The Search for Patterns or What Determines the Increased Competitive Ability of Invasive Non-indigenous Plants?

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European settlement, western agriculture, forestry, and urbanization have resulted in the sometimes dramatic loss of natural North American habitats. More than 99.9% of the area once covered by oak savannas in the midwest has been transformed (Henderson and Epstein 1995) and over 99% of the tall-grass prairies have been lost (Swengel and Swengel 1995). Similar but less dramatic losses occurred for the nation's wetlands (53%, Dahl 1990) and forests (33%, Darr 1995). The shrinking acreage of natural areas is shared by an increasing number of non-indigenous species (NIS) introduced (intentionally or unintentionally) by humans. An estimated 17,000 species of native plants and about 5,000 introduced plants occur outside cultivation in the United States (Morse et al. 1995). The percentage of NIS in different floras varies widely from 6% in New Mexico to 28% in Illinois (U.S. Congress 1993) to 38% in New York (Rejmánek and Randall 1994) but the loss of the uniqueness of natural areas is of increasing concern. In 1950 20% of the flora of the Northeast consisted of NIS, whereas in 1986 NIS increased to 36% in New York (Morin 1995). Replacement plant communities are often dominated by a few successful cosmopolitan species. This is a direct threat to the integrity of National Parks and natural areas that were otherwise protected because of their unique fauna, flora or landscape. NIS often alter geomorphological, biogeochemical, and hydrological processes or fire regimes, thus, preventing the recruitment of native species and accelerating local and global extinction rates (MacDonald et al. 1989). For 160 of 163 federally listed threatened and endangered species the invasion of NIS contributed to their listing. For 53 of these species invasive NIS were a or the major factor for their listing (U.S. Congress 1993).

However, many NIS were imported for agriculture or because they were valued species in the aquarium or nursery industry. Perceived effects of NIS vary depending on the observer's perspective and many NIS have both positive and negative consequences. Some NIS became abundant enough to allow commercial exploitation (e.g. the Salmon fisheries in the Great Lakes. improved hunter harvests of white-winged doves nesting in saltcedar and honey production from honeybees visiting saltcedar or purple loosestrife). The information on the effects of NIS on an ecosystem is often anecdotal, and many effects may remain undetected for extended periods (U.S. Congress 1993). Because only a minority of NIS cause severe harm, attempts to identify the potentially most harmful species have continued for the last 30 - 50 years. Pimm (1989) stated that the ecology of invasive species and of the invaded community determine the success or failure of invasions. He anticipated some simple theoretical and some equally simple general patterns (Pimm 1989). However, attempts to identify attributes of invaders from species traits have been unsuccessful (Gray 1986; Crawley 1987). Invasive species come from a wide range of taxa and life-history forms (Crawley 1987). Similarly, most ecosystems are being invaded and why differences in the proportion of NIS exist lacks satisfactory answers (Crawley 1987). Only recently, seed mass, length of juvenile period, and mean interval between large seed crops were found to be correlated with invasiveness in the genus Pinus (Rejmánek and Richardson 1996). Despite these advances (for a single well-defined genus!), it is currently only possible to make weak, probabilistic predictions about which species will invade however, (Gilpin 1990: Daehler and Strong 1993) or to predict the rate or extent of spread of invasive plants (Kareiva et al. 1996). **[Editor's note:** See Remanek and Richardson 1996, Reichard this Proceedings, for recent efforts to identify such attributes of invaders from species traits.]

A phenomenon that has not received much attention, however, is the observation that, in alien environments, some plants appear more vigorous and taller, producing more seeds than in their native distribution (Crawley 1987). For example, the seed production of *Chrysanthemoides monilifiera* (native to South Africa) in Australia and of *Acacia longifiblia* (native to Australia) in South Africa is an order of magnitude higher where the plants are introduced (Noble 1989). The vigor and success of NIS has been attributed to more favorable environments, and release from natural phytophagous enemies (Crawley 1987).

Recently, Blossey and Nötzold (1995) proposed the evolution of increased competitive ability (EICA) hypothesis, i.e. the success of invasive plants results from a shift in biomass allocation patterns. In the absence of herbivores, selection favors genotypes with improved competitive abilities and reduced resource allocation to herbivore defense. This hypothesis rests on the assumption that plants with limited resources show trade-offs in biomass allocation among maintenance, growth, storage, reproduction, and defense (Coley et al. 1985; Bazzaz et al. 1987; Fagerström 1989; Herms and Mattson 1992; Lerdau et al. 1995, but see Bryant et al. 1988 and Blossey and Nötzold 1995 for a discussion of alternative hypotheses).

The EICA hypothesis predicts: a) that, under identical growing conditions, individuals of a species taken from an area where they have been introduced will produce more above-ground biomass than individuals taken from the species' native range, and b) that specialized herbivores (i.e. those with potential for introduction as biological control agents) will show improved performance on individuals originating from an area where plants have been introduced. In preliminary experiments, Blossey and Nötzold (1995) tested these predictions comparing the growth of *Lythrum salicaria* L. (purple loosestrife) and the performance of two specialized insects on plants from two locations (one with [Europe] and one without [North America] natural herbivory). The results supported predictions that plants from the area with low herbivore pressure show increased vegetative growth and allow improved performance of herbivores (Blossey and Nötzold 1995). Here, this analysis is expanded to test predictions of the EICA hypothesis, comparing plant growth and preference of a leaf feeding chrysomelid among 36 genotypes of L. salicaria collected from three continents.

Experimental Organisms

Purple loosestrife is an Eurasian wetland perennial introduced into North America in the early 1800's. Its spread across the temperate part of the continent has degraded many prime wetlands. Large, monotypic stands eliminate native plant communities and threaten endangered plant and animal species (Thompson et al. 1987; Malecki et al. 1993). Once established, *L. salicaria* populations persist over decades in North America and tend to encroach upon adjacent areas (Thompson et al. 1987). In contrast, populations in Europe are rapidly invaded by other plant species and *L. salicaria* is a regular but infrequent component of mixed wetland communities (Shamsi and Whitehead 1974). Purple loosestrife grows in a wide range of similar habitat-types in Europe and North America and of the 12 main plant species co-occurring with *L. salicaria* five were found on both continents (Blossey and Kamil 1996). In Europe, displacement of purple loosestrife from plant communities is promoted by specialized insects which devastate tissues, both above and below ground, but these insects were absent from North America until 1992 when three species were introduced as biological control agents (Hight 1990; Malecki et al. 1993; Hight et al. 1995).

Galerucella calmariensis L. (Coleoptera, Chrysomelidae) a species distributed throughout the Eurasian range of purple loosestrife (Palm6n 1945; Silfverberg 1974) was used as the model herbivore. The species was introduced into North America in 1992 as biological control agent (Hight et al. 1995) and it's life history and impact are discussed by Blossey (1995a, b).

Methods and Materials

Seeds of *L. salicaria* were collected between 1989 and 1993 from populations in Europe (13), North America (22), and Australia (1). At least 20 individual plants per population were sampled and seeds sent to Cornell University, Ithaca, New York. Seeds were stored dry at room temperature and were germinated in spring 1994 on a mix of potting soil and sand. After 4 weeks, seedlings were transferred into an experimental garden established on the bottom of a drained pond. The area was divided into a grid of 180 identical cells (20 by 20 cm) and seedling location completely randomized within the grid. Each plant (5 replicates per genotype) was placed in the center of a cell directly into the soil. During the next year plants were watered as needed and left undisturbed. *G. calmariensis* had established a free ranging population at the experimental site. Adult beetles colonizing the experimental plants in spring 1995 were collected and removed from the site to keep plants herbivore free. Between mid-June and mid-July 1995 (peak emergence and flight period of newly emerged *G. calmariensis)* each plant was carefully examined ever), or every other day. Adult insects colonizing the experimental plants were counted and collected using an aspirator. On 15 July 1995 all above-ground plant parts were harvested, air dried in a greenhouse until constant weight, and plant mass determined. Data were analyzed with a one factor analysis of variance.

Results

The comparison of the dry shoot biomass of the 36 different genotypes harvested on 15 July 1995 shows that biomass production was highly variable between sites (Fig. 1). With few exceptions, however, genotypes from North America or Australia produced more above ground biomass than genotypes from Europe (Fig. 1). The differences among North America and Europe are highly significant ($F = 25.88$; $df = 1, 146$; $P < 0.0001$) and support the EICA hypothesis. In accordance with predictions of the EICA hypothesis, teneral beetles preferably colonized genotypes from North America (Fig. 2). Again differences between continents are highly significant ($F = 20.32$; $df = 1, 146$; $P < 0.0001$). Since European genotypes produced less biomass, the preference of *G. calmariensis* for plants from North America or Australia may simply be a function of plant size (height, mass, etc.). However, an analysis accounting for size-dependent herbivore attack shows that North American genotypes attract more beetles per g biomass than European genotypes (Fig. 3). Differences between continents are significant ($F = 4.81$; $df = 1, 146$; $P = 0.0296$) and support the predictions of the EICA hypothesis.

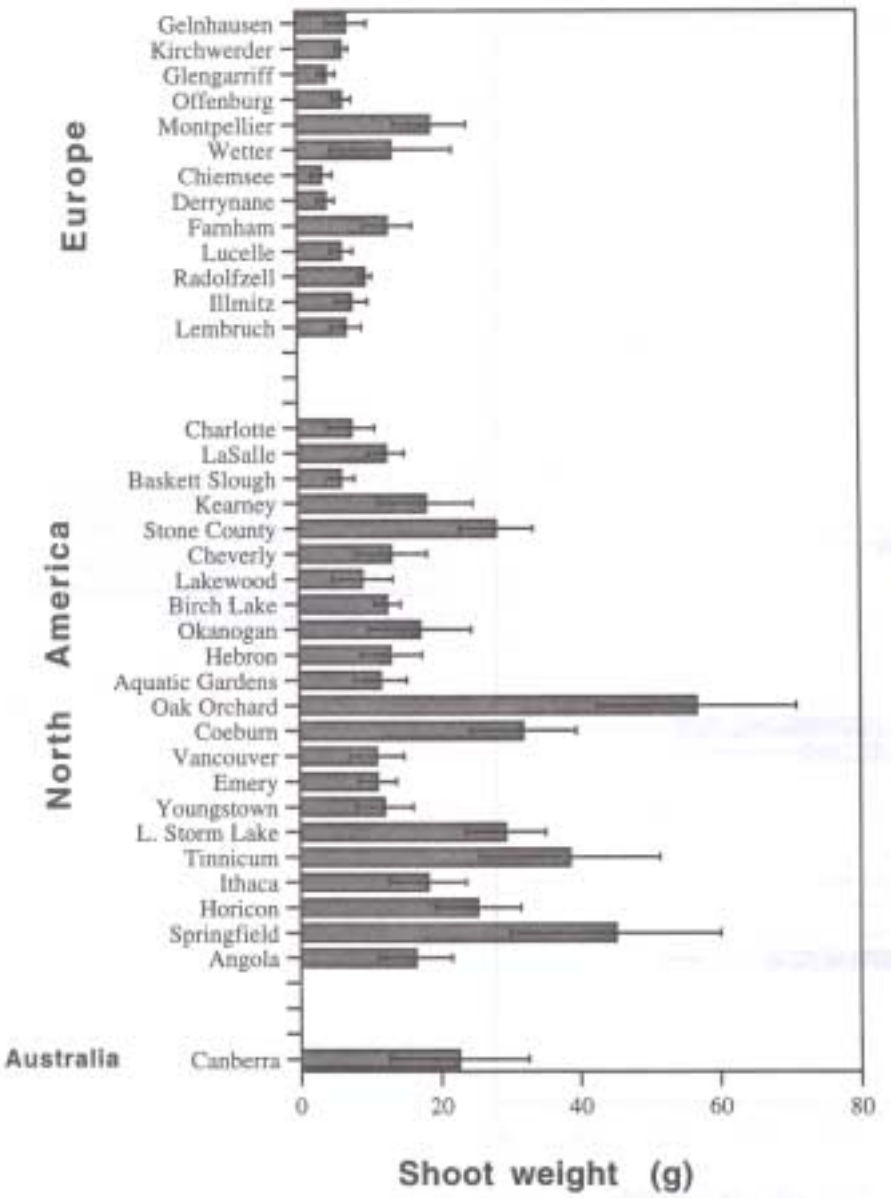

Figure 1. Above ground dry biomass (g) of different genotypes of *L. salicaria* from Europe, North America, and Australia grown in a common garden. Data are means (± SE) of five replicates/genotype.

Discussion

Purple loosestrife occurs throughout similar climatic ranges in Eurasia and North America, occasionally competing with the same species in these separate environments (Blossey and Kamil 1996). Despite these similarities, North American genotypes are competitively superior and persist in invaded wetlands, effectively eliminating recruitment of native plant species. European genotypes on the contrary, are competitively inferior; monospecific stands of purple loosestrife are short-lived and *L. salicaria* is a regular but infrequent species in mixed plant communities (Shamsi and Whitehead 1974).

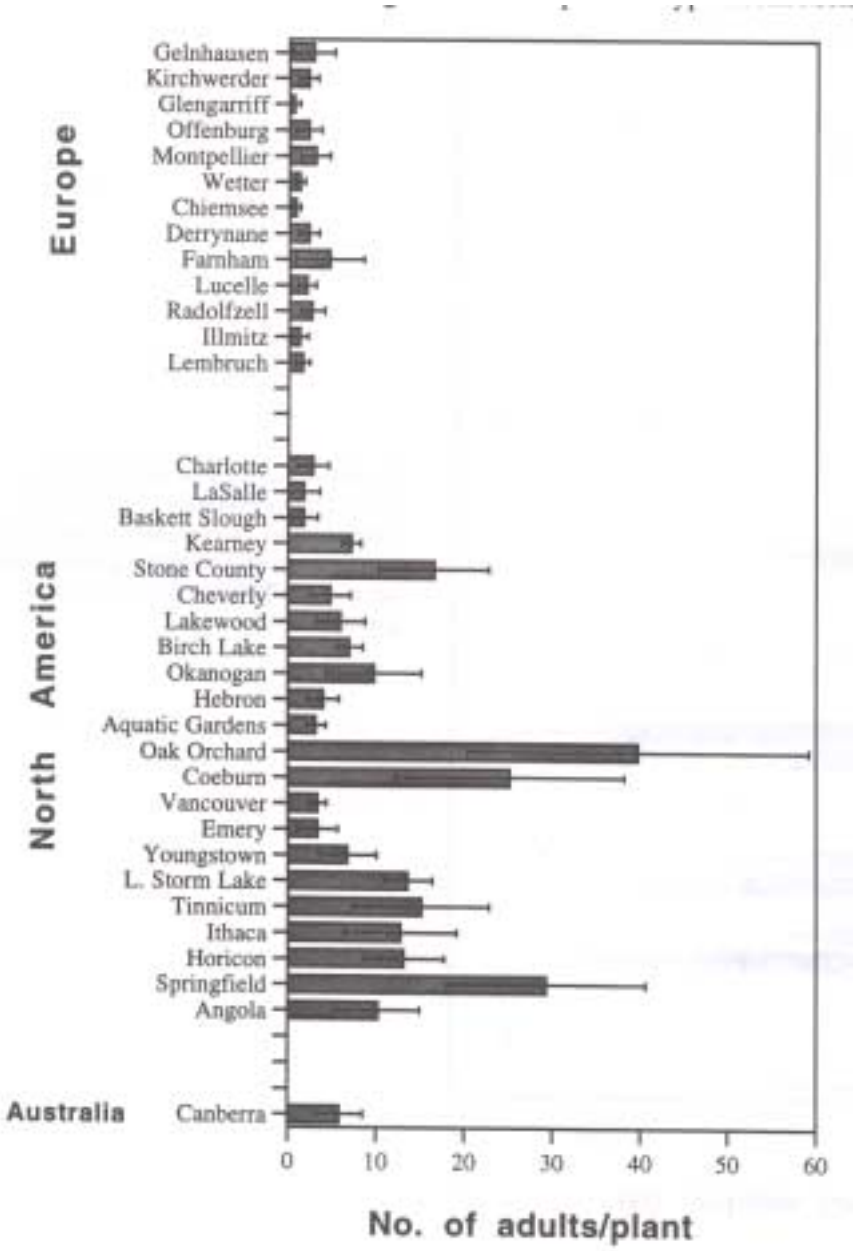

Figure 2. Number of teneral adult *G. calmariensis* collected from different genotypes of *L. salicaria* grown in a common garden. Data are means (± SE) of five replicates/genotype.

The absence of herbivory in North America only partially explains the superiority of *L. salicaria*. The common garden experiment demonstrated that even under identical growing conditions and in the absence of herbivory, North American genotypes show increased vegetative growth. These results suggest that during introduction, establishment, and spread of *L. salicaria* in North America (and Australia?), selection has favored genotypes with increased vegetative growth. Such genotypes exist in European populations, as indicated by better than average growth of genotypes from Montpellier and Wetter, but their frequency is greatly reduced compared to North America. We hypothesize that the attack by specialized natural enemies in Europe should reduce the frequency of genotypes with high vegetative growth since these individuals should be less well defended. Thus, European populations showing increased vegetative growth in our experiment may have been recently established and the herbivores there have not yet completed the selective removal of less well defended genotypes. The preference of *G. calmariensis* for North American genotypes suggests that a shift from herbivore defense to vegetative growth occurred and that *G. calmariensis* can detect this shift. These findings support the EICA hypothesis (Blossey and Nötzold 1995).

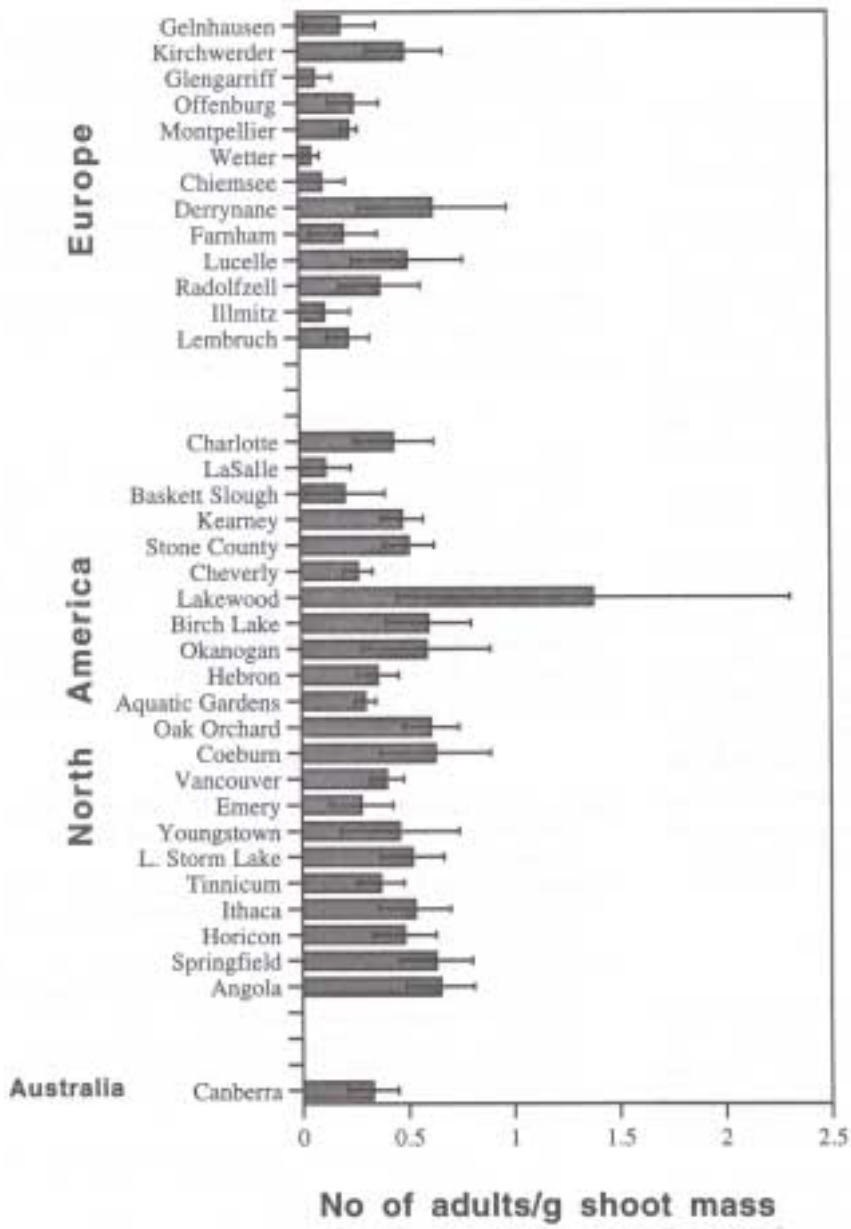

Figure 3. Number of teneral adult *G. calmariensis* per g biomass collected from different genotypes of *L. salicaria* grown in a common garden. Data are means (±SE) of five replicates/genotype.

The EICA hypothesis predicts that insect **performance** should improve on genotypes from an area without herbivory. The preference of teneral adults reported here is an indication (but not a direct test) for the proposed improvement. Overall, in expanding the preliminary findings of Blossey and Nötzold (1995), the reported results support their predictions. We hypothesize that increased vegetative growth results in improved competitive ability of non-indigenous plants. The improved growth, in turn, could be explained through a shift in biomass allocation patterns reducing investment in anti-herbivore defense.

The EICA hypothesis might explain the superiority of invading non-indigenous plants but only about 1% of introduced species actually cause serious problems (Williamson and Brown 1986; di Castri 1989); 99% of the species establish populations in alien environments but remain minor components of their new communities. These discrepancies may be explained by the historic interaction of plants and herbivores in their area of origin that have shaped plant life histories (Grubb 1992). According to the optimal defense hypothesis (see Herrms and Mattson 1992 for details) plants optimize their defense investments in direct proportion to the cost of their loss. Plant populations will reflect their experience of herbivory (frequency and severity) over evolutionary time in their pattern of defense investment (Feeney 1976; Rhoades and Cates 1976). This leads to a second hypothesis: Historic Herbivore Pressure Hypothesis (HHP).

Historic Herbivore Pressure Hypothesis (HHP)

Plant species that are under severe herbivore pressure in their native range are more likely to become invasive as aliens. According to optimal defense theory such plants invest a significant proportion of their resources in defense (Fagerström 1989; Herms and Mattson 1992). After introduction into a habitat without specialized natural enemies, selection will favor genotypes with increased vegetative growth and reduced levels of defense. In the absence of specialized herbivores this shift towards genotypes with superior vegetative growth will be a very rapid process because selection can operate unidirectionally. Plants that are not under severe herbivore pressure and do not expend a lot of energy to defend themselves do not possess a resource pool that can be shifted to improve vegetative growth. They are therefore less likely to respond as successfully to a change in selection pressures. In addition, the selection pressures do not change as dramatically, since the reduction in herbivore pressure is insignificant if herbivores are not an important selection pressure in the native range. For highly attacked species, however, the sudden absence of specialized herbivores represents a major change in selection pressures.

Conclusions

The invasion of non-indigenous plants continues to be a major threat to the integrity of our ecosystems. Currently we are unable to predict the success of a new plant species in a certain environment and far too often purposeful introductions of exotic plants result in environmental disasters. One way of preventing such disasters would be to ban exotic introductions. But even a complete prevention would leave us with hundreds of established undesirable species. The most efficient approach to control non-indigenous plants is at their early stage of establishment. Unfortunately, past control attempts focused on species that had already gotten out of hand. It might be more successful to focus on species with potential to become serious invaders and begin control programs early. The EICA and HHP hypotheses might offer a tool to screen non-indigenous plants and rank species according to their potential to become invasive. This would allow to focus resources on the most important problem plant species. Before such an approach can be implemented, however, we need to test both hypotheses with a number of other species.

In the past, research on invasions and invasive species has focused on species traits or the invaded environment. These factors are important, however, the analysis of environments or species traits has not increased our ability to understand or predict invasion patterns. We need to focus more attention on the processes underlying successful invasions and cannot assume that species experiencing completely different selection pressures remain unchanged. A much better understanding of ecologically and evolutionary processes can be gained by comparing ancestral and invasive populations.

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