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THE EVOLUTION OF AN INVASIVE PLANT: AN EXPERIMENTAL STUDY WITH *SILENE LATIFOLIA*

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Abstract. The damage caused by biological invasions has traditionally been thought to result from alien species taking advantage of ecological differences between the native and introduced ranges. In contrast, the role of evolutionary forces has received relatively little attention. Our results show that evolutionary change in *Silene latifolia*, a North American weed that was introduced from Europe about 200 years ago, can help explain the plant's successful North American invasion. By growing plants from seed collected in 40 populations from Europe and North America under common garden greenhouse and field conditions, we found significant genetic differences in life history, reproductive, and defensive characters. In general, morphological traits and competitive ability remained unchanged, while North American plants germinated earlier, grew faster, produced more flowers, had greater survival, and invested less into defensive traits (trichomes, fruit capsule) than their European conspecifics. We suggest that as *S. latifolia* escaped a suite of specialist enemies, natural selection favored individuals that invest more in growth and reproduction and less in defense.

Key words: alien plant; biological invasion; common garden; EICA hypothesis; escape from enemies; *Silene latifolia*; trichome.

INTRODUCTION

One of the major goals of research on biological invasions is to determine why a species that is a benign component of its native ecosystem exhibits enhanced performance following introduction to a novel location (Elton 1958, Pritchard 1960, Noble 1989, Blossey and Notzold 1995, Pimental et al. 2000, Sakai et al. 2001, Keane and Crawley 2002). The traditional approach to studying invasions has been to focus on ecological factors (Parker 1997, Cox 1999). A common explanation for invasion success is the "enemy release hypothesis" which posits that natural enemies (e.g., pathogens and predators) regulate the species in the native range, but are absent from the introduced range. Surprisingly, only recently have biologists begun to empirically test this hypothesis, and, for a wide range of animals and plants, the level of attack appears to be lower in the introduced range (Wolfe 2002, Mitchell and Power 2003, Torchin et al. 2003, DeWalt et al. 2004; but see Maron and Vila 2001, Agrawal and Kotanen 2003).

While ecological factors have received the bulk of attention from researchers, the role of rapid evolutionary change in biological invasions has been relatively understudied (Baker and Stebbins 1965, Barrett 2000, Ellstrand and Schierenbeck 2000, Lee 2002, Parker et al. 2003). In other words, independent of a plastic re-

sponse to ecological differences in the introduced range, it is possible that an exotic species expresses a genetically based "invasive" phenotype following colonization (Siemann and Rogers 2001, Leger and Rice 2003). One way this may occur is via selection favoring variants that increase investment of resources to important life history traits at the expense of allocation to defense (Blossey and Notzold 1995). If, indeed, there has been a relaxation of enemy pressure, the shift in resources from costly defense/resistance traits to enhanced growth and reproduction should result in enhanced performance in the introduced range.

If post-introduction success is due to genetically based change, it is of interest to consider which phenotypic traits might evolve to confer invasiveness. Dating back to Baker's classic work (1965, 1974), biologists have viewed colonizing or weedy species as having certain traits such as small seeds, rapid germination and growth rates, broad ecological tolerance or phenotypic plasticity, and prolific reproduction via sexual and/or asexual means (Rejmanek and Richardson 1996, Kolar and Lodge 2001). An alternative strategy for an invader might be to display enhanced competitive ability to succeed in closed habitats (Darwin 1859, Crawley 1987, Callaway and Aschehoug 2000).

The purpose of this study was to explore whether evolutionary change has occurred in *Silene latifolia* (hereafter referred to as *Silene*), an invasive agricultural weed that was accidentally introduced to North America from Europe ~200 years ago (Baker 1947, Godwin 1975). Using a common garden approach, we compared morphological, defensive, and life history traits, and competitive ability in plants grown from seed collected

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in European and North American populations. *Silene* is particularly suitable for this type of investigation because of its geographically dependent set of interactions with enemies (Wolfe 2002). The plant is attacked by both generalist (florivores and aphids) and specialist (fruit predator [*Hadena bicruris* Hufn. (Noctuidae)] and the anther smut fungus [*Microbotryum violaceum* (Pers.:Pers.) Deml. & Oberw. (= *Ustilago violacea* (Pers.) Fuckel (Ustilaginales))] enemies in Europe. While damage from enemies can be devastating in the old world, in North America, specialist organisms are either nonexistent or very rare and damage by generalists is low (Wolfe 2002). This escape from enemies certainly suggests that ecological factors impact *Silene*. Yet, it remains to be determined if genetic change also contributes to the plant's successful North American invasion. Given *Silene*'s success in agricultural settings in the introduced range, we predict that natural selection has favored weedier, or *r*-selected, individuals that invest more energy into rapid growth and increased size and reproduction with a concomitant trade-off with defensive structures.

METHODS AND MATERIALS

Silene latifolia Poirlet (= *S. alba* (Miller) E.H.L. Krause = *S. pratensis* (Rafn.) Godren & Gren.) (Caryophyllaceae) is a dioecious, short-lived perennial. While a common field and roadside plant in Europe, *Silene* has become a problematic weed of cultivated fields and disturbed habitats in North America, especially in the northern United States and southern Canada (U.S. Department of Agriculture 1965, McNeil 1977).

We used a common garden approach in the greenhouse and field to assess if genetic differences exist between European and North American plants. The greenhouse experiment was conducted at Georgia Southern University (GSU) to obtain detailed phenotypic measurements and to evaluate whether there were continent-level differences in competitive ability. The field experiment was conducted at Mountain Lake Biological Station (MLBS), Giles County, Virginia, USA to estimate life history characters in a more natural setting. For each experiment, we grew seeds (bulk collections with mixed maternal families) collected between 1999 and 2001 from 20 European and 20 North American populations (10 seeds per population). The year of collection did not influence the probability of ($F_{2,34} = 0.88, P = 0.42$) or time to germination ($F_{2,33} = 0.18, P = 0.84$) at the population level. The sampling spanned the majority of *Silene*'s geographical distribution (Fig. 1), and the same set of populations was used in both experiments.

Greenhouse competition experiment

The greenhouse common garden experiment was initiated in March 2002, and plants were grown in 10-cm pots, using a standard *Silene* soil mix (peat moss, per-

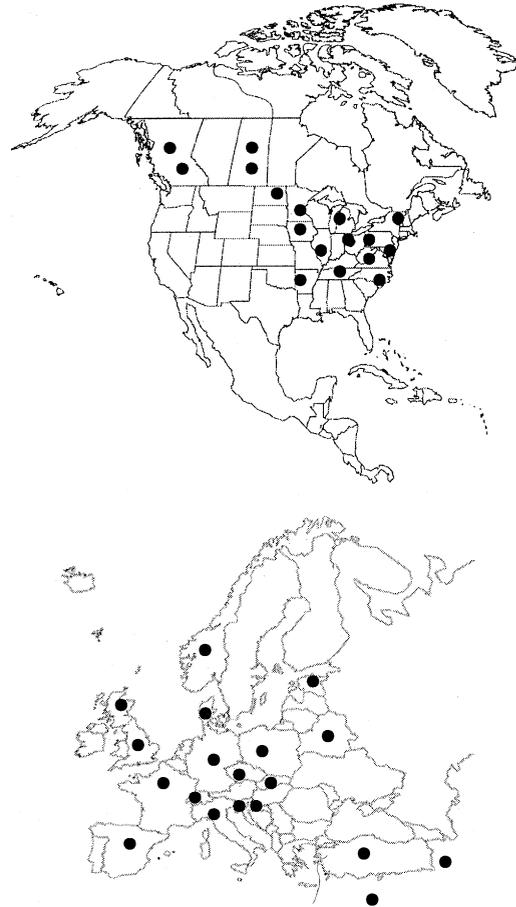


FIG. 1. Map of the *Silene latifolia* seed source populations used in this study.

lite, and pine bark mulch). Of the 400 plants, half (five per population) were grown in interspecific competition with a grass mixture that contained species that occur naturally with *Silene* in both Europe and North America (Pennington Sun and Shade [58% Tall Fescue (*Festuca arundinacea* Schreb.), 18% Red Fescue (*Festuca rubra* L.), 13% Bermudagrass (*Cynodon dactylon* (L.) Pers.), and 11% Perennial Ryegrass (*Lolium perenne* L.)]; Pennington Seed, Inc., Atlanta, Georgia, USA). Each pot was sown with 1.5 mL of grass seed planted immediately below the soil surface. One *Silene* seed was then placed on the surface of the soil. Five plants from each population were grown in separate pots in the absence of competition to act as controls. Pots were arranged randomly in the greenhouse, watered every 2–5 d, and fertilized once per month.

The following traits were measured to test for genetically based differences between introduced and native populations: (1) germination day (the time between planting and full cotyledon expansion); (2) cotyledon area (length and width were measured when the first pair of true leaves was fully expanded; area was calculated using the ellipse equation); (3) leaf size (length

and width of the largest leaf were measured at the onset of flowering; area was calculated using the ellipse equation); (4) plant size (number of fully expanded leaves was counted one month after planting and on the day that each plant began to flower); (5) flower production (total flower number was determined by daily counts during the first flowering season); (6) flower size (length and width of one petal and the calyx were measured on the first flower produced); and (7) underground branches (although *Silene* does not reproduce vegetatively, plants form underground basal branches or rosettes). After approximately one year of growth, we harvested 29 European and 31 North American control plants. Plants were cleaned of soil with a high-pressure hose and the number of branches counted. This measurement provided another estimate of growth.

Mountain Lake common garden

Plants were started in small pots (3.8×14 cm) in the greenhouse with the soil mix described above. Plants were moved to MLBS in May 2002 approximately one month after germination and transplanted into 1-gallon (3.8-L) pots in a fenced deer enclosure. The pots were spaced 0.5 m apart and dug 10 cm into the soil. The naturally occurring vegetation was left intact. Plants received ambient rainfall and fertilizer was applied once a month (teaspoon of Royster Clark 10-10-10 per pot [Royster Clark, Norfolk, Virginia, USA]). To avoid the transfer of foreign pollen to local populations, all *Silene* individuals (escapes from previous experiments at MLBS) within a 1.0 km radius of the enclosure were pulled prior to the flowering of the experimental plants.

For this experiment, we recorded percent germination, survival to flower in the first growing season, overwinter survival after the first growing season, and the probability that plants flowered in the second year. First-year performance was obtained by multiplying population percentages for germination, survival, and flowering. Second-year performance was obtained by multiplying the population percentages for overwinter survival and flowering. The overall performance of individual *Silene* populations was determined by summing the first and second years' performance estimates.

Measurement of defensive traits

The calyces and leaves of *Silene* are covered with trichomes, which are known to deter herbivores in other systems (e.g., Agren and Schemske 1993). We measured trichome density on leaves and calyces at MLBS in 2003. During the middle of the flowering season, one unopened bud (1–2 d from anthesis) was removed from each plant. In the laboratory, the length and width of the calyx were measured, a 3.2-mm² disk was taken from the base of the flattened calyx using a paperpunch, and the number of trichomes was counted under a dissecting microscope. Leaf trichome number was counted

on a 3.2-mm² disk removed near the base of one freshly expanded leaf per plant.

A controlled hand-pollination program was initiated at MLBS to determine if the relative allocation by females to fruit and seeds differed between the two continents. Given that the fruit of *Silene* is the main defense against some forms of *Hadena* attack, we hypothesized that the fruit wall would be thicker in European plants. Within-population crosses were made between bagged male and female flowers. The anthers of one male flower were used to pollinate a single female flower, and female flowers were rebagged upon pollination to ensure no pollen contamination. Ripe fruits were harvested, and seeds and the fruit capsule were weighed independently. The thickness of the fruit wall (taken near the center of the fruit) was measured using a hand-held micrometer caliper.

Data analysis

All statistical analyses were conducted using JMP (SAS Institute Inc., Cary, North Carolina, USA). Throughout this paper we present means \pm 1 SE.

Contingency table analysis (*G* test) was used to compare the proportion of individuals in the two ranges that germinated, flowered, and overwintered. Nested ANOVA was used to determine sources of variation in morphological, life history, and floral characters. *Silene* is dioecious and previous studies have documented how flower size and production differ between the sexes (Carroll and Delph 1996). As preliminary analyses indicated that there were no significant sex \times continent effects (except see *Results* for trichomes), the sex effect was not included in any of our models. In the greenhouse experiment, each trait was the function of the following effects: continent, population(continent), competition, and competition \times continent. A significant competition \times continent interaction would be evidence of a difference in competitive ability between the introduced and native ranges. In the MLBS experiment, each trait was the function of the main effects of continent and population(continent).

All morphological and life history traits measured in the greenhouse and at MLBS varied significantly among populations within each continent (ANOVA, $P < 0.01$ for all traits)—for ease of presentation we do not include these effects in *Results*. All traits were considered fixed effects except population(continent), which was analyzed as a random effect.

Trichome density was the function of the following main effects: sex, continent, and sex \times continent. ANCOVA was used to determine if allocation patterns to seeds and fruit capsules differed between the two continents: log capsule mass was analyzed as a function of the following effects: continent, log seed mass (covariate), and continent \times log seed mass.

RESULTS

Common gardens

The results of our common garden experiments demonstrated that North American and European *Silene*

TABLE 1. Comparison of European and North American *Silene latifolia* grown in a greenhouse common garden experiment.

Plant trait	Europe	N. America	$F_{\text{Continent}}$	df
Morphological				
Cotyledon area (cm ²)	0.064 ± 0.002	0.071 ± 0.002	1.65	1, 36
Largest leaf first flower (cm ²)	5.24 ± 0.32	4.97 ± 0.22	0.41	1, 29
Petal length (cm)	0.44 ± 0.013	0.41 ± 0.009	0.091	1, 29
Calyx length (cm)	0.57 ± 0.016	0.52 ± 0.011	1.66	1, 29
Life history				
Germination day	9.27 ± 0.25	6.89 ± 0.23	43.84***	1, 36
Plant size (1 mo)	3.69 ± 0.17	4.58 ± 0.15	16.16***	1, 36
Plant size (onset of flower)	39.9 ± 3.1	48.8 ± 2.6	5.90*	1, 29
First flower day	74.3 ± 9.7	52.0 ± 6.8	8.42**	1, 29
Flower production	34.52 ± 16.17	70.61 ± 11.18	4.31*	1, 23

Notes: Values are mean ± 1 SE. F values are from nested ANOVA (see *Methods and Materials* for description). Germination day is the time until emergence after planting; plant size is measured by the number of leaves; first flower day is the time from emergence to flowering; and flower production is the total number of flowers produced in the first growing season (non-flowering plants were not included in the analysis).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

have become genetically differentiated. For the most part, morphological traits measured in the greenhouse such as cotyledon size and petal length, were similar between the continents (Table 1). On the other hand, critical life history traits differed significantly between the native and introduced ranges. Under greenhouse conditions, North American plants germinated earlier than European plants and were ~20% larger throughout the juvenile stage, 10% larger at the onset of flowering, and produced ~100% more flowers (Table 1). North American plants also produced significantly more underground branches during the first year of growth (North America = 4.87 ± 0.46 , Europe = 3.90 ± 0.47 , $F_{1,30} = 4.55$, $P = 0.04$). In both the field and greenhouse control treatment, North American plants had greater germination rates and a higher probability of flowering (Fig. 2). Although not statistically significant ($P = 0.10$), North American plants had greater overwintering survival in the field.

At MLBS, North American plants had ~30% greater overall performance (North America = 1.14 ± 0.09 , Europe = 0.83 ± 0.09 ; $t = 2.52$, $P < 0.017$; Fig. 3). There were striking differences in the distribution of performance of the 40 populations: while 65% of European populations were below the overall mean, 89% of North American populations exceeded the global average (Fig. 3).

Competition

Interspecific competition had a significant effect on *Silene*. Plants grown in competition had smaller cotyledons (0.074 ± 0.002 vs. 0.057 ± 0.002 cm², $t = 5.15$, $P < 0.001$), were smaller than control plants at one month after planting (5.14 ± 0.11 vs. 2.72 ± 0.14 leaves; $t = 13.1$, $P < 0.0001$), and at the onset of flowering (55.11 ± 1.91 vs. 16.31 ± 3.22 leaves; $t = 10.35$, $P < 0.0001$). However, there was no evidence for the evolution of competitive ability, as all competition × continent interactions were not significant (Table 1).

Defensive traits

Leaf trichome density did not differ between sexes ($F_{1,103} = 0.001$, $P > 0.97$), continents ($F_{1,103} = 0.356$, $P > 0.55$), or their interaction ($F_{1,103} = 2.51$, $P > 0.15$; Fig. 4). There were, however, significant differences in calyx trichome density. While there were no overall continental differences ($F_{1,113} = 0.482$, $P > 0.48$), females did produce a greater density of trichomes than males ($F_{1,113} = 6.61$, $P < 0.01$). The most interesting result was the significant sex × continent interaction term ($F_{1,113} = 3.84$, $P < 0.04$). Female plants from Europe produced significantly more trichomes than those from North America, but males did not differ in calyx trichome production (Fig. 4).

The construction of fruits differed between the two continents (Fig. 5). European plants made heavier fruits than those from North America ($t = 5.94$, $P < 0.0001$). The mass difference resulted from thicker walls of European capsules ($t = 6.09$, $P < 0.0001$). On the other hand, North American fruits contained greater total seed mass ($t = 6.11$, $P < 0.0001$).

ANCOVA results indicated that the relative response of seed mass to increasing fruit capsule mass was not qualitatively different between the two continents (covariate interaction $F_{1,105} = 0.561$, $P > 0.455$). However, for a given seed mass, European fruit invest significantly more protective capsule tissue.

DISCUSSION

The patterns revealed in this study are consistent with the notion that the success of *Silene* in North America stems, in part, from the action of evolutionary forces. North American *Silene* germinates earlier, forms more underground basal rosettes, and has greater survival than their European counterparts. Flower production by North American plants exceeds what would be expected given the increase in plant size, suggesting a shift in reproductive allometry. We consider a plant that has these qualities to have a weedier (sensu Baker

TABLE 1. Extended.

$F_{\text{Competition}}$	df	$F_{\text{C} \times \text{C}}$	df
41.67***	1, 235	1.74	1, 235
0.26	1, 69	0.004	1, 69
0.14	1, 68	0.019	1, 68
0.002	1, 67	0.069	1, 67
0.86	1, 234	3.05	1, 234
208.45***	1, 234	0.006	1, 234
110.09***	1, 69	0.31	1, 69
11.23**	1, 67	1.64	1, 67
2.86 ⁰⁹	1, 38	0.852	1, 38

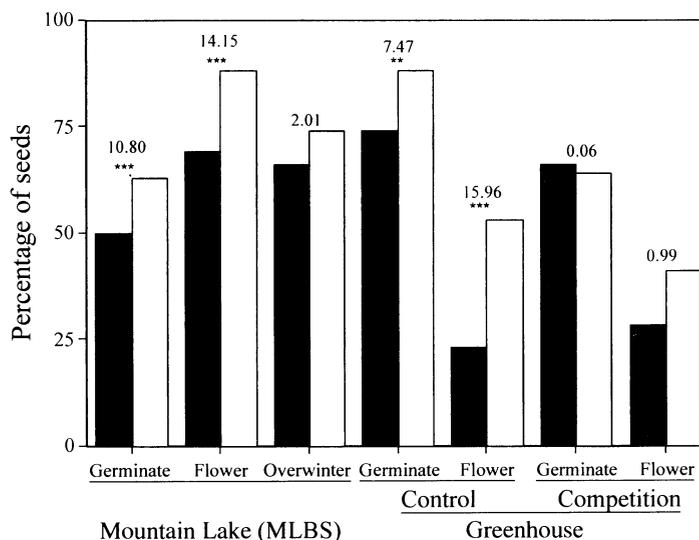
1965) and more invasive phenotype. Overall, it appears that morphological traits remain unchanged while important life history traits evolved. Given that these differences occurred in a common garden, it is possible to rule out phenotypic plasticity and to conclude that there has been a genetic shift since the species' introduction to North America. In an experiment using field-collected seed, it is possible for maternal effects to influence the interpretation of any continent-based differences (Roach and Wulff 1987). However, the differences that emerged at adulthood are not likely the result of environmental maternal effects, as the plants were very similar at the cotyledon stage (Table 1) (see Parker et al. 2003). Additionally, maternal effects are typically expressed early in the life cycle and decrease as plants age (Wolfe 1993).

The question then becomes, how did the invasive phenotype evolve from European ancestors? There are several non-mutually exclusive scenarios, which integrate processes that could have occurred during and/or after *Silene*'s colonization period. First, the patterns suggest that natural selection has increased the ability of *Silene* to invade North American communities. European and North American *Silene* populations expe-

rience profoundly different environments with respect to their exposure to natural enemies (Wolfe 2002). When all enemies are taken into account, *Silene* is 17 times more likely to be damaged in Europe than in North America (Wolfe 2002). Most of the damage found on *Silene* is to reproductive structures caused by various floral herbivores and a fruit predator (*Hadena bicruris*). Natural enemies exert selection that drives the evolution of characters to reduce the adverse effects of attack (Berenbaum 1983, Mauricio et al. 1997, Elle and Hare 2000). If the evolution of plant defense is driven by the balance between costs of resistance and benefits to plant fitness, then selection should favor a reallocation towards growth and reproduction in the absence of natural enemies (Blossey and Notzold 1995, Daehler and Strong 1997). Thus, one working hypothesis is that North American plants are more vigorous because they allocate fewer of their resources to defense. In fact, we do see a significant reduction in investment to defense through lower trichome production in female flowers from North America. This response is exactly what would be expected, a priori, owing to the elimination of floral and fruit damage in North America (Wolfe 2002). The apparent lack of difference

FIG. 2. Life history characters in European (solid bars) and North American (open bars) *Silene latifolia* grown either in a common garden at Mountain Lake Biological Station (MLBS) or in the greenhouse (GH). GH plants were grown individually or in interspecific competition. Values are the percentage of seeds from each continent that germinated, flowered in the first growing season, or overwintered successfully (2002–2003). Values on top of bars are from *G* tests.

** $P < 0.001$; *** $P < 0.0001$.



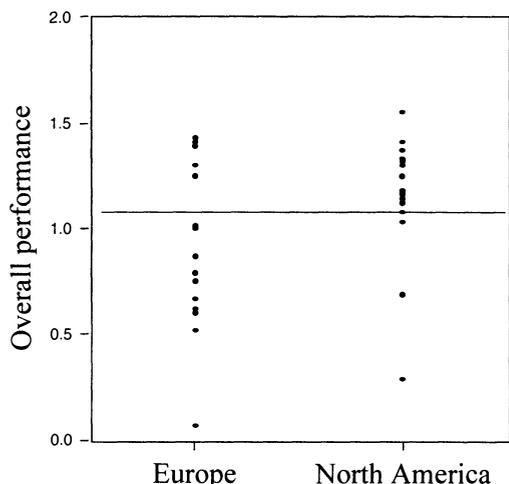


FIG. 3. Overall performance (sum of first- and second-year performance) of individual *Silene latifolia* populations from Europe and North America at MLBS. First-year performance was obtained by multiplying population percentages for germination, survival, and flowering. Second-year performance was obtained by multiplying the population percentages for overwinter survival and flowering. The horizontal line represents the global average.

in leaf trichome density between Europe and North America serves to support the argument that calyx trichome density is a result of altered selection regimes. Relative to the high levels of damage to flowers in Europe, leaves do not appear to be popular targets of attack on either continent (L. M. Wolfe, *personal observation*).

Additional support for an altered defensive strategy comes from the finding that allocation patterns within fruit differ between the two continents. *Hadena* larvae typically develop inside a maturing fruit and then de-

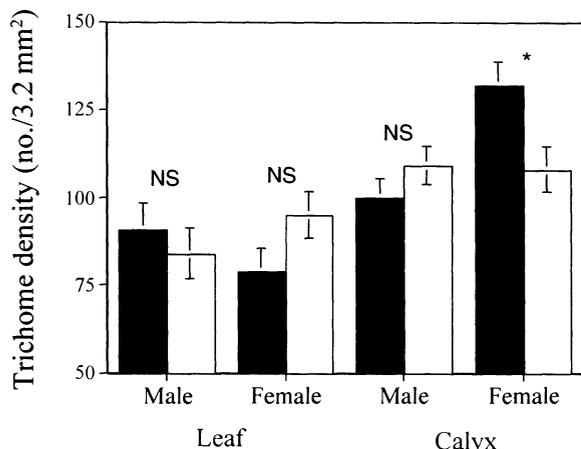


FIG. 4. The production of defensive trichomes on leaves and calyxes of European (solid bars) and North American (open bars) *Silene latifolia*. Values represent the mean (± 1 SE) number of trichomes in a disc with an area of 3.2 mm². * $P < 0.5$.

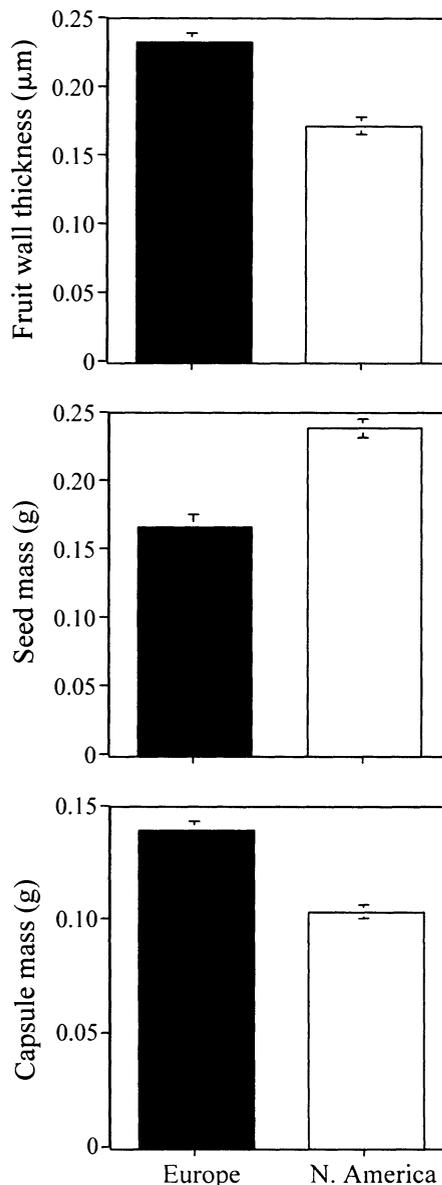


FIG. 5. Patterns of fruit construction by European and North American *Silene latifolia* populations. Values represent means ± 1 SE.

vor the seeds within. After this primary attack, they eat their way out of the fruit, leaving a characteristic exit hole, locate another fruit on the same or neighboring plant, and burrow into the fruit (secondary attack). Under the assumption that thicker-walled fruits are better able to defend themselves against a secondary attack, and given that European plants invest relatively more to the fruit itself than seeds, it appears that European *Silene* allocates more to offspring protection than do North American plants. Similarly, Siemann and Rogers (2003) found that the faster-growing introduced *Sapium sebiferum* (Chinese tallow tree) outperformed the native conspecifics in a common garden

in the introduced range where herbivory is reduced. Levels of foliar tannins were lower in the introduced genotypes than the native genotypes, suggesting that the plants allocated more energy into growth at the cost of defensive structures (Siemann and Rogers 2003).

Genetic variation is requisite for natural selection to act upon. It is plausible that sufficient genetic variation existed in populations in North America to result in the evolutionary changes we have seen. However, it is also possible that the available pool of variation has been enhanced by post-colonization hybridization (Ellstrand and Schierenbeck 2000). If North America was colonized by seed material from multiple, genetically differentiated populations, plants from these previously isolated populations could have come into contact with each other and hybridized, producing novel combinations of genotypes (Ellstrand and Schierenbeck 2000). In fact, evidence suggests that both conditions are met in the case of *Silene*. There is genetic structure in Europe (Vellekoop et al. 1996), and the plant is likely to have been introduced multiple times to North America (D. R. Taylor, *personal communication*).

However, our work does not rule out the possibility that evolution could be the result of stochastic factors. For example, genetic drift is a force thought to have played an important role in other North American invasions, (e.g., fire ants [Tsutsui et al. 2000], purple loosestrife [Eckert et al. 1996]). Typically, genetic bottlenecks are thought to reduce population growth (e.g., Newman and Pilson 1997). However, founder effects during invasion could cause colonists to be a nonrepresentative sample of aggressive lineages from the native range. Assuming there exists among-population variation in Europe in characters associated with invasibility, it is possible that *Silene* phenotypes preadapted to becoming invasive in disturbed or agricultural settings were among the founders in North America. Our future work will attempt to unravel the invasion history using molecular genetic techniques.

In sum, these evolutionary forces (selection, hybridization, and drift) could act independently, or in concert, to alter a suite of morphological, life history, and reproductive traits that together produce a phenotype that exhibits enhanced invasion ability. Only a small number of other studies have adopted a common garden approach to examine the evolutionary basis of invasiveness. Willis et al. (2000) found no differences in four plant species sampled from their native and introduced habitats. In contrast, the results of a long-term study on *Sapium sebiferum* (Siemann and Rogers 2001, 2003) indicated that plants from the introduced range (USA) did in fact exhibit greater size after 14 years of growth than those from the native range. Recently, Leger and Rice (2003) reported no differences in survival or phenotypic traits when native and introduced California poppies were grown under competitive conditions. However, under relaxed conditions with reduced

competition, the invasive poppies did outperform their native conspecifics. While this latter result suggests that there has been post-introduction selection, it is interesting that the invasive poppy phenotype did not evolve increased competitive ability. This is precisely what we found for *Silene* because plants from Europe and North America did not differ in how they performed under competition. However, this result is in direct contrast with the recent findings of van Kleunen and Schmid (2003). In a common garden study with North American (native) and European (introduced) *Solidago canadensis*, they found that the native plants were actually more vigorous than the introduced plants, and in the presence of simulated herbivory, plants from both regions responded similarly (i.e., there has not been a trade-off with defense).

For the past decade an organizing theme in invasion biology has been the EICA (evolution of increased competitive ability) hypothesis (Blossey and Notzold 1995). This idea posits that, in the absence of enemies, more resources should be allocated towards growth and reproduction, and less towards defense. While competitive ability has not evolved per se, the work presented here supports the EICA hypothesis—*Silene* grows more vigorously in the introduced range, and there is evidence that this is a result of a trade-off with defense. Thus it seems that the relative importance of ecological and evolutionary forces is unique to each invasion, but this work demonstrates that, at least in some cases, post-invasion evolution may play a dominant role in the outcome of an introduced species.

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