biology letters

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Biol. Lett. 2006 **2**, 189-193
doi: 10.1098/rsbl.2005.0433

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doi:10.1098/rsbl.2005.0433
Published online 1 March 2006

Novel chemistry of invasive exotic plants

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Of the many exotic plants that have become naturalized in North America, only a small proportion are pests capable of invading and dominating intact natural communities. In the present study, we tested the hypothesis that the most invasive plants are phytochemically unique in their new habitats. A comparison of exotic plant species that are highly invasive in North America with exotics that are widespread, but non-invasive revealed that the invasive plants were more likely to have potent secondary compounds that have not been reported from North American native plants. On average, the compounds found in the invasive plants were reported from fewer species, fewer genera and fewer families than those from non-invasive plants. Many of the unique phytochemicals from invasive plants have been reported to have multiple activities, including antiherbivore, antifungal, antimicrobial and allelopathic (phytotoxic) effects, which may provide the plants with several advantages in their new environments.

Keywords: alien plants; enemy-release hypothesis; plant secondary chemistry

1. INTRODUCTION

In the search for characteristics of exotic plants that might serve as predictors of invasiveness, most studies have examined life-history traits rather than attributes that more directly reflect interactions with potential natural enemies and competitors in the plants' new ranges (Mack 1996). Recent advances have shown that such interactions are critical in determining invasiveness. Exotics escaping pathogens (Mitchell & Power 2003) and herbivores (Carpenter & Cappuccino 2005; Cappuccino & Carpenter 2005) to a greater extent are more invasive than those that are more heavily attacked by natural enemies in their new ranges, suggesting that invasive exotics may be better defended from enemies than non-invasive plants. Interactions with native competitors are also important. For example, root exudates of some invasive plants contain novel allelopathic 'weapons', chemicals that are highly toxic to unadapted native plants (Callaway & Aschehoug 2000; Callaway & Ridenour 2004). By virtue of their better defences and enhanced competitive ability, phytochemically unique exotics—those with secondary compounds that are absent from or uncommon in the North American flora—might be more likely to become invasive than plants with common secondary chemistry (Lockwood *et al.* 2001). To test this hypothesis, we searched online academic and governmental databases to determine the degree to which invasive and non-invasive exotics shared their most active chemical constituents with native North American plants. Because phytochemically unique plants may represent taxa that are likewise unique or underrepresented in North America (Lockwood *et al.* 2001), we also compared the number of native relatives of invasive and non-invasive exotics.

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2005.0433 or via http://www.journals.royalsoc.ac.uk.

2. MATERIAL AND METHODS

Characterizing plants as invasive or non-invasive is unavoidably subjective. Although there are many lists of invasive species published by governmental agencies, inclusion of a given species in the lists may not be entirely free of political motivation. To avoid any such bias, we asked six colleagues who work on invasive plants to name the top 10 highly invasive exotic plant pests of North American natural areas and to list up to 10 non-invasive exotics as well. Our colleagues were not apprised of the hypotheses to be tested until after we had received their lists. We asked them to limit their lists to perennials (monocarpic or polycarpic), out of concern that the non-invasives list would otherwise be dominated by annuals that cannot invade intact natural communities simply because they require disturbance to become established. We excluded grasses (family Poaceae) from the final list, because their secondary chemistry is less well studied. We consulted the US Department of Agriculture (USDA) PLANTS Database (http://plants.usda.gov) to verify that all species were indeed introduced and excluded any species of questionable origin.

There was agreement among the lists of invasive species provided by our colleagues (12 species appeared on more than one list). The lists of non-invasive plants showed almost no concordance, with only a single species being named by more than one expert. After eliminating plants for which phytochemical information could not be found, the final list comprised 21 highly invasive species representing 17 families and 18 non-invasive species representing 13 families (table 1). Eight of the 21 invasive species were also included in the IUCN's list of 100 worst invaders worldwide (table 1), a list that includes animals as well as plants (Lowe *et al.* 2000).

To choose a single prominent secondary compound for each species, the first author compiled a list of secondary compounds for each species by consulting the Phytochemical Dictionary (Harborne *et al.* 1999) and the USDA Phytochemical and Ethnobotanical Database (http://www.ars-grin.gov/duke/) and by conducting searches using Thomson ISI Web of Science (http://www.isinet.com/products/citation/wos/). From those lists of chemicals, the second author then chose a single prominent compound reported to be highly active against insects, fungi, plants and/or microbes (table 1). When several compounds from a phytochemically redundant class were present, the compound typically present in largest amounts was chosen as representative of the class. We then searched the online NAPRAlert database through the scientific and technical information (STN) on the Web (http://stnweb.cas.org/) and the USDA Phytochemical and Ethnobotanical Database for plants from North America containing these compounds (electronic supplemental material). Since not all of the species in the lists generated by these searches were native to North America (some were cultivated or exotic species that were merely collected from North American sites), the USDA PLANTS Database was consulted to eliminate any non-native plants. The final dataset consisted of the following continuous variables for each of the highly invasive and non-invasive exotic plants: the number of native species containing the exotic's prominent secondary compound and the number of genera and families represented by those native species. A binary variable, whether or not each compound has been reported from at least one native North American plant, was also created.

The degree of taxonomic relatedness to the native flora was derived from information obtained from the USDA PLANTS Database. For each exotic species, we tallied the number of native congeners as well as the number of native confamilial genera. A confamilial genus was considered to be native if it contained at least one native species.

Fourteen species in the present study were included in earlier studies of herbivory on exotic plants in Ontario, Canada and the northeastern US (Carpenter & Cappuccino 2005; Cappuccino & Carpenter 2005). We used the average leaf damage from these

Received 4 November 2005
Accepted 14 December 2005

Table 1. Twenty-one highly invasive and 18 non-invasive exotic species naturalized in North America, their taxonomic affinities, their prominent secondary compounds and the number of native North American taxa from which the compound has been reported.

			number of North American taxa from which the compound has been reported		
species	family	prominent secondary compound	species	genera	families
highly invasive exotic plants					
Acroptilon repens (L.) DC.	Asteraceae	cnicin	0	0	0
Alliaria petiolata (Bieb.) Cavara and Grande	Brassicaceae	alliarinoside	0	0	0
Berberis thunbergii DC.	Berberidaceae	berberine	47	24	12
Celastrus orbiculatus Thunb.	Celastraceae	celastrol	1	1	1
Centaurea biebersteinii DC.	Asteraceae	(-)-catechin	0	0	0
Cytisus scoparius (L.) Link	Fabaceae	sparteine	43	11	6
Elaeagnus angustifolia L.	Elaeagnaceae	harman	1	1	1
Euphorbia esula L.	Euphorbiaceae	esulatin	0	0	0
Hypericum perforatum L.	Clusiaceae	hypericin	1	1	1
Linaria dalmatica (L.) P. Mill.	Scrophulariaceae	linarioside	0	0	0
Lythrum salicaria L.	Lythraceae	gallic acid	58	48	29
Melaleuca quinquenervia (Cav.) Blake	Myrtaceae	nerolidol	17	8	4
Pastinaca sativa L.	Apiaceae	xanthotoxin	12	9	2
Polygonum cuspidatum Sieb. and Zucc.	Polygonaceae	piceid	0	0	0
Pueraria montana (Lour.) Merr.	Fabaceae	biochanin-A	13	1	1
Rhamnus cathartica L.	Rhamnaceae	emodin	5	3	3
Sapium sebiferum (L.) Roxb.	Euphorbiaceae	xanthoxylin	1	1	1
Schinus terebinthifolius Raddi	Anacardiaceae	schinol	0	0	0
Tamarix ramosissima Ledeb.	Tamaricaceae	tamarixetin	2	2	1
Ulex europaeus L.	Fabaceae	maackiain	0	0	0
Vincetoxicum rossicum (Kleopov) Barbar.	Asclepiadaceae	antofine	0	0	0
non-invasive exotic plants					
Aesculus hippocastanum L.	Hippocastanaceae	aescin	0	0	0
Cichorium intybus L.	Asteraceae	lactucin	1	1	1
Daucus carota L.	Apicaeae	falcarindiol	1	1	1
Epilobium hirsutum L.	Onagraceae	gallic acid	58	48	29
Gypsophila paniculata L.	Caryophyllaceae	gypsogenin	1	1	1
Lamium amplexicaule L.	Lamiaceae	ipolamiide	8	2	1
Malus pumila P. Mill.	Rosaceae	rutin	61	41	26
Mentha spicata L.	Lamiaceae	carvone	10	7	3
Nepeta cataria L.	Lamiaceae	nepetalactone	0	0	0
Plantago lanceolata L.	Plantaginaceae	catalpol	21	6	2
Sanguisorba minor Scop.	Rosaceae	ellagic acid	16	14	13
Silene vulgaris (Moench) Garke	Caryophyllaceae	gypsogenin	1	1	1
Solanum dulcamara L.	Solanaceae	solasodine	4	3	2
Sorbus aucuparia L.	Rosaceae	rutin	61	41	26
Syringa vulgaris L.	Oleaceae	verbascoside	23	7	4
Trifolium pratense L.	Fabaceae	biochanin-A	13	1	1
Verbascum thapsus L.	Scrophulariaceae	verbascoside	23	7	4
Vitis vinifera L.	Vitaceae	gallic acid	58	48	29

studies to examine whether phytochemical uniqueness is correlated with low herbivory.

All continuous variables were non-normally distributed, so we used non-parametric Wilcoxon rank-sum tests to compare invasive and non-invasive exotics. A log-likelihood χ^2-test was used to test the hypothesis that the prominent phytochemicals of invasive exotics were less likely to have been recorded from the native North American flora. We performed Spearman's rank correlations to examine the relationship between herbivore damage and phytochemical uniqueness quantified by the number of native species, genera and families reported to contain the prominent secondary compound of the exotics. Wilcoxon rank-sum tests were also used to compare leaf herbivory of plants with unique phytochemistry (prominent phytochemical not recorded from native North American plants) and plants sharing their prominent phytochemicals with native plants. The analyses were performed using JMP IN v. 5.1 (SAS Institute, Cary, NC, USA).

3. RESULTS

Almost half (42.8%) of the highly invasive exotics possessed a prominent secondary compound that has not been recorded from native North American plants, whereas only 11.1% of the prominent chemicals from non-native plants were absent from the North American flora (Log-likelihood $\chi^2=5.16$, d.f. $=1$, $p=0.023$). Active secondary compounds from highly invasive exotics were found in fewer native species (figure 1*a*; Wilcoxon rank-sum test: $\chi^2=5.05$, d.f. $=1$, $p=0.024$), representing fewer native genera (figure 1*b*; Wilcoxon rank-sum test: $\chi^2=4.23$, d.f. $=1$, $p=0.040$) and fewer native families

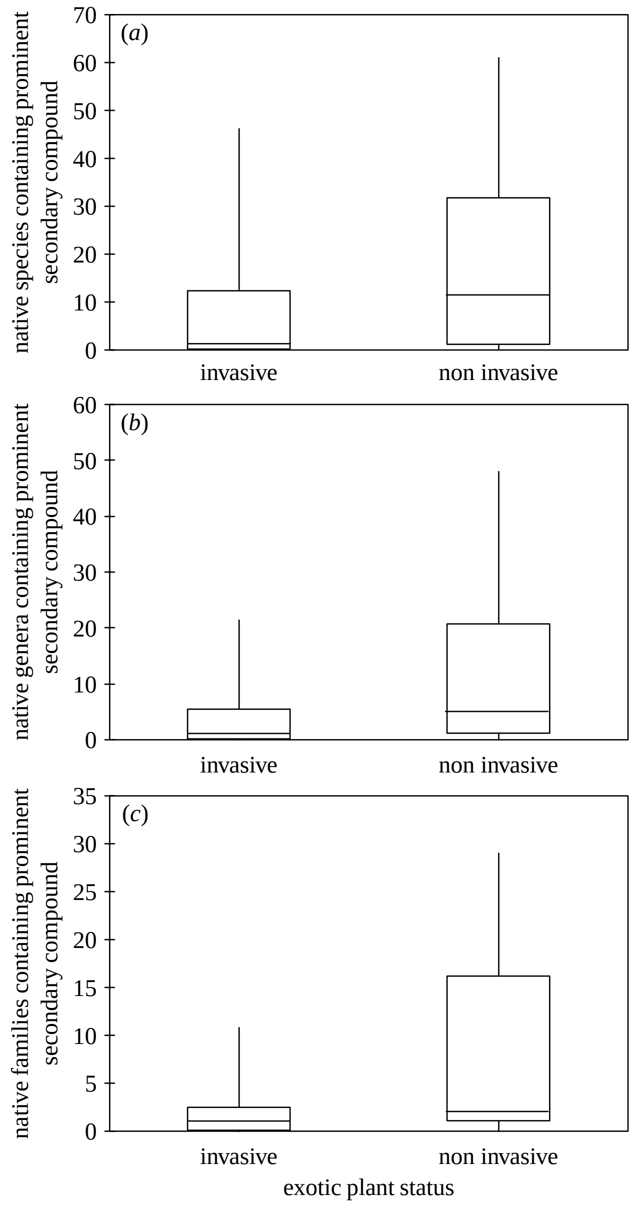

Figure 1. Invasive exotic plants share their prominent secondary chemicals with fewer North American species than non-invasive exotic plants. (*a*) The number of native North American species, (*b*) the number of native genera and (*c*) the number of native families reported in the phytochemical literature to contain the prominent active secondary compounds found in 21 invasive and 18 non-invasive exotic plant species. Boxes depict medians, 25th and 75th percentiles; whiskers extend to 10th and 90th percentiles.

(figure 1*c*; Wilcoxon rank-sum test: $\chi^2=4.78$, d.f.$=1$, $p=0.029$) than compounds from non-invasive exotic plants. Highly invasive exotics did not have significantly fewer native congeners than non-invasive species (Wilcoxon rank-sum test: $\chi^2=1.80$, d.f.$=1$, $p=0.180$) nor did they represent families with fewer native genera (Wilcoxon rank-sum test: $\chi^2=0.198$, d.f.$=1$, $p=0.656$).

Plants with uncommon secondary compounds suffered less leaf herbivory as estimated from previous studies on herbivore damage to exotic plants in Ontario and the northeastern US (figure 2; Cappuccino & Carpenter 2005). For the 14 exotic plant species from those studies, the mean proportion of leaf area damaged was significantly correlated with the number of native species (Spearman's $\rho=0.706$, $p=0.002$), genera (Spearman's $\rho=0.640$, $p=0.008$) and families (Spearman's $\rho=0.635$, $p=0.008$) sharing their prominent secondary compounds. Plants having prominent secondary compounds that were not recorded from native North American plants experienced significantly less leaf damage than those sharing their prominent phytochemicals with native plants (Wilcoxon rank-sum test: $\chi^2=5.19$, d.f.$=1$, $p=0.023$).

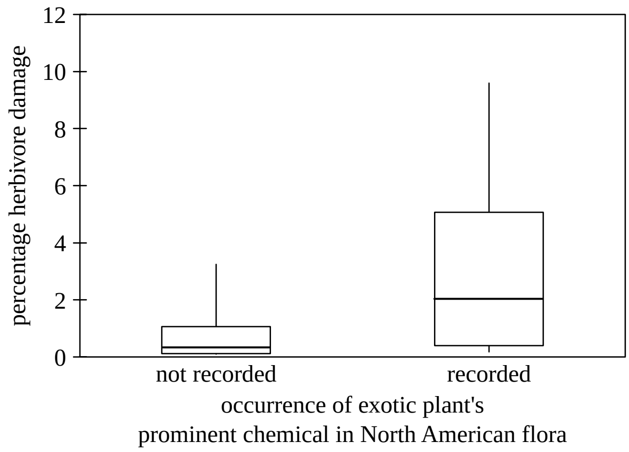

Figure 2. The percentage leaf herbivory on 16 exotic plants from earlier work (Carpenter & Cappuccino 2005) for which the prominent secondary chemicals have either been recorded or not recorded from native North American plants.

4. DISCUSSION

Our results suggest a phytochemical basis for the escape from enemies that has been shown from previous studies to be correlated with invasive potential in exotic plants (Mitchell & Power 2003; Carpenter & Cappuccino 2005; Cappuccino & Carpenter 2005). A plant species introduced to a new habitat can be colonized rapidly by herbivores that recognize it as potential food and have the physiological capability to detoxify its secondary constituents (Strong 1974; Strong *et al.* 1977; Singer *et al.* 1993). Herbivores of native plants often shift onto novel hosts that are phytochemically similar to, but not necessarily related to, their traditional hosts (Strong *et al.* 1984). While some phylogenetically isolated plants have been reported to have impoverished herbivore faunas (Connor *et al.* 1980), and while phylogenetic similarity of exotics to the North American flora was weakly correlated with herbivore damage in our previous work (Cappuccino & Carpenter 2005), in the present study, highly invasive exotics did not have significantly fewer close relatives than non-invasive plants.

Although escape from herbivores as a mechanism of exotic plant invasion has received considerable attention in the literature (Keane & Crawley 2002), with few exceptions (DeWalt *et al.* 2004) the link between herbivore release and exotic plant performance has not been well documented. The enemy-release argument relies on the assumption that herbivores, when present, limit plant abundance and distribution—a question that has generated decades of debate (Keane & Crawley 2002; McEvoy 2002). The relationships we observed between unique chemistry, low herbivory and exotic plant invasiveness suggest an important role for enemy escape; however, other mechanisms that could drive invasiveness, such as allelopathy (Callaway & Aschehoug 2000; Callaway & Ridenour 2004) and the alteration of soil microbial communities (Kourtev *et al.* 2002), are also likely to be important. These mechanisms also depend on novel phytochemistry (Callaway & Ridenour 2004). For some exotic plants, the prominent novel phytochemical may confer multiple advantages, enabling invasiveness through several mechanisms. Over half (57.5%) of the compounds in our dataset have been reported as active against more than one type of organism and several appear to have generalized biocidal effects (electronic supplementary material). This was true for the prominent compounds of both invasive and non-invasive exotics. Allelopathic activity has been reported for only six of the compounds (electronic supplementary material); however, as advanced methods lend new credibility to studies of allelopathy (Hierro & Callaway 2003), it is possible that many more compounds once seen as merely defensive will prove to be 'offensive' as well.

We do not claim that the compounds of invasive plants are in and of themselves more toxic than those of non-invasive plants. They are merely more effective in their new ranges where adapted herbivores, pathogens and competitors are absent. Invasive exotic species are often uncommon or even rare in their native ranges (Callaway & Aschehoug 2000; DiTommaso *et al.* 2005), supporting the argument that these plants are not phytochemically superior in all environments. Furthermore, in their native ranges, plants may produce lower concentrations of their defensive compounds to avoid detection by specialist herbivores, which use the compounds as host-location cues. In the novel range, where chemical uniqueness will decrease the likelihood of attracting preadapted herbivores, production of the novel secondary compounds may be increased, thereby making the plants even more resistant to generalists (Joshi & Vrieling 2005).

Combatting invasive plants is difficult and costly (Pimentel *et al.* 2000). The ability to predict which exotic species are likely to become pests of natural areas would allow managers to initiate proactive control measures before emergent pests spread far from their points of entry. Pest status in other geographic areas where a plant has been introduced has proven to be a useful predictor of its potential invasiveness in a new location (Reichard & Hamilton 1997). For plants that do not have a prior history of invasion, our work suggests that phytochemical isolation from native plants could be used to predict invasiveness.

The authors thank Ragan Callaway and Klaas Vrieling for their helpful comments on the manuscript. This research was funded by an NSERC Discovery grant to N.C.

Callaway, R. M. & Aschehoug, E. T. 2000 Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* **290**, 521–523. (doi:10.1126/science.290.5491.521)

Callaway, R. M. & Ridenour, W. M. 2004 Novel weapons: invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.* **2**, 419–426.

Cappuccino, N. & Carpenter, D. 2005 Invasive exotic plants suffer less herbivory than non-invasive plants. *Biol. Lett.* **1**, 435–438. (doi:10.1098/rsbl.2005.0341)

Carpenter, D. & Cappuccino, N. 2005 Herbivory, time since introduction and the invasiveness of exotic plants. *J. Ecol.* **93**, 315–321. (doi:10.1111/j.1365-2745.2005.00973.x)

Connor, E. F., Faeth, S. H., Simberloff, D. & Opler, P. 1980 Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecol. Entomol.* **5**, 205–211.

DeWalt, S., Denslow, J. & Ickes, K. 2004 Natural enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* **85**, 471–483.

DiTommaso, A., Lawlor, F. M. & Darbyshire, S. J. 2005 The biology of invasive alien plants in Canada. *Cynanchum rossicum* (Kleopow) Borhidi (= *Vincetoxicum rossicum* (Kleopow) Barbar.) and *Cynanchum louiseae* (L.) Kartesz & Gandhi (= *Vincetoxicum nigrum* (L.) Moench). *Can. J. Plant Sci.* **85**, 243–263.

Harborne, J. B., Baxter, H. & Moss, G. P. 1999 *Phytochemical dictionary: a handbook of bioactive compounds from plants*. London, UK: Taylor & Francis.

Hierro, J. L. & Callaway, R. M. 2003 Allelopathy and exotic plant invasion. *Plant Soil* **256**, 29–39. (doi:10.1023/A:1026208327014)

Joshi, J. & Vrieling, K. 2005 The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecol. Lett.* **8**, 704–714. (doi:10.1111/j.1461-0248.2005.00769.x)

Keane, R. M. & Crawley, M. J. 2002 Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170. (doi:10.1016/S0169-5347(02)02499-0)

Kourtev, P. S., Ehrenfeld, J. G. & Haeggblom, M. 2002 Exotic plant species alter the microbial community structure and function in the soil. *Ecology* **83**, 3152–3166.

Lockwood, J. L., Simberloff, D., McKinney, M. L. & Von Holle, B. 2001 How many, and which, plants will invade natural areas. *Biol. Invasions* **3**, 1–8. (doi:10.1023/A:1011412820174)

Lowe, S. J., Browne, M. & Boudjelas, S. 2000 *100 of the world's worst invasive alien species*. Auckland, New Zealand: IUCN/SSC Invasive Species Specialist Group, Auckland.

Mack, R. M. 1996 Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol. Conserv.* **78**, 107–121. (doi:10.1016/0006-3207(96)00021-3)

McEvoy, P. B. 2002 Insect–plant interactions on a planet of weeds. *Entomol. Exp. Appl.* **104**, 165–179. (doi:10.1023/A:1021238030692)

Mitchell, C. E. & Power, A. G. 2003 Release of invasive plants from fungal and viral pathogens. *Nature* **421**, 625–627. (doi:10.1038/nature01317)

Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. 2000 Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**, 53–64.

Reichard, S. H. & Hamilton, C. W. 1997 Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* **11**, 193–203. (doi:10.1046/j.1523-1739.1997.95473.x)

Singer, M. C., Thomas, C. D. & Parmesan, C. 1993 Rapid human-induced evolution of insect–host associations. *Nature* **366**, 681–683. (doi:10.1038/366681a0)

Strong, D. R. 1974 Rapid asymptotic species accumulation in phytophagous insect communities: the pests of cacao. *Science* **185**, 1064–1066.

Strong, D. R., McCoy, E. D. & Rey, J. R. 1977 Time and the number of herbivore species: the pests of sugarcane. *Ecology* **58**, 167–175.

Strong, D. R., Lawton, J. H. & Southwood, T. R. E. 1984 *Insects on plants: community patterns and mechanisms*. Cambridge, MA: Harvard University Press.