

INCREASED PLANT SIZE IN EXOTIC POPULATIONS: A COMMON-GARDEN TEST WITH 14 INVASIVE SPECIES

DANA M. BLUMENTHAL^{1,3} AND RUTH A. HUFBAUER²

¹USDA Agricultural Research Service, Rangeland Resources Research Unit, 1701 Center Avenue, Fort Collins, Colorado 80526 USA

²Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, Colorado 80523 USA

Abstract. The “evolution of increased competitive ability” (EICA) hypothesis predicts that exotic species will adapt to reduced herbivore pressure by losing costly defenses in favor of competitive ability. Previous studies often support the prediction that plants from exotic populations will be less well defended than plants from native populations. However, results are mixed with respect to the question of whether plants from exotic populations have become more competitive. In a common-garden experiment involving plants from two native and two exotic populations of 14 different invasive species, we tested whether exotic plants generally grow larger than conspecific native plants, and whether patterns of relative growth depend on the intensity of competition. We found a quite consistent pattern of larger exotic than native plants, but only in the absence of competition. These results suggest that invasive species may often evolve increased growth, and that increased growth may facilitate adaptation to noncompetitive environments.

Key words: competition; defense; evolution of increased competitive ability (EICA); exotic plant species; invasive species; microevolution; weed.

INTRODUCTION

Understanding why some exotic species are so successful is essential to controlling their populations. The “evolution of increased competitive ability (EICA) hypothesis” suggests that exotic plant populations, with few specialized enemies in their new range, will evolve to allocate resources to growth or reproduction instead of defense against enemies (Blossey and Nötzhold 1995, Müller-Schärer et al. 2004). The primary predictions of the EICA hypothesis are that plants from a species’ exotic range will be less well defended, grow larger, and therefore be more competitive than plants from its native range. If EICA is common, it lends support to the enemy-release hypothesis and the use of biological control: evidence of selection against defensive traits would suggest that enemy release has been important to invader population dynamics, and that poorly defended exotic populations may be particularly susceptible to introduced enemies (Siemann and Rogers 2003).

The EICA hypothesis stems from observations that many plant species appear to grow larger in their exotic range (Crawley 1987, Blossey and Nötzhold 1995, Hinz and Schwarzlaender 2004, Bossdorf et al. 2005; but see Thebaud and Simberloff 2001). Direct tests of EICA involve growing plants from the native and exotic ranges of invasive species in common gardens. Such studies have evaluated defensive and/or growth characteristics of 24 invasive species, comprised of 20 herbaceous dicots

and 4 woody dicots (Bossdorf et al. 2005). The results of these studies tend to support the predictions of EICA with regard to defense. Most measurements of specialist preference, specialist damage, or quantitative defenses effective against specialists, suggest that plants from exotic populations are more susceptible to specialists than are plants from native populations (Blossey and Nötzhold 1995, Daehler and Strong 1997, Willis et al. 1999, Blair and Wolfe 2004, Bossdorf et al. 2004b, Wolfe et al. 2004, Joshi and Vrieling 2005, Stastny et al. 2005). Although susceptibility to generalist enemies is more varied (Willis et al. 1999, Siemann and Rogers 2003, Blair and Wolfe 2004, Bossdorf et al. 2004b, Lankau et al. 2004, Maron et al. 2004a, Wolfe et al. 2004, Buschmann et al. 2005, Joshi and Vrieling 2005, Leger and Forister 2005, Meyer et al. 2005), this would be expected if exotic populations are not released, or are only partially released, from generalist enemies (Maron and Vilà 2001, Keane and Crawley 2002, Müller-Schärer et al. 2004, Parker et al. 2006).

It is not yet clear whether poorly defended plants from exotic populations shift resources from defense to increased growth. While in nine species, exotic plants have been found to be larger or to reproduce more than native conspecifics (Blossey and Nötzhold 1995, Willis et al. 1999, Siemann and Rogers 2001, 2003, Leger and Rice 2003, Blair and Wolfe 2004, Wolfe et al. 2004, Buschmann et al. 2005, Erfmeier and Bruelheide 2005, Joshi and Vrieling 2005, Stastny et al. 2005), seven species show no difference between native and exotic plants (Willis et al. 2000, DeWalt et al. 2004, Maron et al. 2004b, Buschmann et al. 2005, Meyer et al. 2005). Evidence for the reverse pattern, that native plants grow

Manuscript received 20 December 2006; revised 16 April 2007; accepted 11 May 2007. Corresponding Editor: P. Alpert.

³ E-mail: dana.blumenthal@ars.usda.gov

larger or reproduce more than exotic conspecifics, has been found for only three species (Daehler and Strong 1997, van Kleunen and Schmid 2003, Bossdorf et al. 2004a). Differences among studies, particularly in the number of populations sampled, preclude firm conclusions. Nevertheless, as a whole, these results suggest that plants more often evolve increased than decreased size upon introduction to a new range.

Another open question is whether such increases in size are associated with increases in competitive ability in the exotic range. The EICA hypothesis proposes trade-offs between allocation to defense and allocation to traits that enhance invasiveness, and consequently the hypothesis defines competitive ability broadly, to include “vegetative growth or reproductive efforts depending on which is more important for success in a particular new environment” (Blossey and Nötzold 1995:887). To determine how EICA may influence invasion, however, it is important to learn what types of traits are favored in a new range. In particular, there may often be trade-offs between increasing growth rates in the absence of competition, potentially leading to invasion of disturbed environments rich in available resources, and increasing competitive ability (sensu Tilman 1982), potentially leading to invasion of less disturbed plant communities (Chapin 1980). If exotic plants evolve increased competitive ability in this more narrow sense, then including competitors in common-garden experiments would be expected to favor exotic plants over native conspecifics, and therefore accentuate the predicted pattern of larger exotic than native plants. This result, however, has not been observed. Relative to native conspecifics, exotic plants have been found to be larger with and without competition (Blair and Wolfe 2004), of similar size with and without competition (Vilà et al. 2003), larger only without competition (Leger and Rice 2003), and smaller only with competition (Bossdorf et al. 2004a). Furthermore, of the seven species studied under competitive conditions, only two showed exotic plants to grow larger than native conspecifics (Siemann and Rogers 2001, Blair and Wolfe 2004).

In sum, while there is strong evidence for decreased defenses in exotic populations of invasive species, it remains to be determined how these species use resources not allocated to defense. Our objectives in this study were, (1) to determine whether exotic plants grow larger than native conspecifics for invasive species in general, by including multiple invasive species in a single common-garden experiment, and (2) to determine whether exotic plants are more competitive than native conspecifics, by subjecting plants to three levels of interspecific competition: no competition, low competition, and high competition.

MATERIALS AND METHODS

Experimental design

We compared the growth of plants from two populations in the native range and two populations in

the exotic range in each of 14 invasive species (Table 1). We subjected the plants to three competition treatments (see *Competition treatments*, below). To test for a general pattern of evolution among invasive plants, species form the relevant replication. Our design therefore prioritized numbers of species over numbers of populations within species ($n = 2$ populations per range), precluding meaningful within-species analyses. Seed from a given population was typically collected from multiple individuals and stored together as a bulk sample (for seed sources, see *Species selection*, below). Thus, seed from a single population could be comprised of siblings or unrelated individuals. The variation within a population adds an additional source of variation to the statistical error term, making our design conservative. We accounted for some of this additional variation by planting four individuals from a given population in one pot for each competition–population combination. Each pot, rather than each individual plant, was used to assess the performance of invasive and native populations. Thus, our experiment consisted of 14 species \times 2 populations per origin \times 2 origins \times 3 competition treatments = 168 pots. A consequence of this approach was that variation in survival led to variation in intraspecific competition. Therefore, to avoid confounding treatment effects with differences in intraspecific competition, all analyses were limited to data from the 131 pots in which all four individuals survived to harvest (Table 1).

Both species locations within the greenhouse and competition treatments within species were completely randomized. Due to limited greenhouse space and large differences in height among species, the 12 pots for each species were grouped together. This approach allowed us to greatly reduce the variation in light levels reaching different pots of the same species, which we considered to be essential for detecting possibly subtle intraspecific differences among populations. Grouping pots within a species is equivalent to treating species as blocks, and reflects the fact that species effects were not the focus of this study. This intentional blocking by species does not interfere with our ability to draw conclusions about simple effects of origin. However, both species effects and interactions between species and competition or origin must be treated with caution, as each could be caused either by differences among species or differences in greenhouse locations. To limit the contribution of greenhouse location, we rotated species locations within the greenhouse every four weeks, for the duration of the experiment. To further reduce variation within a species, we rotated pots within a species every two weeks.

Species selection

Species selection was based primarily on seed availability. Nevertheless, we were able to obtain a broad array of herbaceous species that are invasive in the United States. The list includes species that invade natural and agricultural ecosystems, grasses as well as

TABLE 1. Collection locations and numbers of populations in each competition treatment at harvest.

Species	Life form†	Collection locations and sources‡		No. native (N) and exotic (E) populations per treatment§		
		Native range	Exotic range	No comp.	Mod. comp.	High comp.
<i>Abutilon theophrasti</i> Medik.	AF	India	USA, USA (C)	2N, 1E	2N, 1E	2N, 1E
<i>Aegilops cylindrica</i> Host	AG	Turkey, Afghanistan	USA	2N, 2E	2N, 2E	2N, 2E
<i>Avena fatua</i> L.	AG	Afghanistan, Pakistan	USA	2N, 2E	2N, 2E	2N, 2E
<i>Bromus tectorum</i> L.	AG	Turkey	USA	2N, 2E	2N, 1E	2N, 1E
<i>Centaurea diffusa</i> Lam.	BF	Russia (A), Ukraine (A)	USA (A)	2N, 2E	2N, 1E	2N, 1E
<i>Centaurea maculosa</i> auct non Lam.	PF	Ukraine (A)	USA (A)	1N, 2E	x	x
<i>Desmodium tortuosum</i> (Sw.) DC.	AF	Brazil	India	2N, 2E	2N, 2E	1N, 2E
<i>Echinochloa crus-galli</i> (L.) Beauv.	AG	Afghanistan; Germany	USA	2N, 2E	2N, 2E	2N, 2E
<i>Elytrigia repens</i> (L.) Gould	PG	Afghanistan, India	USA, USA (C)	2N, 1E	2N, 2E	2N, 2E
<i>Lespedeza cuneata</i> (Dum.-Cours.) G. Don	PF	China, India	USA	2N, 1E	x	1N, 1E
<i>Leucanthemum vulgare</i> Lam.	PF	Finland, Russian Federation	USA	2N, 2E	2N, 2E	1N, 2E
<i>Linaria dalmatica</i> (L.) P. Mill.	PF	Macedonia (A), Novi-Beograd (A)	USA (A)	1N, 2E	x	x
<i>Poa annua</i> L.	AG	Afghanistan, India	Canada	2N, 1E	2N, 1E	2N, 1E
<i>Tragopogon dubius</i> Scop.	BF	Greece	USA	2N, 1E	2N, 1E	2N, 1E

† Life forms include annual grasses (AG) and forbs (AF), biennial forbs (BF), and perennial grasses (PG) and forbs (PF).

‡ Parentheses denote seed obtained from commercial vendors (C), or collected by the authors and their colleagues (A). All other seeds were obtained from the USDA-ARS National Plant Germplasm System.

§ Numbers refer to the number of populations for each species–origin–competition combination used in the analyses. In order to keep intraspecific competition constant, only pots in which all four plants survived were included in analyses. For the three rightmost columns, “comp.” = competition; “x” denotes treatment combinations for which no pots contained four surviving plants.

forbs, and both annuals and perennials (Table 1). Neither annual species nor grasses have been studied in previous EICA experiments. Seed sources included the USDA-ARS National Plant Germplasm System (Beltsville, Maryland, USA), a commercial seed vendor (Valley Seed Service, Fresno, California, USA), and seed collection by the authors and colleagues. From all sources, we only used seed originally collected from wild populations. All four populations for a given species were obtained from the same type of seed source, with the exception of two species in which one exotic population was obtained from the commercial vendor (Table 1). Where many collections were available, we attempted to choose native and exotic collection sites from similar latitudes, and to ensure that different collection sites for a particular species were separated from one another by at least 160 km. The latter criterion could not be met for exotic populations of *L. dalmatica*, and could not be determined for *A. theophrasti*, *B. tectorum*, *D. tortuosum*, *E. crus-galli*, and *T. dubius* due to insufficient information about collection locations.

Competition treatments

We grew plants in the greenhouse under three competition treatments: no interspecific competition (no competition), competition with *Phalaris arundinacea* of similar age (low competition), and competition with previously established *P. arundinacea* (high competition; see Plate 1). These treatments were designed to correspond to the array of competitive environments invasive plants may face, from recently disturbed environments with little competition to relatively undis-

turbed environments with more intense competition. This design differs from previous EICA studies that have varied competition (Leger and Rice 2003, Vilà et al. 2003, Blair and Wolfe 2004, Bossdorf et al. 2004a) primarily in the addition of the high-competition treatment, which allows us to test for competitive ability as measured by differences in growth under conditions of low resource availability (Tilman 1982). We chose *P. arundinacea* as the common competitor because it is a fast-growing perennial, capable of providing both above- and belowground competition (Green and Galatowitsch 2002). It also appears to be native to both Eurasia and North America (Merigliano and Lesica 1998), the native and exotic ranges, respectively, of most of the species in the experiment (Table 1). This reduces the likelihood that native and exotic populations of our study species differ in previous exposure to the competitor.

Experimental setup and maintenance

All plants were grown in 20 cm diameter × 20 cm deep pots, filled with a 1:1 mixture, by volume, of sand and Scotts Metro Mix 200 potting soil (American Clay Works, Denver, Colorado, USA). We established competition treatments by planting five *P. arundinacea* individuals in fixed locations within each pot: the center of the pot and four equally spaced locations 2 cm from the edge. We added invasive species to these competition treatments by transplanting four individuals from a single population into each pot, equally spaced between the five *P. arundinacea* individuals. In the high-competition treatment, *P. arundinacea* was planted by

seed on 22 March 2004, approximately 3.5 months prior to the addition of the invasive species. We sowed multiple seeds at each location within a pot, and thinned and transplanted seedlings as necessary to achieve five seedlings per pot. The low-competition treatment was established with *P. arundinacea* seedlings rather than seed, to maximize similarity in size among *P. arundinacea* seedlings, and between *P. arundinacea* seedlings and invasive species seedlings. We sowed seeds of both the invasive species and *P. arundinacea* for the low-competition treatment into plugs (2-cm diameter \times 2 cm deep) filled with potting soil on 16–17 June. These plugs were transplanted into the larger pots once seedling roots extended below the plugs, between 29 June and 13 July. We transplanted individuals of similar sizes whenever possible. Pots were labeled with codes that obscured population origins to prevent bias during care or harvest.

The greenhouse was set to 25°C during the day and 21°C at night. Plants were watered as necessary to maintain growth, with the size of each application limited to avoid leaching of soil nutrients. To minimize nutrient deficiency, we added 2.5 g of 20:20:20 (N:P:K) fertilizer (Voluntary Purchasing Groups, Bonham, Texas, USA) to all pots in four increments between 1 and 13 October.

Data collection

To enable us to assess the potential contribution of maternal effects arising from differences in seed mass, we weighed five groups of 10 seeds from each population prior to planting. We harvested aboveground biomass of all weed species by pot following flowering or seven months of growth, whichever happened first. Several annual species, *Abutilon theophrasti*, *Avena fatua*, *Echinochloa crus-galli*, and *Poa annua*, flowered within four months of planting. The harvest was limited to aboveground biomass because of the difficulty of accurately separating roots of *P. arundinacea* from those of the target weed species.

Data analysis

To evaluate maternal influences via differences in seed mass, we ran a model including origin (native or exotic) as a fixed effect, and species, origin \times species, and population(origin \times species) as random effects (PROC MIXED [SAS Institute 1997]). The model for aboveground biomass analyses included origin and competition as fixed effects, species and population(origin \times species) as random effects, and the appropriate interactions (Table 2). To meet the assumptions of the analyses, both response variables were square root transformed prior to analysis. We used the Satterthwaite approximation to calculate appropriate degrees of freedom for the *F* tests of fixed effects (Littell et al. 1996). To investigate a significant interaction between competition and origin on aboveground biomass (see *Results*, below), mixed models were run for each of the three



PLATE 1. *Abutilon theophrasti* growing with no competition (upper panel), moderate competition (middle panel), and high competition (lower panel) from *Phalaris arundinacea*. Photo credit: D. M. Blumenthal.

competition treatments. We conducted a post hoc test to examine an apparent interaction between origin and life history (annual, biennial, perennial) in the absence of competition. This model included origin, life history, and origin \times life history as fixed effects, and species(life history), origin \times species(life history), and population(origin \times species) as random effects. We used contrasts to separately test effects of origin for annuals

TABLE 2. Mixed-model analysis for aboveground biomass.

A) Fixed effects			
Source of variation	Type III <i>F</i>	df†	<i>P</i>
Origin	4.57	1, 11.7	0.054
Competition	22.38	2, 24.9	<0.0001
Origin × competition	4.35	2, 19.5	0.027
B) Random effects			
Source of variation	Likelihood ratio‡	df	<i>P</i>
Species	82.00	1	<0.0001
Competition × species	110.19	1	<0.0001
Origin × species	8.91	1	0.0014
Origin × competition × species	0.70	1	0.2014
Population(origin × species)	10.00	1	<0.001

† For *F* tests of fixed effects, degrees of freedom were calculated using the Satterthwaite approximation (Littell et al. 1996).

‡ Using SAS Proc. Mixed, a standard way of testing the significance of random effects is to compare -2 times the residual log likelihood of models run with and without each effect (Littell et al. 1996). This likelihood ratio is evaluated against a chi-square distribution with one degree of freedom (Littell et al. 1996).

and perennials. To hold the total acceptable error rate at 0.05, *P* values for analyses of competition and life history, respectively, were evaluated against Bonferroni-corrected α values of 0.016 and 0.025.

RESULTS

There were no differences in the mass of the seeds we planted between native (0.037 g/seed) and exotic (0.036 g/seed) populations ($F_{1,33.1} = 0.22$, $P = 0.64$). While species differed considerably in seed mass, there was not a significant interaction between species and origin (likelihood-ratio test statistic distributed as $\chi_1 = 0$, $P > 0.05$). Furthermore, including seed mass as a covariate in analyses of aboveground biomass did not qualitatively change the results. Aboveground biomass at harvest varied greatly among species, due to rapid onset of flowering in some annual species. Species harvested at ~ 4 months (*Abutilon theophrasti*, *Avena fatua*, *Echinochloa crus-galli*, and *Poa annua*) averaged 0.15 g/plant, while the remaining species harvested after 7 months averaged 1.7 g/plant. Competition from *Phalaris arundinacea* greatly reduced invasive species biomass (Table 2), from an average of 2.6 g without competition, to 0.75 g with low competition, and 0.14 g with high competition.

Across species, competition interacted with origin to determine aboveground biomass (Table 2, Fig. 1). Analyses within competition treatments indicated that plants from exotic populations grew larger only in the absence of competition ($F_{1,13} = 10.64$, $P = 0.0062$; Fig. 1). Origin had no effect with either low ($F_{1,9.66} = 0.48$, $P = 0.51$) or high competition ($F_{1,13.2} = 0.15$, $P = 0.71$; Fig. 1). Given the smaller number of species in the low- and high-competition treatments (Table 1), the absence of an origin effect within these treatments should be viewed with some caution. However, the

origin × competition interaction demonstrates that the pattern of larger exotic than native plants is either stronger in or limited to the no-competition treatment.

Because the effect of origin in the absence of competition appeared to be strongest among perennials (Fig. 2), we performed a post hoc analysis to examine the effect of life history in the absence of competition. There was a significant interaction between origin and life history ($F_{2,9.15} = 16.25$, $P = 0.001$). Examining that interaction further within life-history types, plants from the introduced range grew significantly larger than plants from the native range for perennials ($F_{1,9.93} = 62.44$, $P < 0.0001$), but not annuals ($F_{1,8.44} = 2.34$, $P = 0.164$). There were too few biennials to warrant further analysis.

Origin also interacted with species, both in the main model (Table 2) and without competition ($\chi_1 = 4.4$, $P = 0.017$). As plants within a species were grouped within the greenhouse, however, greenhouse location could also contribute to species × origin interactions, and therefore inferences regarding this interaction should be made with caution.

DISCUSSION

Unlike previous EICA studies, our experiment tested whether invasive plants generally evolve increased size

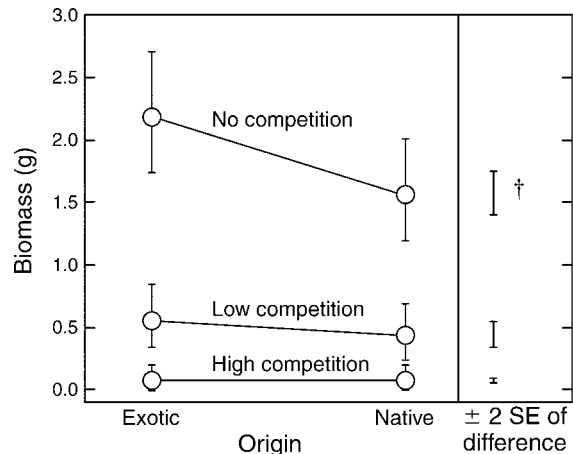


FIG. 1. Interactive effects of competition and origin on aboveground biomass across 14 invasive species. Best linear unbiased predictors (BLUPs) and standard error bars are back transformed from those calculated from square-root-transformed data. BLUPs are used to estimate means of fixed effects in mixed models including random effects. They are the best predictor of linear combinations of the conditional means of both fixed and random effects (Littell et al. 1996). The standard errors associated with each BLUP (left panel) reflect variation among species within each origin and thus are not representative of the errors used to test differences between origins in post hoc analyses where native individuals are compared directly to exotic individuals of the same species, akin to a paired *t* test. Therefore, in the right-hand panel we also show error bars, each representing two standard errors, for the estimated differences between exotic and native range for each level of competition; "†" indicates $P = 0.006$; other differences are not significant ($P > 0.05$).

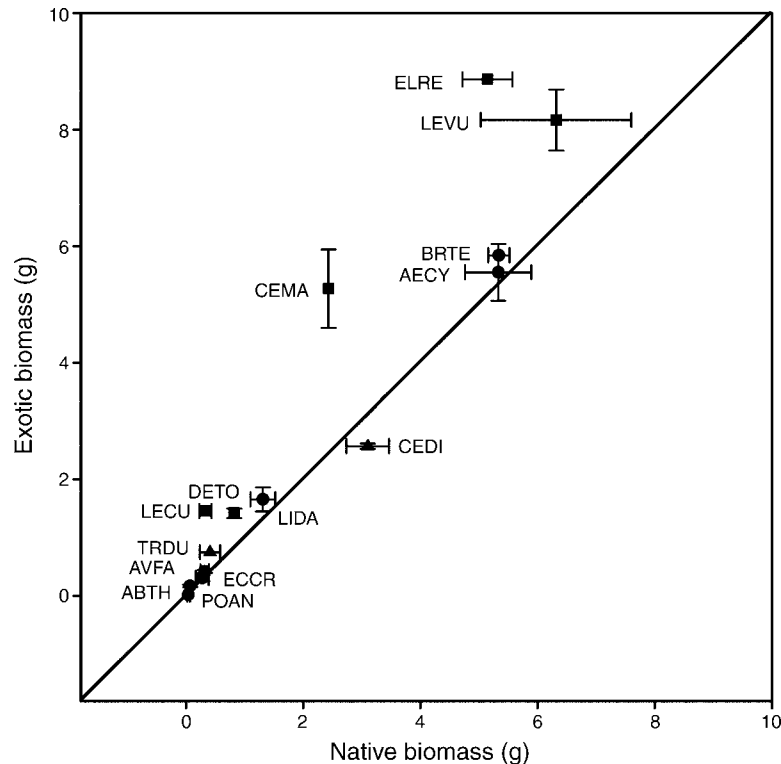


FIG. 2. Size (mean \pm SE) of native and exotic plants for the 14 invasive species grown without competition. Points correspond to individual annual (circles), biennial (triangles), or perennial (squares) species. Species codes are the first two letters of the genus followed by the first two letters of the species (see Table 1). Points above the line of equality represent species for which exotic plants were larger than native plants. Missing error bars represent species \times origin combinations for which plants from only one population germinated and survived to harvest.

and competitive ability by comparing plants from native and exotic populations of 14 invasive species. We found that in the absence of competition, exotic plants were larger, on average, than native conspecifics (Figs. 1 and 2). This pattern is similar to but more consistent than that found by comparing results of previous EICA studies (Bossdorf et al. 2005), and it appears to provide relatively broad support for the role of genetic change in invasion (Blossey and Nötzhold 1995). Although the pattern of increased growth among plants from exotic populations was observed across a range of herbaceous invasive species, post-hoc analyses suggest that it is either stronger in or limited to perennial species (1 grass and 4 forbs). The fact that origin was not significant among annuals (5 grasses and 2 forbs) may represent the absence of an origin effect or a lack of statistical power. Additionally, origin \times species interactions, both in the full model and without competition, suggest that exotic plants are larger than native plants only for some species. It is not possible, however, to draw firm conclusions with regard to differences among species, both because species effects were confounded with greenhouse location, and because limited power precluded meaningful species-specific analyses.

There are two alternative explanations for larger exotic than native plants that we cannot completely rule out. Differences observed in common gardens can reflect maternal effects as well as genetic differences. Maternal effects are often manifested in seed mass (Roach and Wulff 1987), but we found no differences by origin in the mass of the seeds we planted, and treatment effects were robust to the inclusion of seed mass as a covariate. It is also possible that there were biases in seed-collection locations or environments that do not reflect differences between native and exotic ranges. Because the majority of our seed was obtained from the USDA-ARS National Plant Germplasm System, we have incomplete information about collection locations, and therefore cannot fully evaluate this possibility. Nevertheless, given the variety of species and collection locations in this study (Table 1), we expect that a systematic bias in seed collection is unlikely.

The fact that exotic plants consistently grew larger than native conspecifics only in the absence of competition (Fig. 1), both supports the idea that exotic plants may evolve increased growth (Blossey and Nötzhold 1995) and suggests that increased growth may lead to adaptation to open, noncompetitive environments. These results are in accord with those of other EICA

studies that have explicitly varied competition. For example, exotic *Eschscholzia californica* plants grew larger and produced more flowers than native conspecifics, but competition eliminated this difference (Leger and Rice 2003). Competition also decreased the success of exotic relative to native *Alliaria petiolata* plants, leading to exotic plants that were shorter and produced fewer siliques than native plants (Bossdorf et al. 2004a). Although competition does not always inhibit exotic plants more than native conspecifics (Vilà et al. 2003, Blair and Wolfe 2004), it is notable that the opposite result, competition more strongly inhibiting plants from native populations, has not been observed.

Specific traits observed in common-garden experiments also suggest that plants from exotic populations are well adapted to noncompetitive environments. Noncompetitive environments tend to select for traits such as rapid growth and high reproductive allocation, which allow plants to take advantage of high levels of available resources (Chapin 1980). A number of EICA studies have examined such traits. Relative to native *Silene latifolia* plants, exotic conspecifics germinate faster, grow faster, flower earlier, and produce higher vegetative and reproductive biomass (Blair and Wolfe 2004, Wolfe et al. 2004). Similarly, exotic *Rhododendron ponticum* plants germinate earlier and have faster relative growth rates than plants from native populations (Erfmeier and Bruelheide 2005). Such results suggest that genetic differences among ranges can lead to exotic plants with “weedy phenotypes” (Wolfe et al. 2004), and together with results from EICA studies directly manipulating competition, provide considerable evidence for adaptation to noncompetitive environments.

Why might plants become adapted to noncompetitive environments upon introduction to a new range? As Blossey and Nötzhold (1995) state, the specific traits selected for in the introduced range will depend upon the environment. Thus, it is possible that habitats in the exotic range are less competitive than those in the native range (Bossdorf et al. 2004a). Such differences might be common, given that exotic plants are frequently transported by humans, and therefore frequently transported to relatively disturbed, noncompetitive environments. For example, exotic *Eschscholzia californica* plants, which appear to be particularly well adapted to noncompetitive environments, grow primarily in association with human disturbances; in contrast native *E. californica* plants grow in a wide variety of habitats (Leger and Rice 2003). Alternatively, genetic differences observed in this and other studies might be the result of selection by humans (van Kleunen and Schmid 2003, Bossdorf et al. 2005). Given the extent of human activity in agricultural and horticultural systems, particularly regarding international trade, both intentional and inadvertent introductions are likely to select for genotypes adapted to disturbed systems. For species used by humans, plant breeding may further selection for such genotypes.

The results from this and several previous EICA studies suggest that genetic changes, potentially caused by natural or artificial selection, may often contribute to the success of exotic species in open, noncompetitive environments. Inasmuch as these results indicate a general trend among exotic plant species, they suggest that genetic changes may be more likely to contribute to invasion of disturbed or eutrophied environments than of relatively undisturbed plant communities.

ACKNOWLEDGMENTS

We thank A. Gassman, A. Lawrence, R. Sforza, and the USDA-ARS-NPGS for providing seeds for this study; C. Ferrier, E. Hardy, J. Matsuura, J. Reeder, G. Schuman, and P. Westra for contributions to experimental design and maintenance; and A. Blair, O. Bossdorf, J. Fargione, J. Gurevitch, J. Maron, L. Perry, M. van Kleunen, and three anonymous reviewers for helpful comments on earlier versions of this manuscript.

LITERATURE CITED

- Blair, A. C., and L. M. Wolfe. 2004. The evolution of an invasive plant: an experimental study with *Silene latifolia*. *Ecology* 85:3035–3042.
- Blossey, B., and R. Nötzhold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* 83:887–889.
- Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144:1–11.
- Bossdorf, O., D. Prati, H. Auge, and B. Schmid. 2004a. Reduced competitive ability in an invasive plant. *Ecology Letters* 7:346–353.
- Bossdorf, O., S. Schroder, D. Prati, and H. Auge. 2004b. Palatability and tolerance to simulated herbivory in native and introduced populations of *Alliaria petiolata* (*Brassicaceae*). *American Journal of Botany* 91:856–862.
- Buschmann, H., P. J. Edwards, and H. Dietz. 2005. Variation in growth pattern and response to slug damage among native and invasive provenances of four perennial *Brassicaceae* species. *Journal of Ecology* 93:322–334.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233–260.
- Crawley, M. J. 1987. What makes a community invisable? Pages 429–453 in M. J. Crawley, P. J. Edwards, and A. J. Gray, editors. *Colonization, succession, and stability*. Blackwell Scientific, Oxford, UK.
- Daehler, C. C., and D. R. Strong. 1997. Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia* 110:99–108.
- DeWalt, S. J., J. S. Denslow, and J. L. Hamrick. 2004. Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. *Oecologia* 138:521–531.
- Erfmeier, A., and H. Bruelheide. 2005. Invasive and native *Rhododendron ponticum* populations: Is there evidence for genotypic differences in germination and growth? *Ecography* 28:417–428.
- Green, E. K., and S. M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. *Journal of Applied Ecology* 39: 134–144.
- Hinz, H. L., and M. Schwarzlaender. 2004. Comparing invasive plants from their native and exotic range: What can we learn for biological control? *Weed Technology* 18:1533–1541.

- Joshi, J., and K. Vrieling. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters* 8:704–714.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17:164–170.
- Lankau, R. A., W. E. Rogers, and E. Siemann. 2004. Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. *Ecological Entomology* 29:66–75.
- Leger, E. A., and M. L. Forister. 2005. Increased resistance to generalist herbivores in invasive populations of the California poppy (*Eschscholzia californica*). *Diversity and Distributions* 11:311–317.
- Leger, E. A., and K. J. Rice. 2003. Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters* 6: 257–264.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.
- Maron, J. L., and M. Vilà. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361–373.
- Maron, J. L., M. Vilà, and J. Arnason. 2004a. Loss of enemy resistance among introduced populations of St. John's Wort (*Hypericum perforatum*). *Ecology* 85:3243–3253.
- Maron, J. L., M. Vilà, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004b. Rapid evolution of an invasive plant. *Ecological Monographs* 74:261–280.
- Merigliano, M. F., and P. Lesica. 1998. The native status of reed canary grass (*Phalaris arundinacea* L.) in the inland Northwest, USA. *Natural Areas Journal* 18:223–230.
- Meyer, G., R. Clare, and E. Weber. 2005. An experimental test of the evolution of increased competitive ability hypothesis in goldenrod, *Solidago gigantea*. *Oecologia* 144:299–307.
- Müller-Schärer, H., U. Schaffner, and T. Steinger. 2004. Evolution in invasive plants: implications for biological control. *Trends in Ecology and Evolution* 19:417–422.
- Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461.
- Roach, D.A., and R. D. Wulff. 1987. Maternal effects in plants. *Annual Review of Ecology and Systematics* 18:209–235.
- SAS Institute. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.
- Siemann, E., and W. E. Rogers. 2001. Genetic differences in growth of an invasive tree species. *Ecology Letters* 4:514–518.
- Siemann, E., and W. E. Rogers. 2003. Increased competitive ability of an invasive tree may be limited by an invasive beetle. *Ecological Applications* 13:1503–1507.
- Stastny, M., U. Schaffner, and E. Elle. 2005. Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology* 93:27–37.
- Thebaud, C., and D. Simberloff. 2001. Are plants really larger in their introduced ranges? *American Naturalist* 157:231–236.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- van Kleunen, M., and B. Schmid. 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* 84:2816–2823.
- Vilà, M., A. Gomez, and J. L. Maron. 2003. Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L. *Oecologia* 137:211–215.
- Willis, A. J., J. Memmott, and R. I. Forrester. 2000. Is there evidence for the post-invasion evolution of increased size among invasive plant species? *Ecology Letters* 3:275–283.
- Willis, A. J., M. Thomas, and J. Lawton. 1999. Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? *Oecologia* 120:632–640.
- Wolfe, L. M., J. A. Elzinga, and A. Biere. 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*. *Ecology Letters* 7:813–820