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What determines the increased competitive ability of invasive non-indigenous plants?

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Abstract. There are very few valid generalizations about invasive species. It is only possible to make weak probabilistic predictions about which species will invade. A phenomenon that has not received much attention, however, is the observation that many plants in alien environments appear more vigorous, grow taller and produce more seeds than in their native distribution. The increased vigour and success of aliens in the area of introduction has been attributed to more favourable environments, or release from phytophagous natural enemies. The optimal defence hypothesis predicts that plants with limited resources show trade-offs in biomass allocation among storage, maintenance, growth, reproduction, and defence. According to the framework of the optimal defence theory, the invasiveness of non-indigenous plants could be a result of shifts in biomass allocation patterns favouring vegetative growth in the absence of natural enemies. We tested *Lythrum salicaria* (purple loosestrife) genotypes from Europe, North America, and Australia and confirmed predictions that under identical growing conditions plants from the introduced range show increased vegetative growth compared with plants from the native range. In addition, specialized herbivores introduced for the biological control of *L.. salicaria* colonized genotypes from North America and Australia in preference to those from their native range. Our findings support the hypothesis that the success of invasive plants might be explained by selection favouring genotypes with improved competitive abilities (i.e. vegetative growth) and reduced herbivore defence.

Introduction

Non-indigenous plants are a major threat to the integrity of the worlds ecosystems (Drake *et al.* 1989). The proportion of exotic plants in different floras varies widely from 10% in some European countries to about 50% in New Zealand (Heywood 1989). Attempts to identify attributes of invaders from species traits have been unsuccessful (Gray 1986; Crawley 1987). The species come from a wide range of taxa and life-history forms but often tend to form dense monospecific stands, eliminating regeneration by other plants (Crawley 1987). Therefore, it is only possible to make weak, probabilistic predictions about which species will invade (Gilpin 1990; Daehler and Strong 1993).

A phenomenon that has not received much attention, however, is the observation that, in alien environments, some plants appear to be more vigorous, grow taller, and produce more seeds than in their native distribution (Crawley 1987). For example, the seed production of *Chrysanthemoides monilifera* (native to South Africa) in Australia and of *Acacia longifolia* (native to Australia) in South Africa is an order of magnitude higher where the plants are aliens (Noble 1989). The vigour and success of aliens in areas where they have been introduced has been attributed to more favourable environments and release from natural phytophagous enemies (Crawley 1987).

Recently, Blossey and Nötzold (1995) proposed the EICA (evolution of increased competitive ability) hypothesis, i.e. the success of invasive plants results from a shift in biomass allocation patterns. In the absence of herbivores, selection favours genotypes with improved competitive abilities and reduced resource allocation to herbivore defences. This hypothesis rests on the assumption that plants with limited resources show trade-offs in biomass allocation among maintenance, growth, storage, reproduction, and defence (Coley *et al.* 1985; Bazzaz *et al.* 1987; Fagerström 1989; Herms and Mattson 1994; 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 that: (i) under identical growing conditions, individuals of a species taken from an area where they have been introduced will produce more biomass than individuals taken from the species' native range; and (ii) 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 we expand this preliminary analysis and 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 that was introduced into North America in the early 1800s. 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 in North America persist for decades 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; Blossey 1991). In Europe, displacement 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).

Table 1. Relative frequency (%) of the occurrence of purple loosestrife in different habitat-types in Europe (N = 152 sites), Oregon (N = 101 sites), Minnesota (N = 1470 sites) and Wisconsin (N = 2202 sites). Data from Europe after Blossey (1989), from Oregon after Huso and McEvoy (1995), from Minnesota after Skinner *et al.* (1994), and from Wisconsin after Henderson (1987).

Habitat-types	Europe	Oregon	Minnesota	Wisconsin
Ditches	27	15.8	20	35
Lakes and ponds	36.1	9.9	32	14
Pastures and marshes	36.9	32.7	31	27
Creeks and rivers	-	38.6	9	21
Others	-	3	8	3

Purple loosestrife grows in a wide range of similar habitat-types in Europe and North America (Table 1). The most important factor determining the presence of *L. salicaria* at a particular site is the moisture regime especially during germination (Shamsi and Whitehead 1974). Differences between regions are largely due to the availability of certain habitat-types. Lakeshores or ponds are abundant in northern Europe and Minnesota, but are rare in most parts of Oregon. Wet pastures and marshes (spring-flooded, summer-dry) are a preferred habitat for *L. salicaria* across all regions. Rivers or creeks are very important habitats in Oregon (and other areas in the arid mid-west) and are of some importance in Minnesota and Wisconsin. European *L. salicaria* populations are largely dependent on man-made sites (often ditches) because of habitat loss during channeling of almost all creeks and rivers.

A comparison of the abundance classes for purple loosestrife shows surprisingly similar results. About 50-70% of the populations consist of less than 100 plants. The frequency of populations with over 1000 plants is highest in Minnesota (Table 2). In comparing

Table 2. Relative frequency (%) of sites, in four abundance classes, of purple loosestrife in Europe (N = 152 sites), Oregon (N = 101 sites), Minnesota (N = 1470 sites) and Wisconsin (N = 2202 sites). Data from Europe after Blossey (1989), from Oregon after Huso and McEvoy (1995), from Minnesota after Skinner *et al.* (1994), and from Wisconsin after Henderson (1987). * 1-20 plants/site. ** Sites with >100 plants.

No. of plants/ site	Europe	Oregon	Minnesota	Wisconsin
<9	12	24.7	28*	44
10 - 99	40	24.7	22	26
100 - 999	36	36.6	23	30**
>1000	12	14.0	27	–

the abundance of *L. salicaria* in Europe and North America, it is necessary to account for the fact that the species became established only recently in the midwest (around the 1930s) and is still expanding its range and abundance despite massive control efforts (Stuckey 1980; Henderson 1987; Skinner *et al.* 1993).

Of the 12 main plant species co-occurring with *L. salicaria,* five were found on both continents (Table 3). Their relative importance was different but the American survey included entire genera such as *Carex* spp. which were omitted from the analysis in Europe (Thompson *et al.* 1987; Blossey 1989).

We used *Galerucella calmariensis* L. (Coleoptera: Chrysomelidae) a species distributed throughout the Eurasian range of purple loosestrife (Palmén 1945; Silfverberg 1974) as the model herbivore in our experiments. The species was introduced into North America in 1992 as a biological control agent (Hight *et al.* 1995). Adults overwinter in the leaf litter and appear in early spring, feeding on young tips and leaves. The main oviposition period is May and June. Larvae feed primarily on developing leaf- and flower-buds; at high densities entire plants can be defoliated (Blossey 1995). Pupation occurs in the leaf litter beneath the host-plant and the new generation of beetles appear at the end of June.

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 the seeds were 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 four weeks, seedlings were transferred into an experimental garden established on the bottom of a drained pond. We used cotton string to divide an area into a grid of 180 identical cells (20 by 20 cm). Seedling location was completely randomized within the grid and each plant (five replicates per genotype) was placed in the centre of a cell directly into the soil. During the next year, plants were watered as needed and left undisturbed. *Galerucella 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 (the period of peak emergence and flight of newly emerged *G. calmariensis*) we carefully examined each plant, either daily or every second day. Adults colonizing the experimental plants were collected using an aspirator. On 15 July 1995 all of the above-ground plant parts were harvested and air dried in a greenhouse until constant weight, to determine the plant mass.

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

Table 3. Plant species and relative frequency of their co-occurrence with purple loosestrife in Europe and North America. (Data from Europe after Blossey 1989, from North America after Thompson *et al.* 1987).

European sites (N = 110)		North American sites (N = 45)	
Plant species	Occurrence	Plant species	Occurrence
Lysimachia vulgaris	48	*Typha* spp.	51
Phragmites australis	44	*Phalaris arundinacea*	45
Filipendula ulmaria	31	*Carex* spp.	20
Urtica dioica	17	*Scirpus* spp.	16
Comarum palustre	13	*Salix* spp.	11
Juncus effusus	13	*Equisetum fluviatile*	9
Epilobium hirsutum	11	*Phragmites australis*	9
Iris pseudacorus	10	*Cyperus* sp.	7
Phalaris arundinacea	10	*Alisma plantago-aquatica*	5
Typha spp.	9	*Urtica dioica*	5
Mentha aquatica	7	*Sparganium eurycarpum*	2
Alisma plantago-aquatica	5	*Agrostis gigantea*	2

(Fig. 1). These results support the EICA hypothesis.

In accordance with predictions of the EICA hypothesis, teneral beetles preferably colonized genotypes from North America and Australia (Fig. 2). 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.) (Fig. 3). An analysis accounting for size-dependent herbivore attack shows that, in general, North American genotypes of the same size attract more beetles than European genotypes (Fig. 4). These results also support the predictions of the EICA hypothesis.

Discussion

Purple loosestrife occurs throughout similar climatic ranges in Eurasia and North America, occasionally competing with the same species in these separate environments (Tables 1, 2 and 3). Despite these similarities, North American genotypes are competitively superior and persist in invaded wetlands, effectively eliminating recruitment of endemic plant species. European genotypes of *L. salicaria*, on the contrary, are competitively inferior; monospecific stands of purple loosestrife are short-lived and the plant is a regular but infrequent species in mixed plant communities (Shamsi and Whitehead 1974; Blossey 1991).

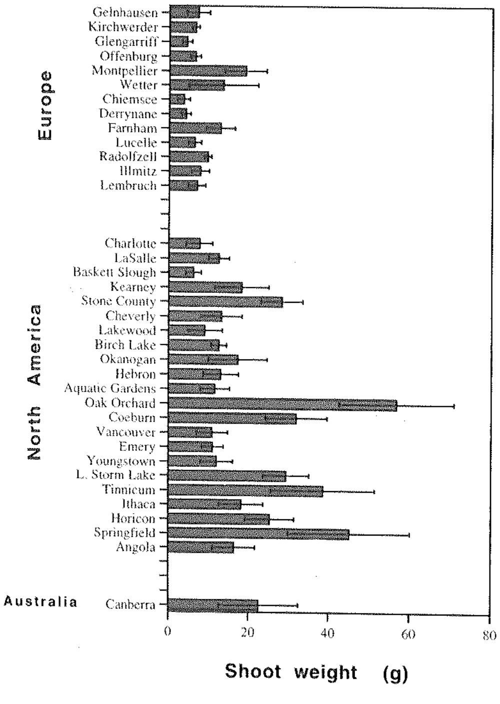

Fig. 1. Above-ground dry biomass (g) of shoots of different genotypes of *L. salicaria* from Europe, North America and Australia, grown in the same garden. Data are means (±SE) of five replicates/genotype.

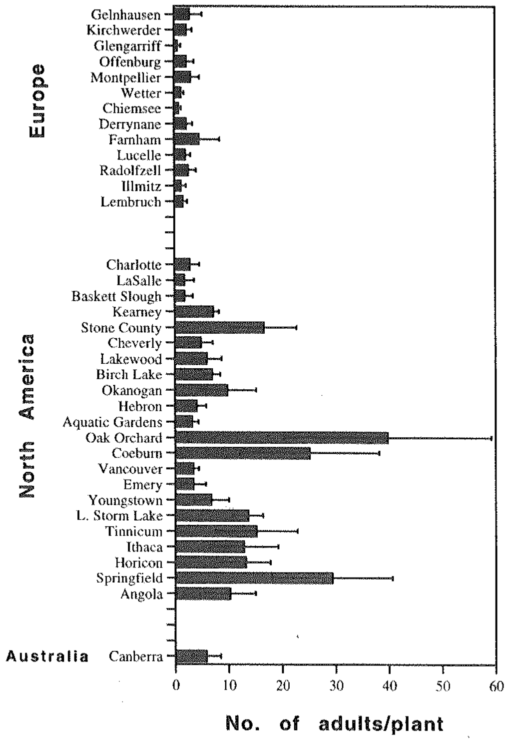

Fig. 2. Number of teneral adult *G. calmariensis* collected from different genotypes of *L. salicaria* grown in the same garden. Data are means (±SE) of five replicates/genotype.

The absence of herbivory in North America only partially explains the superiority of *L. salicaria*. Our experiments demonstrated that even under identical growing conditions and in the absence of herbivory,

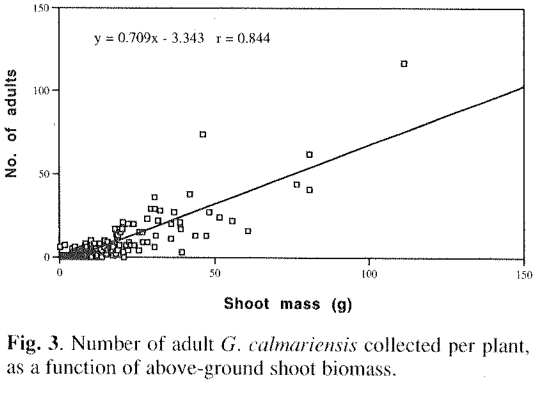

Fig. 3. Number of adult *G. calmariensis* collected per plant, as a function of above-ground shoot biomass.

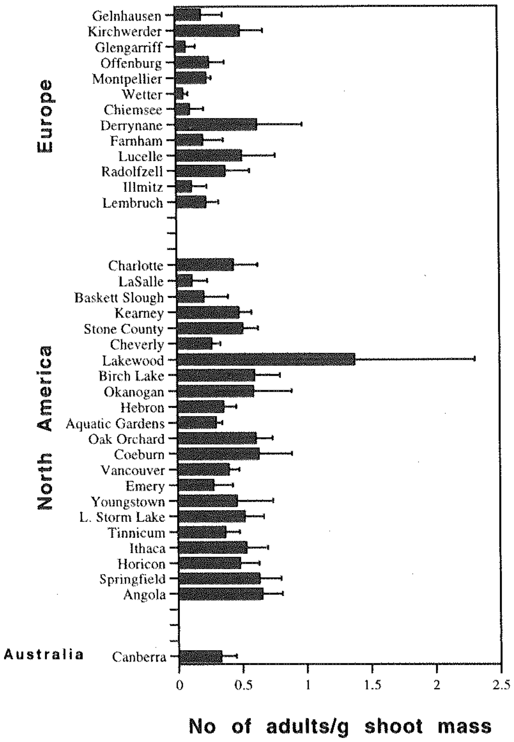

Fig. 4. Number of teneral adult *G. calmariensis* per gram of shoot biomass, collected from different genotypes of *L. salicaria* grown in the same garden. Data are means (±SE) of five replicates/genotype.

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 favoured 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.

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 experiments are, possibly, recently established. In these populations, herbivores 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 defence to vegetative growth occurred. These findings support the EICA hypothesis (Blossey and Nötzold 1995).

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. We attempted to compare the survival, development and weight of *G. calmariensis* larvae on the 36 genotypes by using larval transfers. Unfortunately, coccinellid beetles eliminated most of the larvae from the experimental plants. We were, therefore, unable to collect valid data and we plan to repeat this part of the experiment.

Overall, in expanding the preliminary findings, our results support the predictions of Blossey and Nötzold (1995). The improved competitive ability of non-indigenous plants is a result of improved vegetative growth. This, in turn, could be explained through a shift in biomass allocation patterns reducing investment in anti-herbivore defence.

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 defence hypothesis (see Herms and Mattson 1992 for details) plants optimize their defence 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 defence investment (Feeney 1976; Rhoades and Cates 1976). These arguments lead to a second hypothesis which is described below.

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 defence theory such plants invest a significant proportion of their resources in defence (Fagerström 1989; Herms and Mattson 1992). After introduction into a habitat without specialized natural enemies, selection will favour genotypes with increased vegetative growth and reduced levels of defence. In the absence of specialized herbivores this shift towards genotypes with superior vegetative growth will be rapid because selection will be unidirectional.

Plants that are not under severe herbivore pressure do not possess a resource pool that can be shifted to improve vegetative growth. They are therefore less likely to respond as markedly 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 have resulted 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 is to control non-indigenous plants at an early stage of their establishment. Unfortunately, most control attempts in the past have focused on species that were already widespread and problematic. It might be more successful to focus on species with the potential to become invaders and to begin control programmes early. The EICA and HHP hypotheses might offer a tool to screen non-indigenous plants and to rank species according to their potential to become invasive. This would allow us to focus resources on the most important problem-plant species. Before such an approach can be implemented, however, we need to test both hypotheses on a number of other invasive plant species.

Much previous research on invasions and invasive species has focused on species traits or the invaded environment and 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 we cannot assume that species experiencing completely different selection pressures remain unchanged. A much better understanding of ecological and evolutionary processes can be gained by comparing ancestral with invasive populations.

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