

LETTER

Herbivores and the success of exotic plants: a phylogenetically controlled experiment

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Abstract

In a field experiment with 30 locally occurring old-field plant species grown in a common garden, we found that non-native plants suffer levels of attack (leaf herbivory) equal to or greater than levels suffered by congeneric native plants. This phylogenetically controlled analysis is in striking contrast to the recent findings from surveys of exotic organisms, and suggests that even if ‘enemy release’ does accompany the invasion process, this may not be an important mechanism of invasion, particularly for plants with close relatives in the recipient flora.

Keywords

Congeneric pairs, exotics and aliens, herbivory, invasive species, plant invasions, plant–insect interactions.

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INTRODUCTION

The accidental or intentional introduction of non-native organisms continues to threaten natural and agricultural ecosystems worldwide (Mack *et al.* 2000; Pimentel 2002). Recent studies have demonstrated that exotic plant species have smaller pathogen and herbivore communities in their introduced range than in their region of origin (Fenner & Lee 2001; Wolfe 2002; Mitchell & Power 2003). This reduced-parasite biota potentially gives exotic plants an advantage in comparison with native plants, as predicted by the classic ‘enemy release’ hypothesis for the success of introduced organisms (Keane & Crawley 2002; Wolfe 2002; Mitchell & Power 2003; Torchin *et al.* 2003). Most previous studies, however, lack in direct experimental comparisons of impacts on native vs. exotic organisms in a common habitat (Schierenbeck *et al.* 1994). This comparison is critical because (i) a lower diversity of enemies does not necessarily translate to less damage (Maron & Vilà 2001); (ii) the local processes that control populations of native and exotic plants could be masked in continent-wide surveys; and (iii) measuring native and exotic plants in a common environment ensures that any observed differences are not the product of unmeasured environmental or faunal variation between native and foreign sites.

Old-field habitats of eastern North America are dominated by a mixture of native and exotic herbaceous plant species. To test the impacts of folivorous insects on native vs. exotic plants, a field experiment with 30 taxonomically paired old-field plant species in a common garden was

conducted. Using congeneric pairs factors in a large component of interspecific variation, leaving behind species that are similar except for their native/exotic status.

MATERIALS AND METHODS

Seeds were collected from 30 old-field plant species occurring at or near the University of Toronto’s Koffler Scientific Reserve at Jokers Hill (44°03′N, 79°29′W), near Newmarket in southern Ontario, Canada (Table 1). These 30 species formed 14 congeneric pairs and one confamilial pair, in which one species from each pair was a native, and another was an exotic of Eurasian origin. All the exotic plant species probably have been in the region for less than 200 years. Seeds from each species were germinated in a greenhouse in the spring of 2002 and planted onto a plowed field in a completely randomized design ($n \approx 15$ plants for each of the 30 species). Plants were spaced 1 m apart and the plot was not weeded or irrigated.

Late in the growing season, a survey of percentage leaf damage imposed by naturally occurring insect herbivores was conducted. The percentage leaf damage was estimated on 24 September 2002 by destructively harvesting 10 random leaves, while looking away, from each of the 390 surviving plants and by visually scoring each leaf for percentage damage to the nearest 10%. The percentage damage of each plant was then estimated as the mean per cent of leaf area missing as a result of herbivory.

A laboratory bioassay of resistance to a generalist lepidopteran (*Spodoptera exigua* Noctuidae) was also conducted.

Table 1 Species employed in the experiment. The presence of wild plants at our study site is indicated by an 'x' under JH; all other plants occur in southern Ontario. Native or alien origin follows Morton & Venn (1990) and nomenclature follows Gleason & Cronquist (1991). LH, life history from Newmaster *et al.* (1998); 'A' = annual, 'B' = biennial, 'P' = perennial. The numbers in parentheses refer to the taxonomic pair shown in Fig. 1. Under the numbers in parentheses and family name, the results from an individual *t*-test on that pair alone are provided. See Fig. 1 for the mean differences in herbivory

Plant family	Species	Origin	JH	LH
(1) Asclepidaceae (<i>t</i> = 3.1, d.f. = 26, <i>P</i> < 0.01)	<i>Asclepias syriaca</i>	Native	x	P
	<i>Cynanchum rossicum</i>	Alien	x	P
(2) Asteraceae (<i>t</i> = 1.7, d.f. = 27, <i>P</i> = 0.10)	<i>Lactuca canadensis</i>	Native	x	B
	<i>Lactuca serriola</i>	Alien	x	BA
(3) Asteraceae (<i>t</i> = 1.1, d.f. = 16, <i>P</i> = 0.29)	<i>Senecio pauperculus</i>	Native		P
	<i>Senecio vulgaris</i>	Alien	x	A
(4) Asteraceae (<i>t</i> = 3.0, d.f. = 21, <i>P</i> < 0.01)	<i>Artemisia campestris</i>	Native		B
	<i>Artemisia biennis</i>	Alien	x	B
(5) Brassicaceae (<i>t</i> = 0.7, d.f. = 28, <i>P</i> = 0.47)	<i>Lepidium densiflorum</i>	Native	x	A
	<i>Lepidium campestre</i>	Alien	x	AB
(6) Campanulaceae (<i>t</i> = 4.6, d.f. = 19, <i>P</i> < 0.01)	<i>Campanula rotundifolia</i>	Native	x	P
	<i>Campanula rapunculoides</i>	Alien	x	P
(7) Caryophyllaceae (<i>t</i> = 1.7, d.f. = 31, <i>P</i> = 0.09)	<i>Cerastium arvense</i>	Native		P
	<i>Cerastium fontanum</i>	Alien	x	P
(8) Caryophyllaceae (<i>t</i> = 1.5, d.f. = 29, <i>P</i> = 0.14)	<i>Silene antirrhina</i>	Native	x	B
	<i>Silene vulgaris</i>	Alien	x	P
(9) Chenopodiaceae (<i>t</i> = 0.9, d.f. = 18, <i>P</i> = 0.37)	<i>Chenopodium simplex</i>	Native	x	A
	<i>Chenopodium album</i>	Alien	x	A
(10) Plantaginaceae (<i>t</i> = 2.6, d.f. = 27, <i>P</i> = 0.02)	<i>Plantago rugelii</i>	Native	x	AP
	<i>Plantago major</i>	Alien	x	AP
(11) Poaceae (<i>t</i> = 0.2, d.f. = 25, <i>P</i> = 0.91)	<i>Bromus kalmii</i>	Native		P
	<i>Bromus inermis</i>	Alien	x	P
(12) Poaceae (<i>t</i> = 1.8, d.f. = 29, <i>P</i> = 0.08)	<i>Elymus trachycaulus</i>	Native		P
	<i>Elymus repens</i>	Alien	x	P
(13) Rosaceae (<i>t</i> = 1.7, d.f. = 24, <i>P</i> = 0.11)	<i>Geum aleppicum</i>	Native	x	P
	<i>Geum urbanum</i>	Alien	x	P
(14) Rosaceae (<i>t</i> = 1.3, d.f. = 15, <i>P</i> = 0.22)	<i>Potentilla arguta</i>	Native	x	P
	<i>Potentilla recta</i>	Alien	x	P
(15) Rubiaceae (<i>t</i> = 3.0, d.f. = 25, <i>P</i> < 0.01)	<i>Galium boreale</i>	Native	x	P
	<i>Galium verum</i>	Alien	x	P

Spodoptera exigua is a widely employed generalist herbivore known to feed on plants in well over 20 families. This test examines whether there are differences between the native and exotic plants, irrespective of their fauna of enemies; these differences may have evolved since invasion or may simply reflect different evolutionary histories of the plants. To assay resistance, a single leaf of each of the field plants was cut and placed in a 90 mm Petri dish lined with moist filter paper in a cooler. Petri dishes were brought back to a non-air-conditioned laboratory and one *S. exigua* neonate was introduced to each dish. Petri dishes were sealed with parafilm and the larvae were allowed to feed for 5 days at ambient temperature. After this assay period, mortality of the herbivore and growth of the survivors were assayed. Growth was assayed by weighing frozen wet mass of larvae to the microgram.

Fixed-factor factorial ANOVAS were employed for the analyses. Arcsine square root transformed values for the percentage leaf damage were used. The effect on larval mortality in the bioassay was assessed with a paired *t*-test on arcsine square root transformed percentage larval death on each plant species by taxonomic pair.

RESULTS AND DISCUSSION

Contrary to the predictions of the enemy release hypothesis, the census of leaf damage revealed that there were greater levels of herbivory by naturally occurring herbivores on exotic plants than on natives (Fig. 1; 7.5% compared with 5.3% herbivory, $F_{1,360} = 7.391$, $P = 0.007$). Herbivore damage varied significantly among genera ($F_{14,360} = 25.073$, $P < 0.001$), supporting the decision to pair congeners for the analysis. Although overall levels of herbivory were low, and pairs did significantly vary in the relative level of herbivory on native vs. exotics (interaction term: $F_{14,360} = 2.027$, $P = 0.015$), the pattern of greater herbivory on exotics was found in 11 of the 15 taxonomic pairs. The finding of the present study rejects the hypothesis that exotic plants generally have lower levels of herbivory than natives (Fig. 1). It is unclear whether the higher levels of damage on the exotic plants was a product of higher diversity of herbivores compared with natives. The correlation between herbivore diversity and damage is an issue requiring further study.

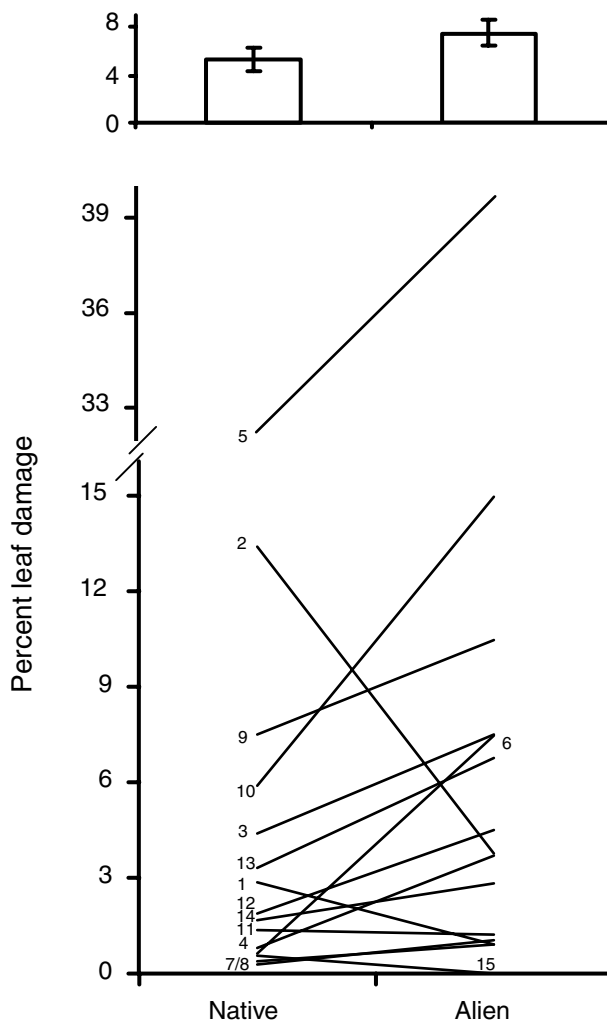


Figure 1 Effects of plant origin on herbivory by naturally occurring insects in a common garden plot (Koffler Scientific Reserve at Jokers Hill, University of Toronto). The top panel summarizes the effects across all species (raw mean \pm SEM), while the bottom panel shows the means for each of the 15 taxonomic pairs. The taxonomic identity of each pair in the bottom panel is given by the number and corresponds to Table 1.

Plant abundance was not a clear explanatory variable for the patterns of herbivory. All species in the present study are considered common to very common in Ontario (abundances ranked by the Ontario Natural Heritage Information Centre, <http://www.mnr.gov.on.ca/MNR/nhic/nhic.cfm>). Similarly, invasiveness did not strongly correlate with variation in herbivore damage [invasiveness ranked by Ontario Society for Ecological Restoration (OSER), <http://www.ser-ontario.org/publica.htm>]. For example, OSER ranks both *Campanula rapunculoides* and *Bromus inermis* as category 4, exotic species that do not pose a serious threat. Yet, in comparison with their native congeners, alien *Campanula* had nearly

12 times more damage, while alien *Bromus* has a slightly lower level of damage (Fig. 1).

In the bioassay of resistance with a single generalist herbivore, neither larval mass of the survivors ($F_{1,87} = 1.280$, $P = 0.269$) nor larval mortality ($t = 1.189$, d.f. = 14, $P = 0.254$) were affected by native vs. exotic origin. This result indicates that exotic species are no more resistant to herbivores than native congeners, although the mortality data tended to be lower on exotics, which is consistent with patterns of leaf damage (per cent mortality of *S. exigua* \pm SEM on native plants was 78 ± 5 vs. 64 ± 7 on exotic plants). This similarity between natives and exotics is probably a consequence of the chemical and physical similarity between congeners, and may not apply to exotics that are more phylogenetically distant from the native flora. Such 'phylogenetically isolated' species may be more likely to escape enemies in new regions (Darwin 1859; Rejmánek 1999; Duncan & Williams 2002), perhaps contributing to the evidence of predator escape produced by broad but phylogenetically uncontrolled surveys (e.g. Mitchell & Power 2003). One limitation of using congeneric pairs is that inference is limited to highly similar species, potentially biasing results against finding the patterns evident in phylogenetically broader studies. However, even congeneric plants often differ in invasiveness: Mack *et al.* (2000) indicate that 'guilt by [taxonomic] association has proven imprecise at predicting invasive potential'. Thus, we contend that the benefits of phylogenetic control outweigh the costs, as significant variation in invasiveness remains even after unwanted noise is reduced by phylogenetic correction.

Had the enemies other than invertebrate folivores been examined, it would have been possible to find different results. For example, Mitchell & Power (2003) considered foliar pathogens and viruses, Wolfe (2002) assayed several herbivore and pathogen guilds, and Fenner & Lee (2001) focused on insect seed predators. However, Blaney & Kotanen (2001) obtained results similar to the present study, in an experiment designed to assess the impacts of fungal seed pathogens on native and exotic congeners, including most of the pairs included in our experiment. This study found that fungi caused significant losses of seeds in wet meadows, but that these losses did not differ between native and exotic plant species. Finally, Maron & Vilà (2001) documented numerous cases of attack by native enemies on exotic plants, suggesting that even successful escape from some enemies may not translate to less damage or better performance in the novel environment. Ultimately, the net impact on plant fitness (summing across plant resistance and tolerance to attack) will determine the role of enemies in the success of exotic plants (Strauss & Agrawal 1999).

The present report challenges the enemy release hypothesis, as exotic flowering plants appear to be

experiencing greater levels of attack across a broad range of families, compared with their native counterparts. Although the identity and origin of the herbivores responsible is unknown, their identity will be critical to make conclusions about the causes of the patterns observed in this study. The finding that exotic plants are less able to escape herbivory than congeneric natives indicates that native plants may be better adapted to the local herbivore fauna than non-natives (Shea & Chesson 2002), as asserted by the 'new association' hypothesis of biological control (Hokkanen & Pimentel 1989).

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REFERENCES

- Blaney, C.S. & Kotanen, P.M. (2001). Effects of fungal pathogens on seeds of native and exotic plants: a test using congeneric pairs. *J. Appl. Ecol.*, 38, 1104–1113.
- Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection*. Murray, London.
- Duncan, R.P. & Williams, P.A. (2002). Darwin's naturalization hypothesis challenged. *Nature*, 417, 608–609.
- Fenner, M. & Lee, W.G. (2001). Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand. *NZ. J. Ecol.*, 25, 95–99.
- Gleason, H. & Cronquist, A. (1991). *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd edition. New York Botanical Garden, Bronx, New York.
- Hokkanen, H.M.T. & Pimentel, D. (1989). New associations in biological control – theory and practice. *Can. Entomol.*, 121, 829–840.
- Keane, R.M. & Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.*, 17, 164–170.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.*, 10, 689–710.
- Maron, J.L. & Vilà, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, 95, 361–373.
- Mitchell, C.E. & Power, A.G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature*, 421, 625–627.
- Morton, J.K. & Venn, J.M. (1990). *A checklist of the Flora of Ontario – Vascular Plants*. University of Waterloo Biology Series 34. Department of Biology, University of Waterloo, Waterloo, Ontario.
- Newmaster, S.G., Lehela, A., Uhlig, P.W.C., McMurray, S. & Oldham, M.J. (1998). *Ontario Plant List*. Forest Research Paper No. 123. Ontario Forest Research Institute, Sault Sainte Marie, ON, Canada.
- Pimentel, D. (2002). *Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species*. CRC, Boca Raton, Florida.
- Rejmánek, M. (1999). Invasive plant species and invulnerable ecosystems. In: *Invasive Species and Biodiversity Management* (eds Sandlund, O.D., Schei, P.J. & Viken, A.). Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 79–102.
- Schierenbeck, K.A., Mack, R.N. & Sharitz, R.R. (1994). Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, 75, 1661–1672.
- Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.
- Strauss, S.Y. & Agrawal, A.A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.*, 14, 179–185.
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J. & Kuris, A.M. (2003). Introduced species and their missing parasites. *Nature*, 421, 628–630.
- Wolfe, L.M. (2002). Why alien invaders succeed: support for the escape-from-enemy hypothesis. *Am. Naturalist*, 160, 705–711.

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