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Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L.

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Abstract The evolution of increased competitive ability hypothesis predicts that introduced plants that are long liberated from their natural enemies may lose costly herbivore defense, enabling them to reallocate resources previously spent on defense to traits that increase competitive superiority. We tested this prediction by comparing the competitive ability of native St John's wort (*Hypericum perforatum*) from Europe with introduced St John's wort from central North America where plants have long grown free of specialist herbivores, and introduced plants from western North America where plants have been subjected to over 57 years of biological control. Plants were grown in a greenhouse with and without competition with Italian ryegrass (*Lolium multiflorum*). St John's wort from the introduced range were not better interspecific competitors than plants from the native range. The magnitude of the effect of ryegrass on St John's wort was similar for introduced and native genotypes. Furthermore, introduced plants were not uniformly larger than natives; rather, within each region of origin there was a high variability in size between populations. Competition with ryegrass reduced the growth of St John's wort by >90%. In contrast, St John's wort reduced ryegrass growth <10%. These results do not support the contention that plants from the introduced range evolve greater competitive ability in the absence of natural enemies.

Keywords Biological control · Evolution of increased competitive ability hypothesis · Evolution · Invasion · Plant vigor

Introduction

The evolution of increased competitive ability (EICA) hypothesis states that the vigor and success of introduced plants may in part be due to shifts in their resource allocation patterns (Blossey and Nötzold 1995). Specifically, EICA postulates that introduced plants that are no longer under selection by specialist herbivores may lose costly traits that confer resistance to these herbivores, enabling them to reallocate resources previously spent on defense to traits that increase competitive superiority. This predicts that under identical growing conditions, introduced plants that have long been free from herbivore pressure may be larger or otherwise more competitive than native conspecifics (Blossey and Nötzold 1995). Thus far, results of tests of the EICA hypothesis have been contradictory. Some evidence suggests that both purple loosestrife (*Lythrum salicaria* L.) and Chinese tallow (*Sapium sebiferum*) are larger in the introduced versus native range (Blossey and Nötzold 1995; Blossey and Kamil 1996; Siemann and Rogers 2001). However, from a common garden study it was found that four other biennial species that are exotic in Australia and New Zealand have not evolved a larger size compared to their native European conspecifics (Willis et al. 2000). Similarly, Thébold and Simberloff (2001) found no consistent evidence that stem heights published in European and American flora books were significantly different between the native and the introduced range, respectively.

To determine whether introduced plants have evolved greater competitive abilities than their native counterparts requires not only common garden experiments, in which the size of native and introduced genotypes are compared, but also competition experiments in which interspecific competitive ability of native and introduced genotypes is determined (Grace 1990). In this context, competitive ability is best determined by the reduction in growth caused by the presence of an interspecific competitor (Goldberg 1990). If the EICA hypothesis holds true, the size of the plants from the introduced range should be less

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reduced by competition than that of plants from the native range.

Here we describe the results of a greenhouse experiment in which we compared the competitive ability between St John's wort (*Hypericum perforatum* L.) collected from introduced North American and native European populations. Among introduced populations we compared the competitive ability of plants from populations that have likely been exposed to some history of biological control and from populations where biological control was never applied. The EICA hypothesis predicts that plants from the introduced range should be larger and less affected by competition than plants from the native range. Within North America, plants from populations that experienced biological control should be smaller and more affected by competition than plants that have never been exposed to specialist herbivores during their history in North America.

Materials and methods

Study species

Hypericum perforatum L. is a short-lived perennial, native to Europe, Northern Africa and Asia. St John's wort was first introduced into the eastern USA in 1793 (first reported in Lancaster, Pennsylvania); it was first found in the western USA between 1840 and 1850 (Campbell and Delfosse 1984). St John's wort spread rapidly in overgrazed rangeland in the western USA and, by 1945, occupied over 6 million ha in California. In an effort to control this weed, in 1945, a chrysomelid beetle, *Chrysolina quadrigemina* (Coleoptera: Chrysomelidae) was introduced as a biocontrol for St John's wort (Huffaker and Holloway 1949; Holloway and Huffaker 1951). Within 5 years of their introduction, biocontrol beetles had markedly reduced St John's wort populations in the west. Besides *C. quadrigemina* additional biological control agents have been introduced (Holloway and Huffaker 1953; Julien and Griffiths 1998). In central North America, St John's wort was never very invasive, and biocontrol agents have only been introduced into Minnesota and Ontario, Canada (Julien and Griffiths 1998). However, these introductions have been made more recently than those in the west, and therefore some populations from central North America have had a much more limited exposure to biocontrol agents than have plants from western North America.

Seed collection

Seeds were collected in late summer, 1998 and 1999. Mature capsules were collected from ten St John's wort plants within each of ten native populations in Europe, ten western North American populations (California, Oregon, Washington and Montana) and ten introduced populations from central North America (Illinois, Michigan, Wisconsin, Minnesota, and Ontario) (Table 1). Populations span much of the broad latitudinal distribution of the species within each region. All populations were separated by >20 km to reduce the probability of gene flow between populations. In the laboratory, we opened dried seed capsules and extracted the seeds. Seeds were stored at room temperature in coin envelopes until experimentation.

Table 1 Information on St John's wort (*Hypericum perforatum* L.) seed populations used in the study

Range	Country/State	Locality	Code	Latitude (°)	
Native	Czech Republic	Prague	CZ 19	50.08	
	France	Assass	FR 7	43.70	
	France	Clapier	FR 8	44.10	
	Germany	Bonn	GE 20	50.73	
	Italy	Bolzano	IT 4	46.51	
	Netherlands	DeStleg	ND 17	52	
	Spain	Granera	SP 1	41.73	
	Spain	Selva de Mar	SP3	41.21	
	Switzerland	Adliswil	SW 10	47.30	
	England	Silwood	UK 15	51.40	
	Introduced exposed to biocontrol	California	Bass Lake	CA 2	38.66
		California	Meadow	CA 3	39
		California	Vista		
		California	Sierra Field	CA 4	39.25
		California	Covelo	CA 8	39.88
		California	Mt Shasta	CA 11	41.30
		Montana	Ravalli	MT 19	47.30
		Oregon	Ashland	OR 14	42.20
		Oregon	Gold Hill	OR 15	42.45
		Oregon	Winchester	OR 17	43.26
	Washington	Mima Prairie	WA 20	46.63	
Introduced not exposed to biocontrol	Illinois	Tuscola	IL 1	39.80	
	Michigan	Keweenaw	MI 5	44.61	
	Michigan	ESGR	MI 11	45.50	
	Michigan	Radrick	MI 12	45.50	
	Minnesota	Afton	MN 7	44.90	
	Ontario	Rideau River	ON 8	45	
	Wisconsin	Green Lake	WI 3	43.85	
	Wisconsin	Point Beach	WI 4	44.26	
	Wisconsin	Gillett	WI 6	44.26	
	Wisconsin	Wausaukeee	WI 10	45.45	

Greenhouse experiment

On 20 March 2001 we initiated a greenhouse experiment to compare St John's wort performance when grown alone and with *Lolium multiflorum* Lam (Italian ryegrass, hereafter ryegrass). Ryegrass was chosen as a competitor because of its fast growth and because its structure is suitable to confer above and belowground interference. Moreover, this grass often co-occurs with St John's wort in native habitats. Ryegrass seeds were bought from a commercial supplier (Naster variety; Semillas Fitó, Barcelona). We evaluated the competitive ability of the ten St John's wort individuals sampled from each population by comparing the biomass of plants grown in pots with and without ryegrass. Multiple St John's wort seeds from each maternal plant were sown in two pots containing a 4:2:2:1 mixture of peat:perlite:vermiculite:sand. Pots were 1.05 l in volume, 14 cm in diameter and 20.5 cm tall. Soil acidity was neutralized with 3 g CaCO₃/l. Pots were watered liberally prior to St John's wort germination. After germination, pots were watered with a dilute Hoagland solution. One of each paired pots was randomly chosen to receive several ryegrass seeds. When seeds germinated we removed all but one seedling of St John's wort and ryegrass. In total, the experiment consisted of 600 pots containing St John's wort, 300 with ryegrass and 300 without ryegrass.

In order to determine whether ryegrass growth was affected by the presence of St John's wort, we seeded 15 additional pots with several ryegrass seeds and when they germinated we removed all but one seedling (control ryegrass plants hereafter). Early in

summer (25 June–5 July), when ryegrass plant had already flowered and before they senesced, we harvested, dried at 65°C and weighed aboveground biomass of both species. At this time St John's wort growing in pots without competition were on average 32.5 ± 0.6 cm tall, had 12.93 ± 0.31 ramifications and only 24.33% of the plants had flowered.

A wide set of competition intensity indexes are available for estimating the intensity of the effect size of competition. We used the relative competition index (RCI) that measures the proportional decrease in plant performance due to competition (Goldberg et al. 1999). We calculated the RCI for St John's wort as $[(B_0 - B_1)/B_0] \times 100$, where B_0 is the aboveground biomass of the St John's wort at the end of the experiment growing without ryegrass and B_1 is the aboveground biomass of the half-sib St John's wort growing with ryegrass. RCI has no minimum (negative) value but has a maximum value of 100 indicating maximal competition. If $RCI=0$ there is no competition. If $RCI<0$ the performance of St John's wort is higher in the presence of the ryegrass (facilitation). If $RCI>0$ ryegrass has a negative effect on St John wort (competition in the broad sense). Similarly, we calculated the RCI for ryegrass.

Statistical analysis

Differences in aboveground St John's wort biomass (hereafter biomass) were analyzed using a nested ANOVA with region (Europe, western North America and central North America) and competition (plants growing with or without ryegrass) as fixed factors and population nested within region as a random factor. Nested ANOVAs were also performed for St John's wort grown with and without ryegrass with region as the fixed factor. Differences in the RCI for St John's wort and for ryegrass and in aboveground ryegrass biomass were also analyzed using a nested ANOVA with region and population nested within region as the main effects. We used the mean square for population nested within

region in the denominator of the F -test for region effects, since population was a random factor. Data were transformed prior to analysis when necessary to satisfy parametric assumptions (Zar 1984).

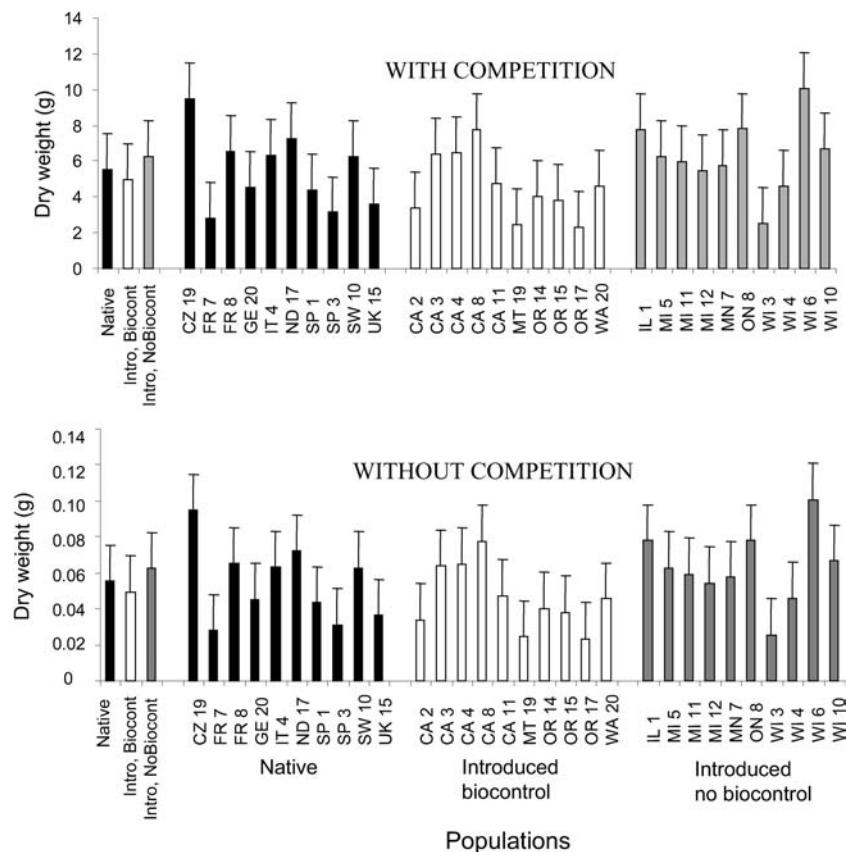
Results

Introduced and native St John's wort did not differ in biomass, regardless of whether plants were grown with or without ryegrass ($F_{2, 27}=1.93$, $P=0.16$ and $F_{2, 27}=2.3$, $P=0.12$, respectively). Thus, we found no evidence that introduced genotypes had evolved a larger size as predicted by the EICA hypothesis.

Within regions, there were significant differences in St John's wort biomass among populations ($F_{27, 477}=6.80$, $P<0.0001$) (Fig. 1). A significant Spearman correlation coefficient ($r_s=0.65$, $P=0.0005$) between biomass of plants grown with and without ryegrass indicated that regardless of the competitive environment certain populations consistently produced larger plants than other populations.

Competition with ryegrass significantly affected St John's wort biomass ($F_{1, 27}=1473.09$, $P<0.0001$), reducing St John's wort biomass by >90% (Fig. 2). However, the intensity of the competition was not significantly different based on region of plant origin ($F_{2, 27}=1.14$, $P=0.33$) although it was marginally different between populations within a region ($F_{27, 213}=1.53$, $P=0.05$).

Fig. 1 Mean aboveground biomass (+SE) of *Hypericum perforatum* plants from native European populations, from introduced North American populations that have either a history of exposure to biocontrol (western North America) or have never been exposed to biocontrol (central North America). All plants were grown under the same greenhouse conditions with or without competition with *Lolium multiflorum*. The three bars to the left are the regional means that were computed by taking the mean of the population means for each region. Native mean value for European populations; Intro, Biocont mean value for western North American populations; Intro, NoBiocont mean value for central North American populations



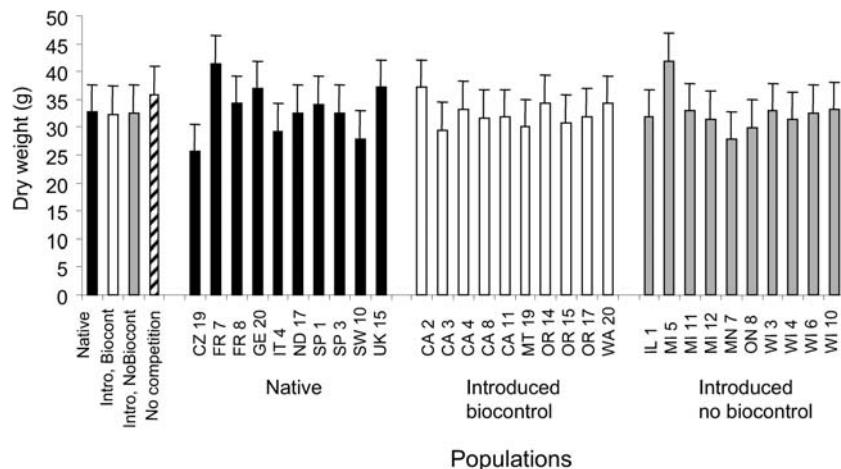


Fig. 2 Mean aboveground biomass (+SE) of *Lolium multiflorum* grown with *Hypericum perforatum* plants from native European populations, from introduced North American populations that have a history of exposure to biocontrol (western North America) or from those that have never been exposed to biocontrol (central North America). All plants were grown under the same greenhouse conditions. The four bars to the left are the mean for each

treatment. *Native* Mean value of *Lolium* plants grown with *Hypericum* from European populations; *Intro, Biocont* mean value of *Lolium* plants grown with *Hypericum* from western North American populations; *Intro, NoBiocont* mean value of *Lolium* plants grown with *Hypericum* from central North America; *No competition* mean value of *Lolium* plants grown in isolation

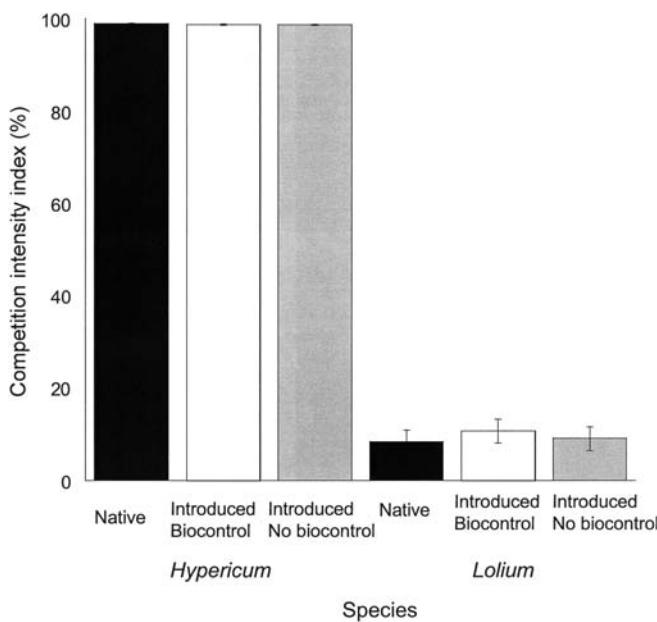


Fig. 3 Mean relative competition index (RCI) (+SE) for *Hypericum perforatum* and *Lolium multiflorum* plants grown under the same greenhouse conditions with or without competition with their counterparts. *Hypericum* plants come from native European populations, from introduced North American populations that have a history of exposure to biocontrol (western North America) or that have never been exposed to biocontrol (central North America). RCI values were computed by taking the mean of the population means for each region

The region of origin of St John's wort did not have a significant effect on ryegrass biomass ($F_{2,27}=0.26$, $P=0.77$). The identity of the St John's wort population within a region had no significant effect on ryegrass biomass ($F_{27,223}=1.25$, $P=0.19$) (Fig. 2). On average

(\pm SE), St John's wort decreased ryegrass biomass by $9.36\pm1.48\%$. Region and population within region had a no significant effect on the intensity of competition ($F_{2,223}=0.25$, $P=0.77$, $F_{27,223}=1.47$, $P=0.07$, respectively) (Fig. 3).

Discussion

Introduced St John's wort from both central and western North America were not larger than native European genotypes. This result mirrors those from multi-year common garden experiments with St John's wort that we have performed in both the native and introduced range (Maron et al., in revision). Results from previous experiments comparing the size of native and introduced conspecifics grown in common environments have been mixed. Blossey and Nörzold (1995) found that *Lythrum salicaria* L. plants from introduced population in Ithaca (New York, USA) were larger than the ones from native populations in Switzerland. However, few differences were found in a comparison of a larger number of populations in the introduced and native range (Willis and Blossey 1999). Similarly, in a transplant experiment conducted in a common garden experiment, Willis et al. (2000) found that four biennial species introduced into Australia and New Zealand were not larger than plants from European populations.

Within a region, plants from different populations varied in size. This variability seems to be constant irrespective of the competition treatment because RCI is only marginally significant among populations. Such phenotypic variability within a region has been also found for other invasive species (Anderson 1989; Rice and Mack 1991; Weber 1997). For example, St John's wort

populations introduced into New South Wales (Australia) had high morphological variability. Broader-leaved plants were taller and more robust than narrow-leaved plants (Campbell et al. 1997). Population variability advocates the need to assay evolutionary consequences of plant invasions by comparing a large number of introduced and native populations that encompass large portions of the native and introduced range (Campbell et al. 1997; Willis and Blossey 1999).

The EICA hypothesis states that introduced plants should evolve increased competitive ability. We have found that the negative impacts of competition with ryegrass were not different for introduced and native St John's wort. As such, our results do not support the contention that introduced plant populations evolve a superior competitive ability. Competition between ryegrass and St John's wort was asymmetric. Ryegrass had a greater negative effect on St John's wort than did St John's wort on ryegrass (Weiner 1990). This asymmetry could have masked regional differences in competition intensity. It is unclear whether our results would have differed had we performed competition experiments with a less robust competitor than ryegrass. If competition is strongly asymmetrical, it may be difficult to detect differences in competitive ability between genotypes of the inferior competitor (in our case, St John's wort; Keddy 2001).

Remarkably little work has been done that investigates differences in competitive ability between native and introduced conspecifics or the effect of competition on introduced plant phenotypes. A notable exception is research by Leger and Rice (2003) who found that introduced California poppy (*Eschscholzia californica*) from Chile were larger and more fecund in common gardens without competition than native poppy populations from California. Experiments are needed that investigate the response to and the effect of competition among introduced and native conspecifics. By comparing both components of competition (i.e. response and effect) in the native and introduced range of aliens, we may learn that escape from a particularly potent competitors is as important as escape from natural enemies in the success of introduced plants. Furthermore, experiments involving native and introduced genotypes that are grown together in a common competitive environment are needed to determine whether increased competitive ability evolves during invasion.

Overall, we found that introduced St John's wort from North America are not larger or more competitive than native conspecifics from Europe. Therefore, our results do not support the notion that introduced plants rapidly evolve greater size or competitive ability.

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