability between the populations and even individual plants within the population in some of plant characteristics (e. g. dry weight of roots) in comparison with the others probably indicate that these characteristics are more plastic in individual plants responses to changing environmental conditions than the others. Plasticity in e.g. roots growing responses may to act as a factor important for the plants' adaptation to local environmental conditions or in competition in plant communities. Significant dependence of most of the plant growth characteristics on the latitude of the plants' geographical location and higher variability explained at the geographical location



than at populations level suggest that a natural gradient exists in the variability of *Lythrum salicaria*. This variability must have resulted from long-term selection and local adaptation to prevailing conditions in the respective habitats (Peacock and McMillan 1968, Oneil 1999). One factor of great importance that is highly variable with latitude and influenced plant life history characteristics is the photoperiod (Peacock and McMillan 1968, Kudoh et al. 1995, Armstrong and Adkins 1998, Li et al. 1998, Pollard et al. 2001). Ray and Alexander (1966) found a strong photoperiodic adaptation to latitude in *Xanthium strumarium* in North America. The plants from southern latitudes were characterised by longer critical night lengths and flowered later under naturally varying photoperiod than plants from northern latitudes. Weber and Schmid (1998) described differences in morphological and life-history characteristics between populations of two *Solidago* species originating from different latitudes in Europe. Plants of populations originating from northern locations flowered earlier and reached a smaller size at maturity than plants from southern locations. The same applies to plants of *Phragmites australis* from different latitudes in Europe, which were cultivated at a site in the middle of the north-south gradient. This variability in phenology and life-history characteristics was genetically based and strongly correlated with physiological requirements for floral initiation in the plants (Véber 1978). Also *L. salicaria* is reported as being sensitive to photoperiod. Shamsi and Whitehead (1974b) described the effect of variation in daylength on growth of *L. salicaria* plants. Plants in short-day treatment were small with reduced stems, very high proportion of roots, small number of internodes and lateral branches, and with small leaves. In long-day treatments, the total plant dry weight increased about 50 times in comparison with short-day plants. The long-day plants had erect stems with long internodes and opposite hairy leaves. Together with elongation of the main stem, rapid growth of lateral branches was observed. The differences between plants from northern and southern populations in my experiment correspond to those between short-day and long-day plants described by Shamsi and Whitehead (1974b). Plants originating from Sweden were semi-prostrate with small leaves and their lateral branches were almost as thick as the main stem. These plants flowered only rarely and their inflorescences, if present, were loose and weak. Shorter days in central Europe, where the experiment was carried out, were highly probable responsible for prostrate growth of these plants, which originated from a location with long days during the growing season. On the other hand, plants from Israel were tall, had vigorous, erect main stem and lateral branches. This is in accordance with results of Blossey and Kamil (1996) and Willis and Blossey (1999) and with our expectation that plants originated from southern latitudes will grow more vigorously and flower later than their conspecifics from the

northern Europe. From this point of view, there is a similarity between the invasive North American and native south European *L. salicaria* plants. Experiments testing the variability of invasive plants across geographical gradients and similarity of invasive genotypes with native ones showing vigorous vegetative growth are a part of an ongoing study on *Lythrum salicaria* plants.

Absence of flowering in most of the plants from Sweden and all plants from Israel may have few reasons. In agreement with the origin of the Swedish and Israeli populations from opposite ends of the latitudinal gradient, the plants reached different developmental stages at the end of the experiment. No elongation of either the main stem or lateral branches during the last month of the experiment was indicative of terminated shoot growth in the plants from Sweden. Adaptation to a shorter growing season in these plants was evident from early senescence of their leaves, which started to fall off already in the middle of August. In the plants from Israel, on the other hand, rapid elongation of the main stem continued until the end of the experiment, without any apparent leaf senescence. These plants did not form flower buds until the end of the experiment although the photoperiod is longer in central Europe than in Israel. In a greenhouse (Kubátová and Bastlová, unpublished data) and thus in conditions more similar to those in south locations, flowering induction was observed in Israeli plants, but they flowered the latest of all tested populations (end of September). I therefore assume that the shorter or colder central European growing season rather than unfulfilled photoperiodic requirement did not allow these plants to terminate their seasonal cycle of shoot development in the garden experiment.

### **Conclusions**

The present study shows the differences between native populations of *L. salicaria* originating from the north-south geographical gradient. Dependence of most of the life history characteristics on the latitude from which the plants were collected confirmed existence of natural gradient in the species variability. Populations from southern localities consisted of plants that were taller, had higher above-ground dry weight and their respective parts (dry weight of lateral branches and roots), higher number of lateral branches and roots, larger leaf area and flowered later than did the plants from northern localities. From this point of view, these plants were more similar to the invasive plants in North America than plants from northern localities. The variability in life history characteristics across the north-south gradient within the native range may result from long term adaptation to prevailing geographical conditions, probably a day-length. In some plant characteristics (e.g. dry weight

of roots) relatively high proportion of variability was found also between and within populations, which indicates probably plastic growth responses to the local environmental conditions.

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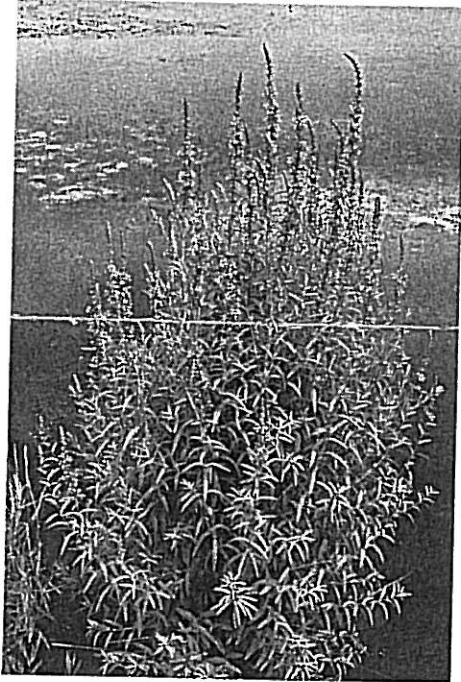
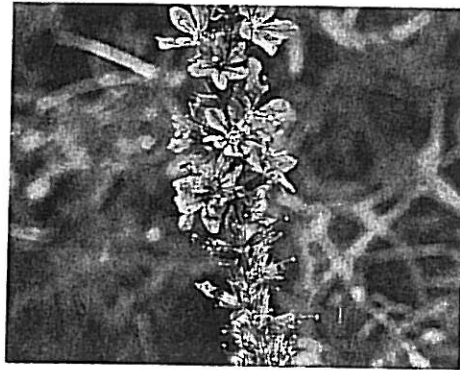
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# **Príloha**



# IDENTIFYING PURPLE LOOSESTRIFE



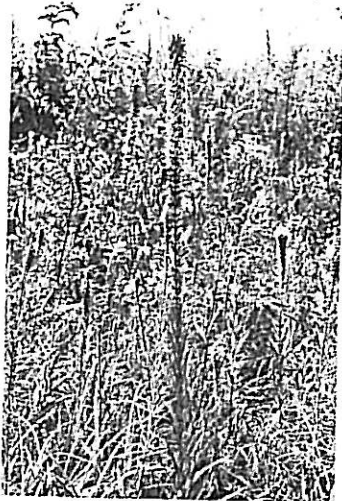
## PURPLE LOOSESTRIFE CHARACTERISTICS

- Height:** 3 to 10 feet  
(5 foot average)
- Leaves:** opposite or 3 in a whorl without teeth.
- Stems:** 4 angles, semi-woody at base
- Flowers:** with 5 to 7 purple petals, in long spikes at the ends of branches
- Flowering season:** early July to early September

Flowering plants are very conspicuous and can be identified at 100 yards. Native loosestrife grows in similar sites but averages 2 feet tall, has its' flowers more widely spaced and usually has its' upper leaves alternate instead of opposite.



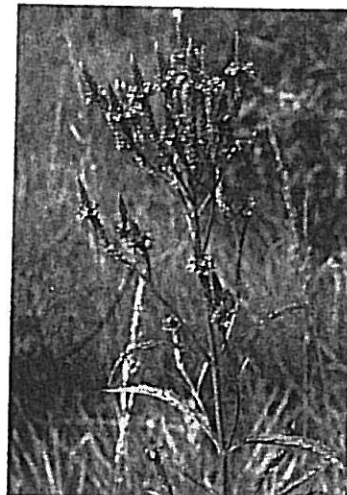
Don't confuse purple loosestrife with these look-a-like native plants:



BLAZING STAR



NATIVE LOOSESTRIFE



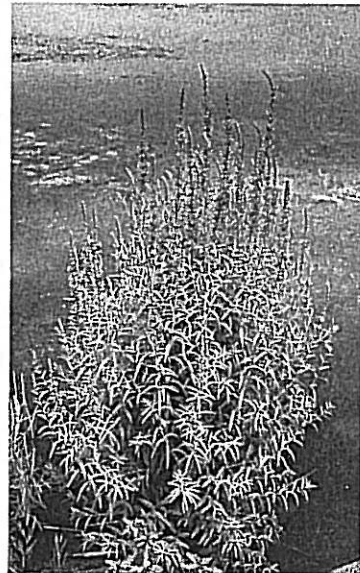
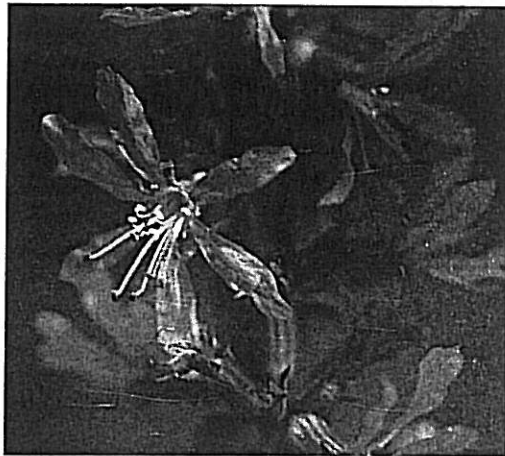
BLUE VERVAIN



Illinois  
Department of  
Conservation  
life and land together

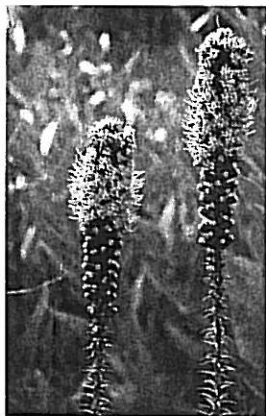
# WANTED: Purple Loosestrife Observations

Purple loosestrife is an aggressive plant that is invading our wetlands and...



- replacing valuable wetland plants;
- eliminating food and shelter for wildlife;
- choking waterways.

Don't Be Confused By These Purple Loosestrife Look-a-Likes



Blazing Star



Fireweed



Blue Vervain

## REPORT FORM—DETACH AND SEND

NAME: \_\_\_\_\_ ADDRESS: \_\_\_\_\_ Diagram (shows roads, distances, and outline of the loosestrife patch).

PHONE: \_\_\_\_\_

### LOCATION OF PURPLE LOOSESTRIFE

County: \_\_\_\_\_

Township: \_\_\_\_\_

Nearest Road Intersection: \_\_\_\_\_

### TYPE OF AREA (check one)

- 1-marsh or wetland  5-meadow or pasture   
 2-pond or lake  6-roadside   
 3-stream or river  7-other (specify)   
 4-ditch

Send me more report forms.  
 Yes \_\_\_\_\_ How many \_\_\_\_\_ No \_\_\_\_\_

Form 8100-82  
 7-85  
 8512

DNR USE ONLY

- NUMBER OF PLANTS (check one)  
 less than 20  100-999   
 20-99  more than 1,000

## WHAT YOU CAN DO ABOUT PURPLE LOOSESTRIFE

Report locations you have observed on the attached form, so we can determine the statewide distribution of the plant.

### INSTRUCTIONS

- Please fill out one card for each patch of purple loosestrife.
- Please read the card before filling it out.
- You may be contacted by phone for additional information on the exact location of the plants.

DETACH THIS STUB BEFORE SENDING REPORT FORM

# Three Bee Plants: Purple Loosestrife, Vetch, and Safflower

by RICHARD DALBY  
Box 6  
Levan, UT 84639

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*Some consider Purple Loosestrife (Lythrum salicaria) nothing more than a weed. Fortunately, honey bees pay no attention to such human concepts and make ready use of the plant as a source of nectar. This square-stemmed woody perennial can be found in wet locations from Nova Scotia south to Virginia and westward to Minnesota and Missouri.*

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## Purple Loosestrife

The long, showy, spiked blossoms of Purple Loosestrife, which vary from red to deep purple to rose, make for a vivid sight. The blossoms occur in three different forms, though never on the same plant. Purple Loosestrife typically grows in extensive dense patches, blooming from June to September. The clasping, opposite leaves are narrow and lance-shaped. The plant can attain 5 feet or more in height. A single mature specimen can produce 2 to 3 million seeds per season. Purple Loosestrife can also spread by its root system. It has a tendency to replace less aggressive native plants. And, its tough stems and roots can impede boats and wildlife. For these reasons some states have adopted control measures including application of glyphosate herbicides and the introduction of parasitic insects that attack the roots and leaves.

Purple Loosestrife is native to Europe. It was brought to America in the 1800s as an ornamental, but soon escaped from cultivation. The ancient Greeks took notice of the plant. They believed that an ox team hung with garlands of Purple Loosestrife would plow together more harmoniously.

Closeup of purple loosestrife with bee working it.▶



Although found over much of the U.S., reports of significant honey production from purple loosestrife are most common from the Northeastern U.S.