

Spring 2004

Role of Hybridization in a Biological Invasion: An Experimental Study with *Silene Latifolia*

Lindsay Heaton

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**THE ROLE OF HYBRIDIZATION IN A BIOLOGICAL INVASION: AN
EXPERIMENTAL STUDY WITH *SILENE LATIFOLIA***

by

LINDSAY HEATON

(Under the direction of Lorne M. Wolfe)

ABSTRACT

Biological invasions are now the second leading cause of loss of biodiversity. Recently, hybridization has been hypothesized as a mechanism for invasion success. The combination of individuals from different gene pools may create novel genotypes having increased invasibility. The goal of my research was to examine the role that intraspecific hybridization may play in invasion success by using the agricultural weed *Silene latifolia* as a model. I used a common garden experiment to examine whether crossing parents of different ancestry results in offspring with differing quality. Plants were pollinated in three treatments reflecting parent plants within the same population (P), between-populations, within-continent (R), and between-continent (C). Plants which had been produced by mating plants located intermediate distances apart (R) germinated faster, and had a greater probability of germinating and surviving. This thesis contributes to our knowledge of the potential role hybridization may play in a successful invasion.

INDEX WORDS: Invasive species, hybridization, inbreeding depression, outbreeding depression.

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by

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B.S., Georgia Southern University, 2002

M.S., Georgia Southern University, 2004

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in
Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

STATESBORO, GA

2004

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EXPERIMENTAL STUDY WITH *SILENE LATIFOLIA*

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DEDICATION

To my parents, Eddie and Gwen Heaton, for always reminding me to keep chasing my dreams.

ACKNOWLEDGEMENTS

I thank my advisor, Dr. Lorne M. Wolfe for his help in all facets of this thesis. I also thank my committee, Dr. Danny Gleason and Dr. Lissa Leege for their advice and suggestions with this research. I thank Dr. Ray Chandler for not only his statistical help, but also for being such an outstanding graduate director who has been a mentor to me as an undergraduate and graduate student.

I thank Dr. Steve Vives for providing me with a graduate assistantship as a teaching assistant. I am extremely grateful for having the opportunity to work for Liz Elliot. She was not only an outstanding leader, but became a trusted friend who I feel very lucky to have known. I thank Dr. Boole for the Irene Burt Boole Botany Scholarship I received in fall of 2003. I thank Smith Baggett for his hard work in the greenhouse. I will never forget all the long days we worked replanting 900 seedlings in extremely hot temperatures.

Finally, I thank my parents Gwen and Eddie Heaton. This degree would have never been possible without their never-ending love and support. Their belief in me has been the strength and motivation I depend on every day. I am unbelievably blessed and proud to have the most amazing parents in the whole world.

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CHAPTER 1

INTRODUCTION

Invasive species are defined as introduced species that cause negative impacts on native plants and animals (Lee 2002). Biological invasions are considered one of the greatest threats to biodiversity, and are thought to be responsible for as much as 25% of the anticipated extinctions of native flora and fauna world wide (Cox 1999). Economically, the US spends more than \$137 billion per year for control and prevention of these pests (Pimentel et al. 2000). To better understand the mechanisms by which introduced species become invasive, we must focus on identifying the characteristics of a species that make it successful (Blossey and Notzold 1995, Ellstrand and Schierenbeck 2000). A better understanding of invasions is key to protecting biodiversity and eventually controlling invasive species.

Many studies have documented that plants in the introduced part of a species' range exhibit enhanced vigor or 'weedy growth' when compared to those in their native range (Blossey and Notzold 1995, Cox 1999, Keane and Crawley 2002). Such weedy traits include faster germination, enhanced growth, greater seed production, and smaller seed size (Pritchard 1960, Blossey and Notzold 1995, Fowler et al. 1996, Crawley et al. 1997). Several studies have found these weedy traits in North American populations which have been introduced from Europe. For example, Nobel (1989) found that invasive populations of *Chrysanthemoides monilifera* as well as *Acacia longifolia* exhibit higher seed production than in their native range. Rejmanek and Richardson (1996) showed invasive pine species had smaller seed mass, a shorter juvenile period, and shorter intervals between seed crops than native pines. Recently Leger and Rice (2003) found that invasive *Eschscholzia californica* had larger shoots and produced more seeds than plants in their native range.

Past research on invasive species has traditionally focused on ecological causes for invasion success. One hypothesis, commonly called escape from enemies, suggests that when a species leaves its native range, it leaves behind natural pathogens and predators (Lawton and Brown 1986, Blossey and Notzold 1995, Crawley 1997). Several studies have documented the absence of natural enemies in nonindigenous habitats (Lawton and Brown 1986, Crawley 1987, Blossey and Notzold 1995). Wolfe (2002) found that *Silene latifolia* is 17 times more likely to be attacked in its native range than in its introduced range because of the absence of several enemies. Torchin et al. (2003) compared the parasites of exotic species in their native and introduced range using 26 host species of molluscs, crustaceans, fishes, birds, mammals, amphibians, and reptiles and found that the number of parasite species present in native populations is twice that seen in introduced populations. Mitchell and Power (2003) also tested the escape from enemies hypothesis by comparing the incidence of fungal and viral pathogens in 473 plant species introduced into the USA from Europe. On average they found 84% fewer fungi and 24% fewer virus species infected species in their introduced range than in their native range. In cases such as these, organisms may be able to capitalize on the release from enemies and increase in growth and reproduction. In enemy-free space, resources previously used for herbivore defense become available and can be reallocated toward increased growth and reproduction (Bazzaz et al. 1987, Herms and Mattson 1992, Blossey and Notzold 1995). As a result of change in predation pressure, it is possible that relaxed selection may lead to evolutionary changes.

Although ecological causes for invasion success have been well studied, evolutionary aspects have only been recently explored. Evolution of traits may be due to several events that occur during the introduction phase including genetic drift, natural selection, or hybridization. Genetic drift is an important

potential pathway for invasion success (Maruyama and Fuerst 1984, Eckert et al. 1996). It is possible that certain genotypes in the native range are preadapted for being successful in the introduced habitat. In this scenario, the invasive phenotypes are already present in the native range. Since colonizing individuals make up only a fraction of the introduced population, the preadapted phenotypes could be the ones that comprise the colonists. Several studies have documented evidence of genetic drift leading to successful invasions (Maruyama and Fuerst 1984). Eckert et al. (1996) found evidence of genetic drift when studying the maintenance of flower morphs in the invasive populations of the tristylous species *Lythrum salicaria*. The success of the highly invasive Argentine ant is due to a bottleneck which occurred upon introduction into North America. Following introduction, genetic diversity was lost, resulting in reduced intraspecific aggression and the formation of interspecifically dominant supercolonies (Tsutsui et al. 2000).

Evolution via natural selection may occur after introduction. In this case, several different phenotypes may be introduced yet natural selection favors those with characteristics which are better suited for the new environment. Since environmental conditions would likely be different in an introduced range, the phenotypes that are the most fit in the introduced range survive and reproduce (Cox 1999, Roy 2000). Evolution of competitive ability may also occur because of differences in enemy level in native and introduced ranges. Blossey and Notzold (1995) hypothesized that in the absence of native herbivores, selection will favor individuals with reduced resource allocation to herbivore defense and increased competitive abilities. Several studies have documented the increased vigor of introduced populations and decreased defense mechanisms when grown in a common garden compared with native plants (Blossey and Notzold 1995, Vila and Gimeno 2003). Daehler and Strong (1997) found reduced

resistance in invasive *Spartina alterniflora* after plants had been living herbivore-free for more than 100 years. When grown in a common garden, introduced plants suffered 50% more damage by leaf eaters and 37% greater mortality than plants from their native range. Siemann and Rogers (2003) conducted a 14 year common garden experiment with native and introduced varieties of *Sapium sebiferum* and found invasive plants had lower concentrations of defense chemicals in the foliage of mature trees and higher growth rates compared to native plants.

Finally, another scenario for invasion success via evolution may be hybridization. Success of hybrids may be due to increased genetic variance, masking or unloading of deleterious recessive alleles, or the transfer of favorable genes (Ellstrand and Schierenbeck 2000). Examples of adaptations resulting from hybridization include the acquisition of herbicide resistance in weeds from genetically engineered crops, and possibly the transfer of cold tolerance (Snow 1999, Milne and Abbott 2000). Several studies have documented positive effects of hybridization on invasibility, such as faster growth, greater size, and increased aggression (Ellstrand and Schierenbeck 2000, Perry et al. 2001). Daehler and Strong (1997) used random amplified polymorphic DNA markers to test for hybridization between native and introduced *Spartina* species in the field and greenhouse. They found high numbers of hybrid plants in the field and high levels of fertility among hybrids that were backcrossed with one parent. It appeared from his field study that hybrid *Spartina* were more vigorous and morphologically intermediate than either parental species.

The combination of individuals from different gene pools may create a novel genotype having increased invasibility. Other studies have shown matings between populations that are genetically different may lead to new adaptive systems, able to fit into new ecological niches. *Rhododendron ponticum* has been

able to colonize areas in much colder than its native range in Spain and Portugal. This broader ecological amplitude is thought to be gained by hybridization in Britain with the cold tolerant *R. catawbiense* from North America (Milne and Abbott 2000). Neuffer et al. (1999) studied hybridization between *Viola* species and found introgressive hybrids between *V. reichenbachiana* and *V. riviniana* that invaded pine forest in Germany which were heavily affected by calcareous pollutants. It was concluded from morphological, cytological, and molecular data that recurrent hybridization and backcrossing resulted in novel genotypes adapted to the polluted pine forest.

Other studies have documented deleterious fitness traits associated with hybrids. Hybrid plants are sometimes vegetatively weak and show decreased competitive ability (Cummings et al. 1999, Snow 2001, Fritz et al. 2003). This may occur when organisms are locally adapted to their environment. Offspring produced between parents from different populations may have phenotypes which are disadvantageous in any environment (Rhymer and Simberloff 1996). Cummings et al. (1999) found hybrid *Helianthus annuus* plants had significantly higher levels of insect damage than wild plants. Hybrid radish was found to have lower fitness than wild plants due to lower pollen fertility, fewer seeds per plant, and delayed flowering (Snow et al. 2001). Fritz et al. (2003) compared damage by 13 insect herbivores and one herbivorous mite on hybrid and parental willows and observed a breakdown of resistance genes in hybrid plants.

Studies such as those outlined above have documented evidence of interspecific hybridization, which occurs between two different introduced species, or between a native and introduced species. Very little work has been done on intraspecific hybridization between different populations of the same species. Although populations of the same species may not be taxonomically

distinguishable, they may differ genetically or phenotypically (Rhymer and Simberloff 1996).

The role of hybridization in invasion success has seldom been studied (Ellstrand and Schierenbeck 2000). The goal of my research is to learn more about the possible pathway that hybridization may create for invasive plants. This study explores evolutionary aspects of invasion success by using the plant *Silene latifolia* (hereafter referred to as *Silene*) as a model. The plant is native to Europe and was introduced to North America in the mid 1800s (McNeill 1977). Recent research indicates that *Silene* has undergone evolutionary change following invasion (Blair 2003). This research found that introduced plants exhibit a more invasive phenotype in some life history traits. Invasive *Silene* showed faster germination, larger size as juveniles, and earlier flowering than native plants. Given that *Silene* has escaped its enemies in North America (Wolfe 2002), it is possible that relaxed selection could have led to evolutionary changes.

The purpose of this study was to experimentally explore the role that hybridization may play in *Silene*'s invasion. I examined whether crossing parents of different ancestry results in offspring of differing quality. *Silene latifolia* has a broad geographic distribution, and as the plant spread from Europe to North America, it is possible that populations became increasingly genetically differentiated. Thus populations that are separated by large distances may be most different. Matings between material from different source populations could result in the production of higher quality phenotypes. On the other hand, it is possible that populations that are widely separated are locally adapted, and have become so differentiated that hybridization would result in outbreeding depression (Rhymer and Simberloff 1996). In this case, cross-population mating could produce offspring with phenotypes unfit for any environment.

CHAPTER 2

MATERIALS AND METHODS

Study Species and Source Material

Silene latifolia Poiret (= *S. alba* (Mill.) E.H.L. Kraus = *S. pratensis* (Rafn.) Godren & Gren.) (Caryophyllaceae) is a dioecious, short-lived perennial that grows along roadsides and the margins of agricultural fields (Baker 1947). The plant originated in Europe and was accidentally introduced into North America in the early part of the nineteenth century with the spread of agriculture (McNeill 1977). *Silene* is considered a noxious, troublesome weed in Canada and the USA (McNeill 1977). A US Department of Agriculture survey as early as 1965 reported that the plant was one of the five worst weeds in pastures and hay crops in six states, and that infestations were rapidly increasing (McNeill 1977).

Much is already known about the biology of the plant, such as its pollination biology, metapopulation structure, and genetic structure (Baker 1948, Alexander and Antonovics 1995, McCauley et al. 1996, Altizer et al. 1998). *Silene* is an ideal plant to use in my study because much of its biology differs between North America and Europe. As previously stated, many of *Silene's* native enemies do not occur in its introduced range (Wolfe 2002). The anther-smut fungus *Microbotryum violaceum* sterilizes male and female plants by transforming their reproductive parts into spore producing parts (Baker 1947). *Microbotryum violaceum* is widespread in Europe, but restricted in North America to populations in Virginia (Wolfe 2002). *Hadena bicruris* occurs only in Europe and is a specialist predator that consumes developing fruit throughout its larval stage.

Overview of Methods

I used a common garden experiment to compare life history traits of European and North American plants, as well as plants crossed in three treatments. These treatments were designed to learn more about the relative fitness of progeny produced by crossing closely related and distantly related plants. The seed material I used in this experiment had already been produced in a two-generation controlled hand pollination program by Dr. Lorne Wolfe. This program was begun by growing seed from 20 European populations and 20 North American populations (see Figure 1 and Table 1). These seeds were germinated in the greenhouse and at flowering adult female plants were subjected to one of three pollination treatments. 1) Within-population crosses were performed on plants from the exact same population (P); 2) Between-population, within-continent crosses were done on plants from different populations but from the same continent (R); and 3) between-continent crosses were performed on plants which came from different continents, Europe and North America (C). All crosses were replicated on each female plant. When ripened, fruit was collected and these seeds were the source for my experiments.

Consequences of crossing history

Generation I

This experiment was initiated in the Georgia Southern University greenhouse on March 3, 2003). I planted ten seeds from each of the three treatments described above, from five maternal plants, from six populations in two continents; ($10 \times 3 \times 5 \times 6 \times 2 = 1800$ seeds). Seeds were planted in small circular pots (3.8 cm diameter, 14 cm depth) with a 50/50 mixture of potting soil and MetroMix 360. Seeds were misted twice a day for two weeks. After two weeks,

plants were watered every 2-3 days, depending on the weather conditions.

Plants were transferred to larger square pots (10 cm width, 12 cm depth) two months after germination. The following traits were measured to assess fitness differences between plants.

- ◆ Germination day - Time between planting and full cotyledon expansion.
- ◆ Percent germinated - The proportion of plants that germinated out of those planted.
- ◆ Biomass - A random sample of plants was taken after three months of growth, and above-ground plant material as well as roots were dried and weighed on an analytical scale to the nearest .
- ◆ Height - The height of each plant was recorded at first flower.
- ◆ Flowering date - Time between planting and appearance of the first flower.
- ◆ Sex - The sex of each plant (male or female) was recorded.
- ◆ Percent flowered - The proportion of plants that flowered out of those that germinated.
- ◆ Flower size - Length and width in cm of a petal and sepal was taken on the second flower produced on each plant.
- ◆ Leaf number - Leaf number was counted on each plant at the time of first flower and four months after planting.
- ◆ Flower production - Number of flowers were counted four months after planting.
- ◆ Whitefly damage - Whitefly damage was recorded on July 28, 2003 examining damage to leaves. A damaged leaf was counted as one with any visual damage. Each plant was given a number 0-3 which corresponded to the level

of damage present. (0= no leaves damaged, 1= 25% leaves damaged, 2= 50% leaves damaged, 3= 75% or greater leaves damaged).

- ◆ Survival - The proportion of individuals that survived four months after planting.
- ◆ Cumulative success - A measure of success calculated for each population. (probability of germination) x (probability of flowering) x (probability of survival for four months).

Creation of Generation II

In order to examine the consequences of a second generation we extended this experiment. In nature we often see different results in progressive generations. Hybrid breakdown has been found to be much more common in F2 hybrids (Ellstrand 1992). Pollinations were conducted and the resulting seeds were planted. Upon flowering, each female plant was pollinated in three treatments mentioned previously (within-population crosses, between-population within-continent crosses, and between-continent crosses). Three flowers on each female plant were chosen and each was pollinated with one of the three treatments. Therefore, each female plant had one flower crossed by each treatment. Hand pollinations were conducted at night when the flowers were fully opened by wiping pollen from one just-opened male flower onto stigmas. The first flowers that open were chosen to be pollinated on each plant. Pollinated flowers were tagged to record which cross had been performed. Fruit was considered to be ripe when a small pore was visible and teeth had begun to open. Upon ripening, fruit was collected and the following measurements were taken.

- ◆ Capsule mass - The weight of the fruit capsule was recorded, without the seeds.

- ◆ Total seed mass.
- ◆ Individual seed mass - The weight of one seed was calculated by weighing 10 seeds, then dividing that weight by 10.
- ◆ Width of capsule - Width of capsule wall (thickness) was measured with micrometer calipers. A small section near the top of the fruit was measured.

Generation II

Seeds were planted on 11-4-03 in the Georgia Southern greenhouse in the same manner as in the Generation I. The same treatments were used in this generation; within-population (P), between-population, within-continent (R), and between continents (C). Ten seeds from each of three treatments were planted from 5 populations and then replicated for each continent; (10x3x5x2=600 seeds). These plants are hereafter referred to as Generation II. The following life history traits were measured.

- ◆ Germination day - Time between planting and full cotyledon expansion.
- ◆ Percent germinated - The proportion of plants that germinated out of those that were planted.
- ◆ Plant size - Leaf number was counted on each plant four months after planting.
- ◆ Survival- The proportion of individuals that survived after four months of germination.

Data Analysis

All statistical analyses were conducted using JMP (SAS Institute Inc., 3.0.2, 1994). Before analysis, all data were tested for normality and transformed if necessary, however these transformations made no significant difference in the subsequent analysis. Throughout this thesis, data are presented as non-transformed means \pm standard error. Throughout the text, the term 'continent' refers to Europe vs. North America. The term 'treatment' refers to the three types of crosses (P= within-population , R= between-population within-continent, C= between-continents).

Contingency table analysis (G test) was used to compare the proportion of individuals that germinated, survived after four months, and flowered. T tests were used to compare European and North American plant traits. When comparing regions between-continent crosses (C) were not analyzed because they were produced by crossing one parent from each country. One way ANOVA was used to determine sources of variation in morphological, life history, and floral characters. In both Generation I and Generation II, each trait was the factor of the following effects: continent, and treatment.

CHAPTER 3

RESULTS

Generation I

Treatment Comparisons

Significant differences among the three treatments (P= within-population crosses, R= between-population within-continent, and C= between continent) were detected in three traits. R crossed plants germinated 4% faster than P plants and 9% faster than C plants (Table 2 and Figure 6). Although they germinated slowest, C plants had the highest number of leaves after four months (Table 2 and Figure 6). Significant differences were seen in enemy damage among the three treatments (Table 2 and Figure 6). R plants suffered the most whitefly damage, followed by C plants, and then P plants.

No significant differences were detected in any of the other traits measured (Table 2 and Figures 6, 7 and 8).

Continental Comparisons

Significant continental differences were detected in several life history and morphological traits (Table 2). North American plants had a higher overall cumulative success than European plants (Table 2 and Figure 5). On average, North American plants germinated 0.6 days faster than plants from Europe (Table 2 and Figure 3). North American plants were also first to flower, averaging 11.65 days earlier than European plants (Table 2 and Figure 3). North American plants had an average of 49% more flowers than European plants (Table 2 and Figure 4). Significant differences in petal width were also found

between the two continents. North American flowers had wider petals than European flowers (Table 2 and Figure 4).

A significantly greater proportion of North American plants flowered than those from Europe (Figure 5). A greater proportion of North American plants survived up to four months than European plants (Figure 5).

European plants produced wider (thicker) fruit capsules than North American plants (Table 2 and Figure 9). On average European capsules were 20% thicker than North American capsules. Fruit capsules produced by European plants weighed an average of 28% more than those produced by North American plants (Table 2 and Figure 9).

Whitefly damage was greater in North American plants than European plants (Table 1 and Figure 3).

No significant differences between the continents were found in biomass, height, petal length, leaf number at four months, total leaf number, or percent germinated (Table 2 and Figures 3, 4 and 5)

Sexual Comparisons

The proportion of male and female plants was almost evenly distributed. Female plants accounted for 51% of the plants that flowered, while males accounted for 49%. Sexual dimorphism was seen in only one morphological or life history trait. Male plants produced 41% (18.51 ± 1.12) more flowers than female plants (13.15 ± 1.03) at four months.

Generation II

Treatment Comparisons

Significant differences in germination time were detected among the three treatments (Table 3 and Figure 12). On average, R plants germinated 1.34 days earlier than P plants and 3.39 days earlier than C plants.

A significantly higher proportion of R plants germinated than any other treatment. Second most abundant to germinate were P plants. C plants germinated least often (Figure 12). A significantly higher proportion of R plants survived to four months than the other treatments (Figure 12).

No significant differences between treatments were found in individual seed mass, total seed mass, or leaf production (Table 3 and Figure 12).

Continental Comparisons

On average, North American plants germinated 1.09 days faster than plants from Europe (Table 3 and Figure 11). The number of leaves at four months was found to be greater in North American plants (Table 3 and Figure 11). North American plants had an average of 11% more leaves than European plants.

Significant differences in survival were found between the two regions (Figure 11). A greater proportion of European plants survived until four months than North American plants.

No significant differences were detected between continents in individual seed mass, total seed mass, or percent germinated (Table 3 and Figure 11).

CHAPTER 4

DISCUSSION

Overview

Silene latifolia has become an aggressive, problematic weed in North America since its introduction 200 years ago (McNeil 1977). Recently, it has been found that North American populations exhibit a more invasive, weedy phenotype than native populations (Blair and Wolfe 2004). My research supports these data. I found that North American plants germinated faster, flowered earlier, and produced more flowers than European plants. Determining the evolutionary event that may have allowed this phenotype to develop is of interest for future prevention and control of this and other invasives.

Recently, hybridization has been suggested to be a potential pathway for invasion success (Ellstrand and Schierenbeck 2000). The combination of individuals from different gene pools may create novel genotypes that have increased invasibility and/or the ability to fit into new ecological niches. The goal of this study was to examine the role that intraspecific hybridization may play in the invasion process. By crossing plants of different relatedness I was able to determine differences in fitness between the offspring produced. Plants which had been produced from parents located the intermediate distance apart, (between-population within-continent), showed higher overall performance in several traits. Lack of success of the other two treatments could indicate inbreeding depression is occurring among close neighbors, as well as outbreeding depression in long distance crosses. These data indicate that

intraspecific hybridization creates higher quality, more successful plants in *Silene*.

Crossing distance effects on fitness

Intermediate distance crosses; R (between-population within-continent) showed the most frequent success when compared to the other treatments. I measured a total of 19 morphological and life history traits. Significant differences among treatments were found 5 times. In 4 times out of 5, R treatment plants showed the highest performance. Regional plants germinated faster than P, or C plants in both generations. In Generation II, a greater proportion of R seeds germinated, and survived than either of the other treatments. Eighteen other traits were measured that did not show significant differences among treatments. However, 5 of these traits showed a trend toward higher performance values in R plants. Despite their success, the level of enemy damage was highest in R plants. These data support the idea that there is a tradeoff between growth and defense. In general, matings between-population and within-continent seem to produce a more invasive plant which devotes more resources toward growth and less toward defense.

One of the most conclusive pieces of data that points to greater invasibility in R plants, may be germination time, because both generations showed significant differences among treatments. Faster germination is seen in many successful invasive plants and may be crucial to plants facing competitive pressures (Baker 1948, Rejmanek and Richardson 1996). Other characteristics include smaller seed size, faster flowering, and more vigorous growth (Baker 1974, Blossey and Notzold 1995, Crawley 1997). Although significant differences

were not detected in these traits, perhaps in subsequent generations differences in morphological and life history traits would be more pronounced.

A significantly higher proportion of R plants germinated in the second generation. More R plants also germinated in Generation I however this value was not significant. This could signify a better quality seed being produced by R crosses. Because environmental conditions were kept constant in the greenhouse we must assume differences in germination rates coincide with seed viability. R plants also had greater survival in both generations, although this value was not significant in the first generation. A greater probability of survival is important as it could lead to greater flowering and offspring.

The level of enemy attack differed significantly among treatments. Regional plants exhibited the highest level of whitefly damage among the three treatments. It is unknown whether *Silene* has some type of defense against enemies such as whiteflies. Previous research has found that European plants have some resistance toward anther-smut (Blair and Wolfe 2004). It is likely that some form of unknown chemical resistance exists to combat other enemies. It seems that R plants may have devoted less energy toward defense and more effort toward increased growth.

The success of R plants indicates that matings between parents with an optimal level of relatedness could yield the most fit progeny. Several studies similar to this have been done in which inbreeding and outbreeding depression was apparent in within population crosses. When both of these deleterious effects occur within a population, there is likely to be an intermediate distance at which two mating plants are located, to produce offspring with the highest fitness (Price and Waser 1979, Waser 1993). This phenomenon, commonly called

optimal outcrossing, has been seen in several plant species (Price and Waser 1979, Waser and Price 1983, Schemske and Paulter 1984, McCall et al. 1988, Sobrevila 1988, Waser and Price 1989). Waser and Price (1994) reported the presence of inbreeding and outbreeding depression in *Delphinium nelsonii*. They found progeny produced from intermediate crossing distances grew approximately twice as large and survived almost a year longer on average as inbred and outbred progeny. Trame et al. (1995) also reported optimal outcrossing in *Agave schottii*. Plants produced from intermediate crossing distances had the greatest seed set, mean number of seeds per fruit, and relative fitness (fruit set x absolute seed set x percentage germination).

Researchers theorize that the phenomenon of optimal outcrossing is due to an inverse correlation between genetic similarity and physical proximity (Price and Waser 1979, Waser and Price 1989). Pollen and seeds of plants are often dispersed close to the parental plants (Handel 1983, Levin 1989). Therefore plants which are closer to one another are thought to be more genetically similar than plants located further apart (Levin 1984, Waser and Price 1994). Plants which exhibit maximum fitness when optimally outcrossed experience both inbreeding when crossed with near neighboring plants because of relatedness between parents, and outbreeding depression when long distance crosses are performed because adaptation to local selection regimes is disrupted (Waser and Price 1989).

Past research has studied within population crosses on a much more local scale than my study. I have extrapolated these crosses to consider many populations, some of which are separated by hundreds of miles. The crosses in my study do not occur naturally, however I am essentially recreating one

possible invasion scenario which may have contributed to *Silene*'s success.

Ellstrand and Schierenbeck (2000) have correlated the evolution of invasiveness with multiple introductions and lag times often observed in successful introductions. These two phenomena occur quite frequently and are thought to be a prerequisite for many species to meet and incur genetic variation (Moody and Mack 1988). It is likely that *Silene* had multiple introductions into North America (Taylor personal correspondence). These populations could have come together and hybridized, creating a more invasive plant with an increased capability of becoming successfully established.

Compared to R plants, P and C plants performed relatively poorly. This points to some degree of inbreeding occurring among close neighbors, as well as outbreeding depression in long distance crosses. Inbreeding depression has been reported in many species, (Levin 1984, Schemske and Paulter 1984, Fenster 1991, Wolfe 1993) and is most likely due to relatedness between parents (Waser and Price 1994). Plants that live within a population tend to be somewhat related because of the distance pollen and seeds are distributed (Levin 1984, Souto et al. 2002). Matings between plants located within the same population may create inbreeding depression in offspring.

Outbreeding depression may be explained by local adaptation, or by significant divergence between populations. In a recent study, Wolfe (2002) found that European populations of *Silene* are 17 times more likely to be attacked in North America because of the absence of several enemies. As a result of a change in predation pressure, native and introduced populations may have evolved quite different resource allocation strategies that correspond to their respective environments. Mating of two different ecotypes such as these may

create an intermediate phenotype which is unfit in any environment. If sufficient divergence has taken place between native and introduced populations after *Silene*'s introduction, matings between continents may cause the breakup of coadapted gene complexes in favorable epistatic relationships (Mayr 1963, Rymer and Simberloff 1996). This thesis, as well as previous research (Blair and Wolfe 2004) indicates that significant genetic differences exist between European and North American plants. These differences may be too significant to produce offspring with optimal fitness by mating plants from different continents.

Evolution of morphological and life history traits

Continental Differences

Several studies have documented that plants in the introduced range exhibit enhanced vigor or 'weedy growth' compared to those in their native range (Blossey and Notzold 1995, Cox 1999, Keane and Crawley 2002). North American plants exhibited more invasive 'weedy' growth than European plants. Although genetic differences were found in previous research, my study is important because it involved seed which was collected from greenhouse crosses. Blair (2003) used seed which had been field collected. The results in her study could have been confounded by maternal effects. This research provides additional support that North American plants do outperform European plants.

These data find that North American plants have a higher overall cumulative success than European plants. Cumulative success is a valuable indicator to assess fitness because it takes into account the success of the plant at several life stages. North American seeds germinated significantly faster than seeds from Europe. Faster germination is important for plants facing competitive pressure. North American plants produced smaller seeds than did

European plants. On average, a seed from Europe weighed 17% more than a seed from North America. Smaller seed size has been correlated with higher seed production, and faster growth, a typical strategy seen in many weeds (Baker 1965). North American plants also flower before European plants. Generation I plants flowered an average of 11.65 days faster than European plants. Earlier flowering could result in greater floral output, and greater seed production in introduced plants (Baker 1965). Indeed, significantly greater floral output was observed in North American plants, which produced an average of 49% more flowers. North American plants also had a significantly greater probability of flowering and surviving in Generation I than did European plants. This success shows North American plants stand a better chance of leaving offspring than European plants.

North American plants had a greater level of whitefly damage than European plants. A recent study indicates that North American populations, which have been virtually freed from enemy attack, devote less investment in defense and greater resource allocation to growth and reproduction. Blair and Wolfe (2004) examined the number of trichomes on the calyx of European and North American plants and found that North American plants had 19% fewer trichomes, which are thought to function in flower protection (Bopp 1999). Another study compared the level of enemy attack between continents and found that North American plants suffered a greater level of enemy attack than did European plants in a common garden in Europe (Wolfe et al. 2004). Interestingly, this study found North American plants still outperformed European plants. My study parallels these data by finding that in both Generation I and Generation II a greater proportion of North American plants

survived. Although North American plants were attacked more, they germinated faster, flowered earlier, had more total flowers, and flowered with greater frequency.

Significant differences in fruit and seed morphology were also seen between the two continents. European fruit capsules weighed 28% more, and had 20% thicker walls than North American capsules. These more formidable capsules may serve as a defense mechanism against enemy attack. *Hadena bicuris* is a specialist predator that consumes developing fruit throughout larval stages by creating a hole in the fruit wall. This enemy is completely absent in North America. Perhaps in the absence of enemies such as *Hadena*, *Silene* has evolved a strategy of lower allocation toward defense (i.e. thinner, less protected capsules). My research as well as past studies suggest that North American populations may be allocating fewer resources toward defense, and more toward growth and reproduction.

Summary

This thesis confirms the evolution of a more invasive phenotype in introduced populations of *Silene*. This weedy phenotype may have evolved through genetic drift, natural selection, or hybridization. My research finds that intraspecific hybridization at an intermediate distance, creates a more successful plant in *Silene latifolia*. Progeny produced from matings between plants located the intermediate distance germinated faster than progeny produced from plants located in close proximity and long distances apart. Matings of intermediately related plants also resulted in offspring with a greater probability of germinating, and surviving. Although R plants were more successful, they had a higher level of attack than either of the other treatments. These data is consistent with the

idea that there is an inverse relationship between allocation to growth and defense. Mating plants between-population and within-continent creates offspring that devote more energy toward growth and less toward defense. The implications of this thesis are that a species' colonization history could be a significant pathway for the evolution of invasiveness. This study indicates that intraspecific hybridization may have played a role in the successful invasion of *Silene latifolia*.

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Table 1. Location of source populations.

	<u>Population</u>	<u>Detailed Location</u>	<u>Collector</u>
N. America	AR	Washington Co.	J. Gentry
	BC 1	Naramata, BC	E. Elle
	BC 2	Naramata, BC	E. Elle
	IL	DeKalb Co.	A. Blair
	IA 1	Okoboji, IA	A. Blong
	IA 2	South Jones Co.	A. Blair
	MD		D. Parrish
	MI 1	East Lansing, MI	A. Jarosz
	MI 2	Hickory Corners, MI	J. Conner
	MN	Houston Co.	A. Blair
	NC 1		D. Parrish
	NC 2		D. Parrish
	OH		D. Parrish
	PA		D. Parrish
	Saskatoon 1	Saskatoon	P. Ryan
	Saskatoon 2	Duck Lake	P. Ryan
	TN		D. Parrish
	VT	Windsor Co.	R. Chandler
	VA 1	Giles Co.	L. Wolfe
	VA 2	Giles Co.	L. Wolfe
Europe	Armenia	Desgh, Tumanian	D. Taylor
	Belarus	Minsk, Prilutchki	D. Taylor
	Croatia		D. Taylor
	Czech Republic		D. Taylor
	Denmark		L. Wolfe
	Estonia		D. Taylor
	France	Begoux	L. Wolfe
	Germany	Mainz Sands	O. Fragman
	Hungary	Cegled	D. Taylor
	Italy	Padova	D. Taylor
	Norway	Barum, Haslum	Univ. of Oslo
	Poland	Wroclaw	A. Klibel
	Scotland	Nairn	F. Wilson
	Slovakia		D. Taylor
	Slovenia		D. Taylor
	Spain 1	Ternel	L. Wolfe
	Spain 2	Collformic	L. Wolfe
	Switzerland		Fenaco
	Turkey	Ankara, Pinigra	Harslan
	UK	Worcesheshire	H. Goddard

Table 2. Sources of variation in life history and vegetative characters for *Silene latifolia* (Generation I) grown in a greenhouse common garden. Continent = Europe or North America, Treatment = P (within-population crosses), R (between-population within-continent crosses), or C (between-continent crosses).

A. Germination time (days)

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	46.44	11.01	0.001
Treatment	2	49.85	3.53	0.029

B. Days to flower

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	12814.95	89.93	<0.0001
Treatment	2	674.20	2.57	0.077

C. Leaf number at four months

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	22.72	0.608	0.436
Treatment	2	35.44	0.428	0.652

D. Total leaf production

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	313.07	1.82	0.178
Treatment	2	1985.90	5.34	0.005

E. Root biomass

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.019	1.26	0.268
Treatment	2	0.040	1.22	0.301

F. Shoot biomass

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.000	0.142	0.708
Treatment	2	0.000	0.319	0.728

G. Plant height at four months

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	82.30	1.31	0.253
Treatment	2	121.07	1.07	0.342

H. Whitefly damage

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	5.48	6.11	0.016
Treatment	2	5.99	3.57	0.031

I. Petal width

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.798	8.70	0.003
Treatment	2	0.001	0.008	0.991

J. Petal length

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.163	2.44	0.119
Treatment	2	0.129	0.696	0.498

K. Total flower production

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	2531.00	8.83	0.003
Treatment	2	788.78	1.54	0.215

L. Capsule mass

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.002	11.84	0.0008
Treatment	2	0.000	1.18	0.311

M. Width of capsule

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.007	8.21	0.007
Treatment	2	0.000	0.125	0.883

N. Cumulative Success

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.250	5.51	0.021
Treatment	2	0.065	0.739	0.481

Table 3. Sources of variation in life history and vegetative characters for *Silene latifolia* (Generation II) grown in a greenhouse common garden study. Continent = Europe or North America, Treatment = P (within-population crosses) , R (between-population within-continent crosses) , or C (between-continent crosses).

A. Individual seed mass

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.000	2.78	0.098
Treatment	2	0.000	0.030	0.970

B. Total seed mass

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	0.003	2.08	0.152
Treatment	2	0.009	2.87	0.060

C. Germination time (days)

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	87.09	4.70	0.031
Treatment	2	525.60	7.32	0.0008

D. Leaf number at four months

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>P</u>
Continent	1	17.91	9.55	0.002
Treatment	2	5.78	1.40	0.248

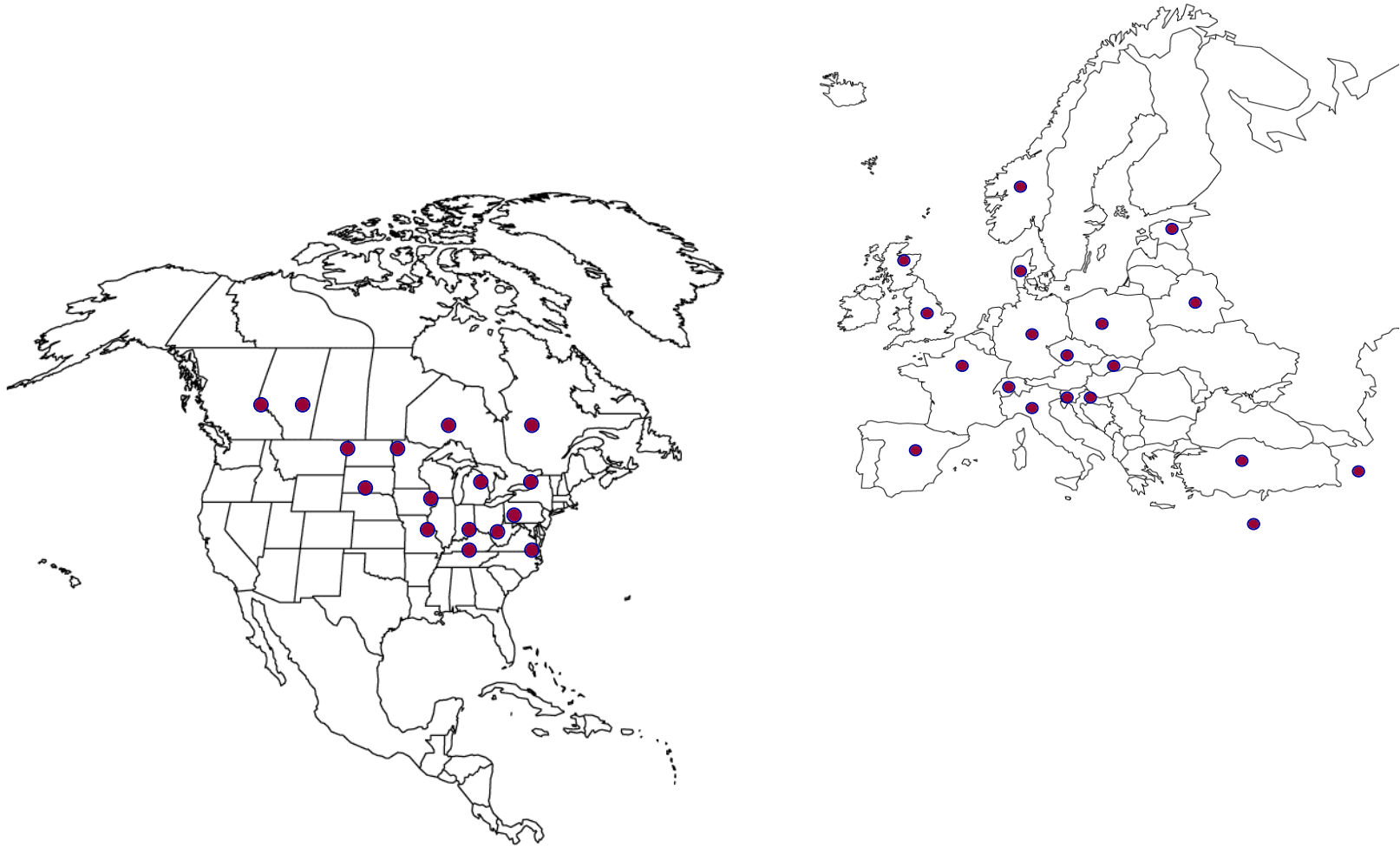


Figure 1. Locations where source seed was collected.

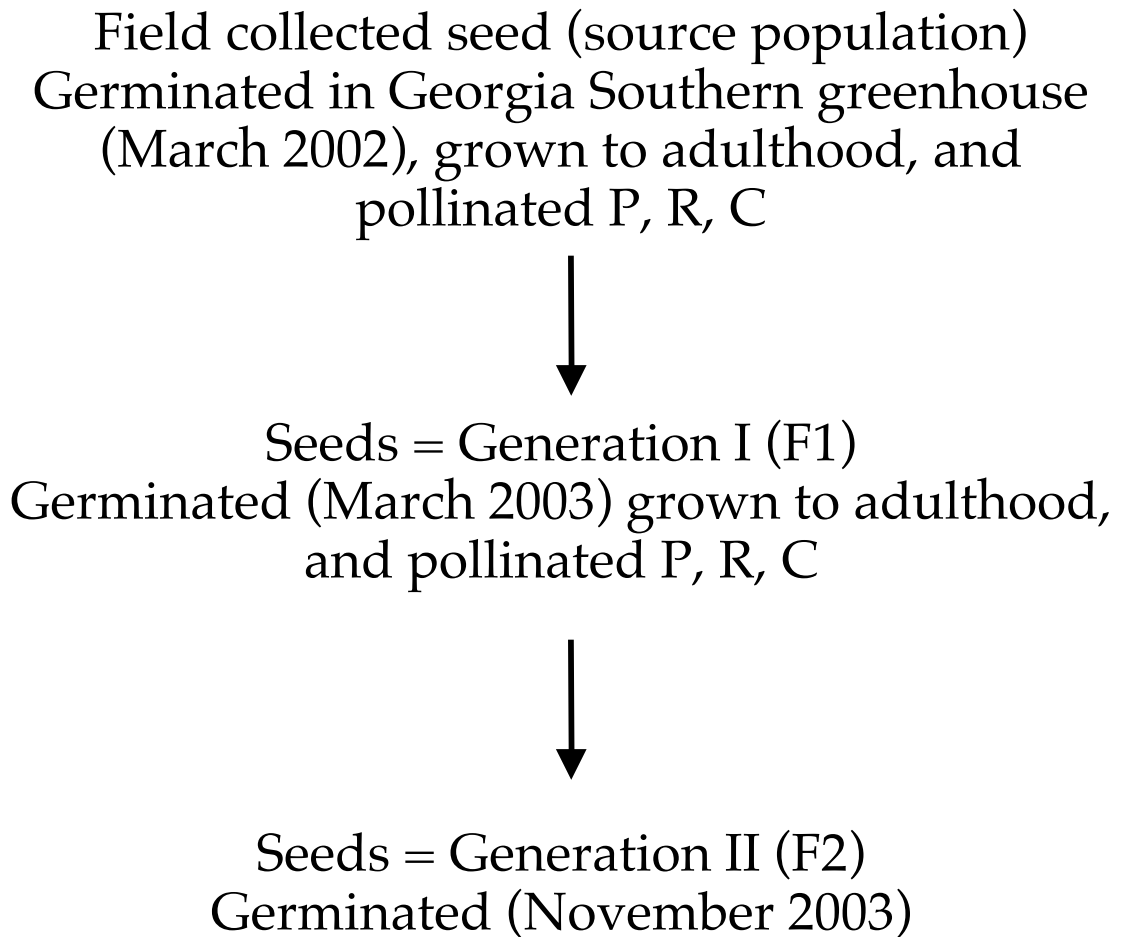


Figure 2. Diagram showing successive generations in this study

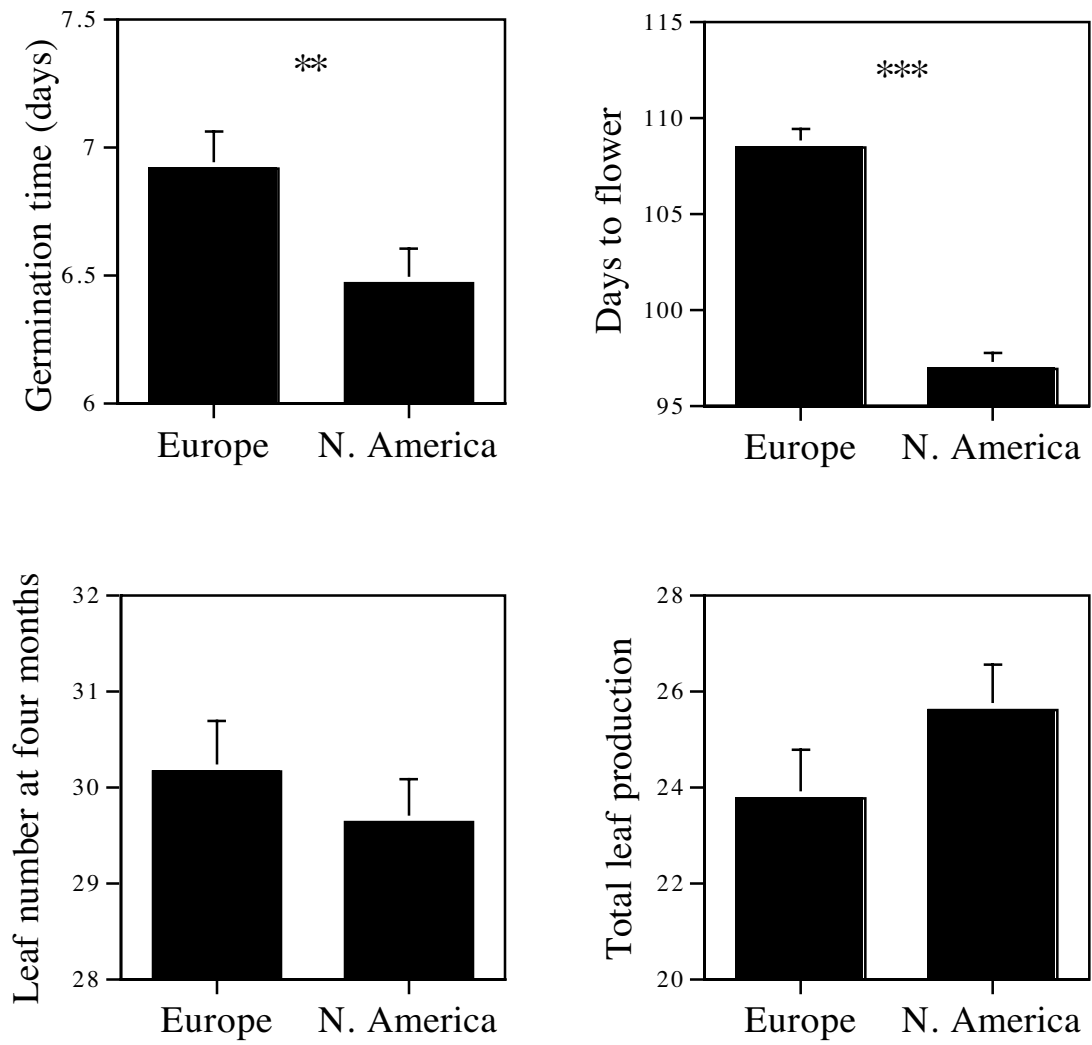


Figure 3. Vegetative traits (means \pm S.E.) of European and North American *Silene latifolia* grown in Generation I in a greenhouse common garden experiment. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.00$. The values for the graphs in this figure are in Appendix A.

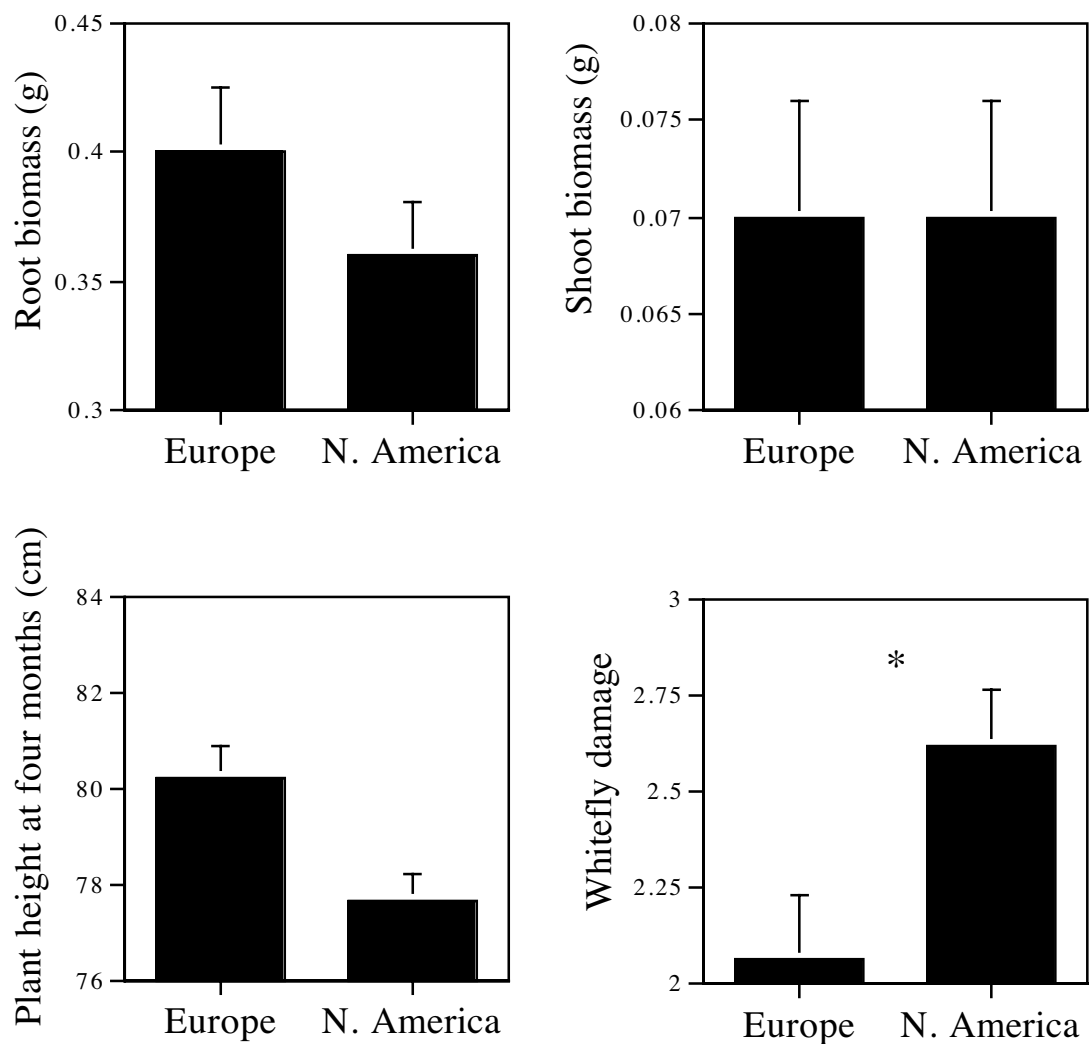


Figure 3 continued.

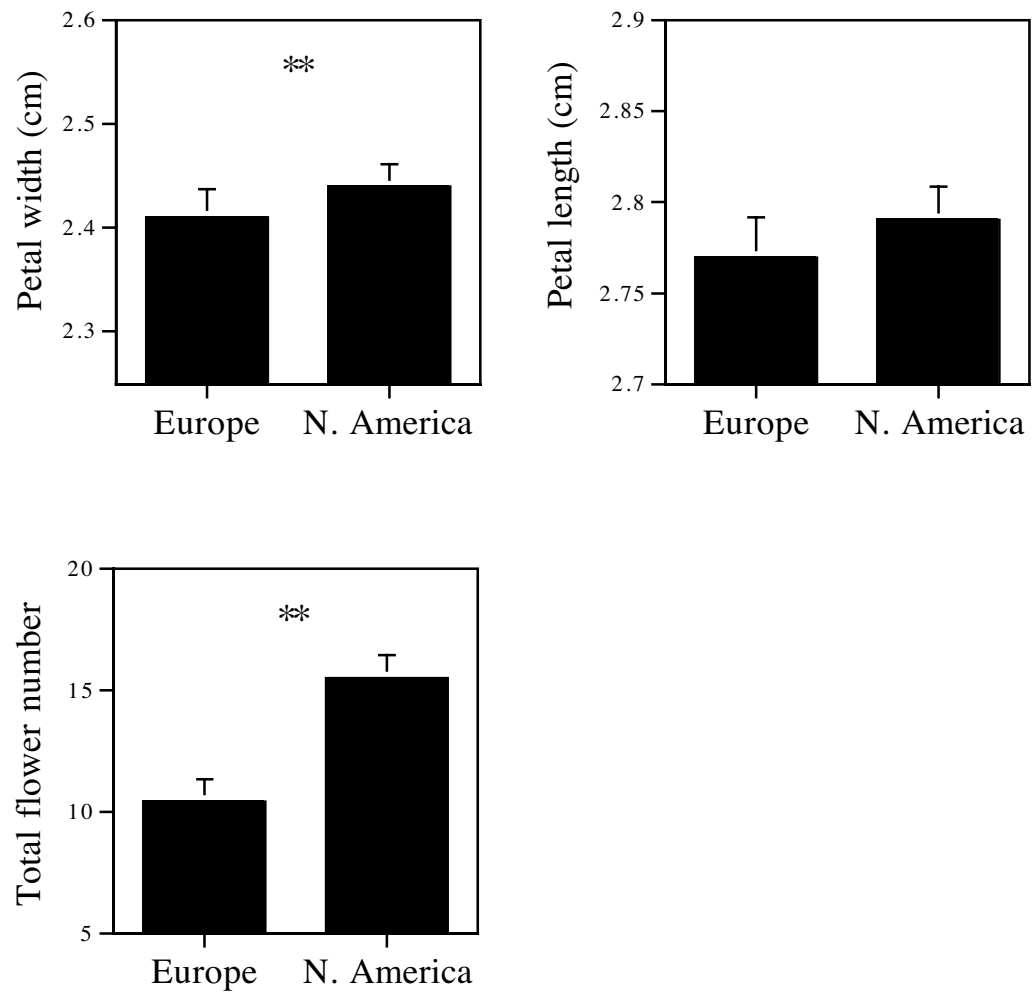


Figure 4. Floral traits (means \pm S.E.) of European and North American *Silene latifolia* grown in Generation I in a greenhouse common garden experiment. *P < 0.05, **P < 0.01, ***P < 0.001 calculated from the ANOVA model. The values for the graphs in this figure are in Appendix A.

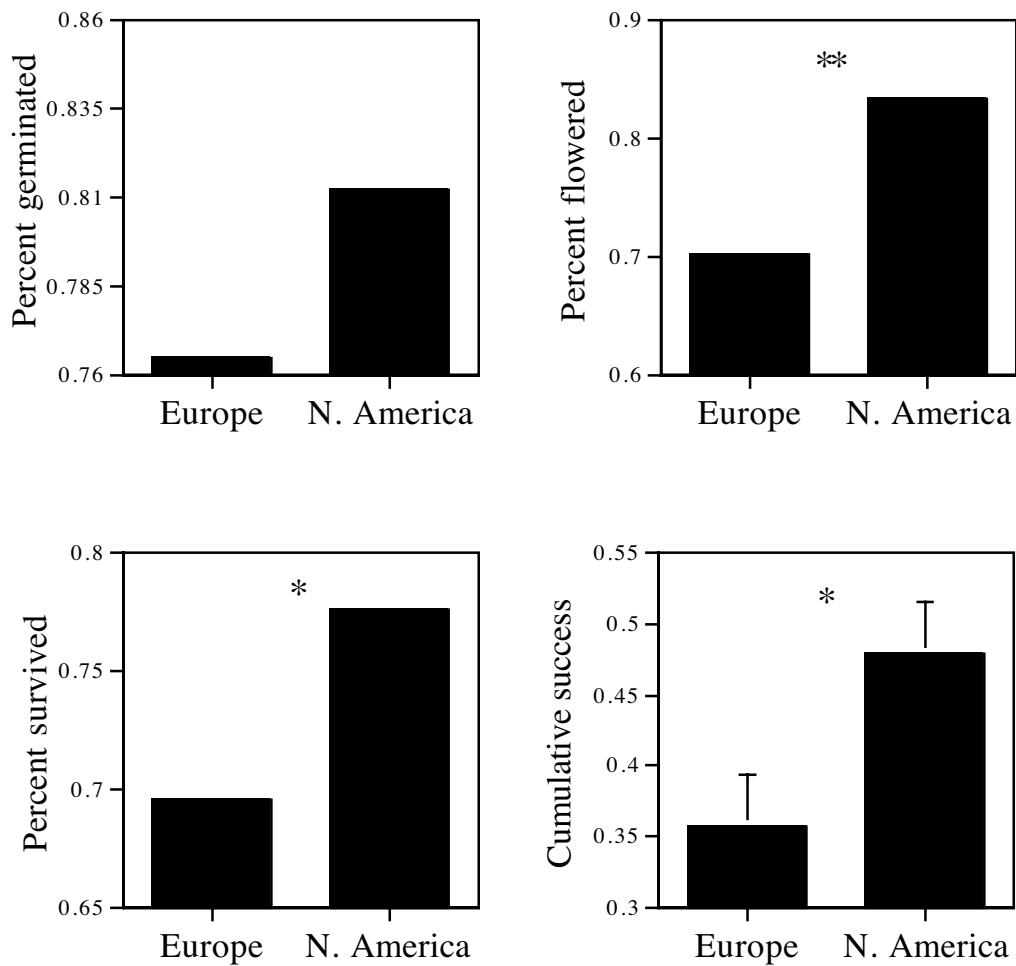


Figure 5. The germination, flower, survival, and cumulative success of plants from Europe and North America grown in Generation I. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.00$. The values for the graphs in this figure are in Appendix C.

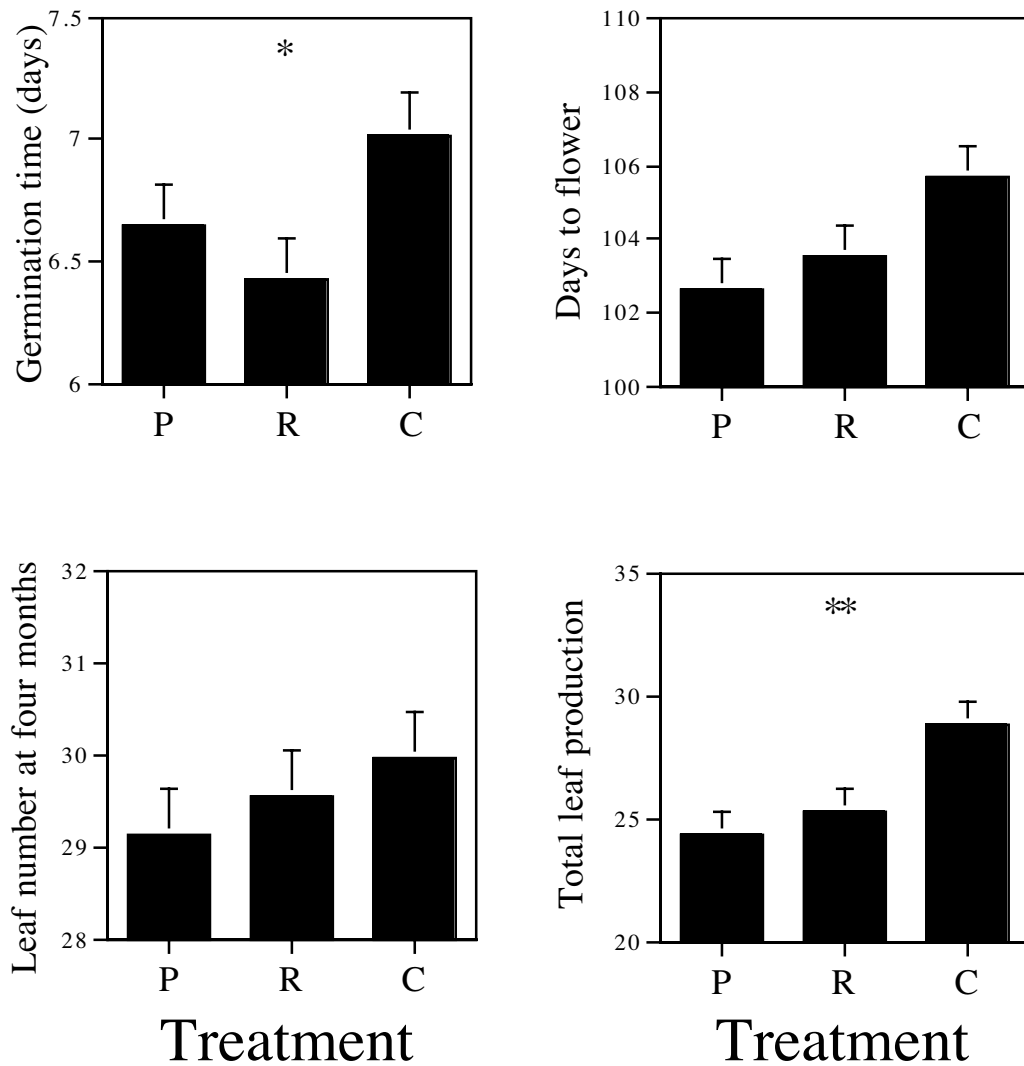


Figure 6. Vegetative traits (means \pm S.E.) of *Silene latifolia* comparing offspring performance for treatments that vary in their crossing history; P (within-population), R (between-population within continent), and C (between continent). Grown in Generation I in a greenhouse common garden experiment. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The values for the graphs in this figure are in Appendix A.

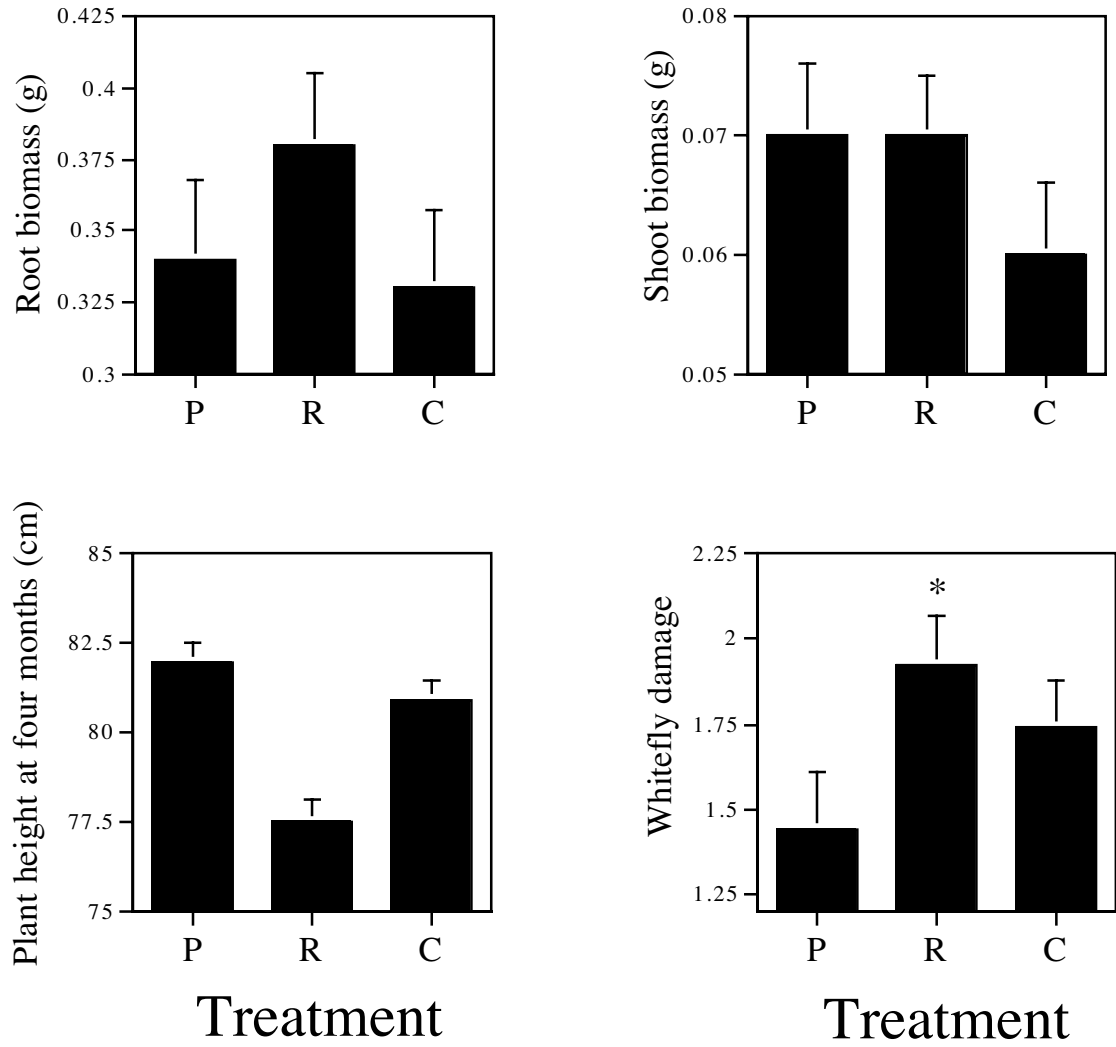


Figure 6 continued.

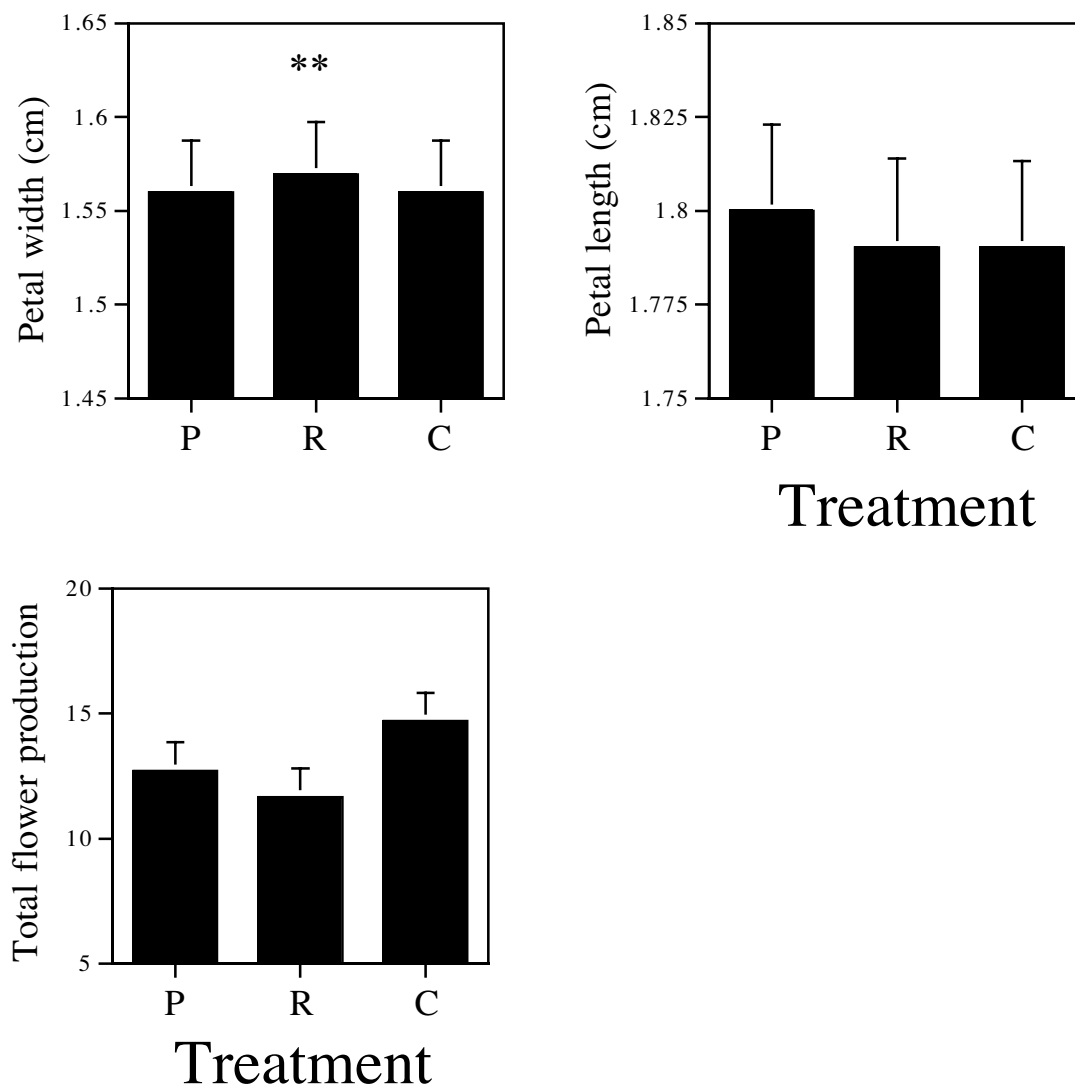


Figure 7. Reproductive traits (means \pm S.E.) of *Silene latifolia* comparing offspring performance for treatments that vary in their crossing history; P (within-population), R (between-population within continent), and C (between continent). Grown in Generation I in a greenhouse common garden experiment. *P <0.05, **P <0.01, ***P <0.001. The values for the graphs in this figure are in Appendix A.

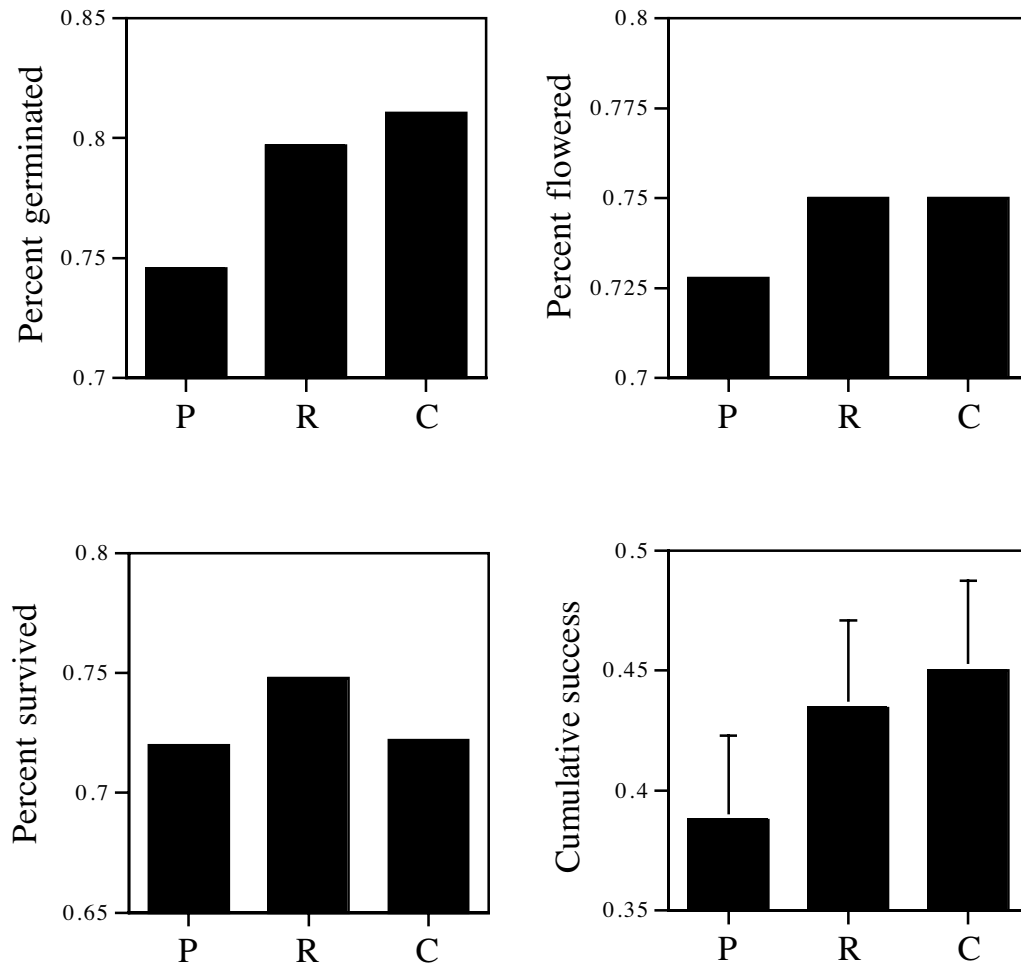


Figure 8. The germination, flower, survival, and cumulative success of plants grown in treatments that vary in their crossing history; P (within-population), R (between-population within continent), and C (between continent). Grown in Generation I. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The values for this figure are in Appendix A and C.

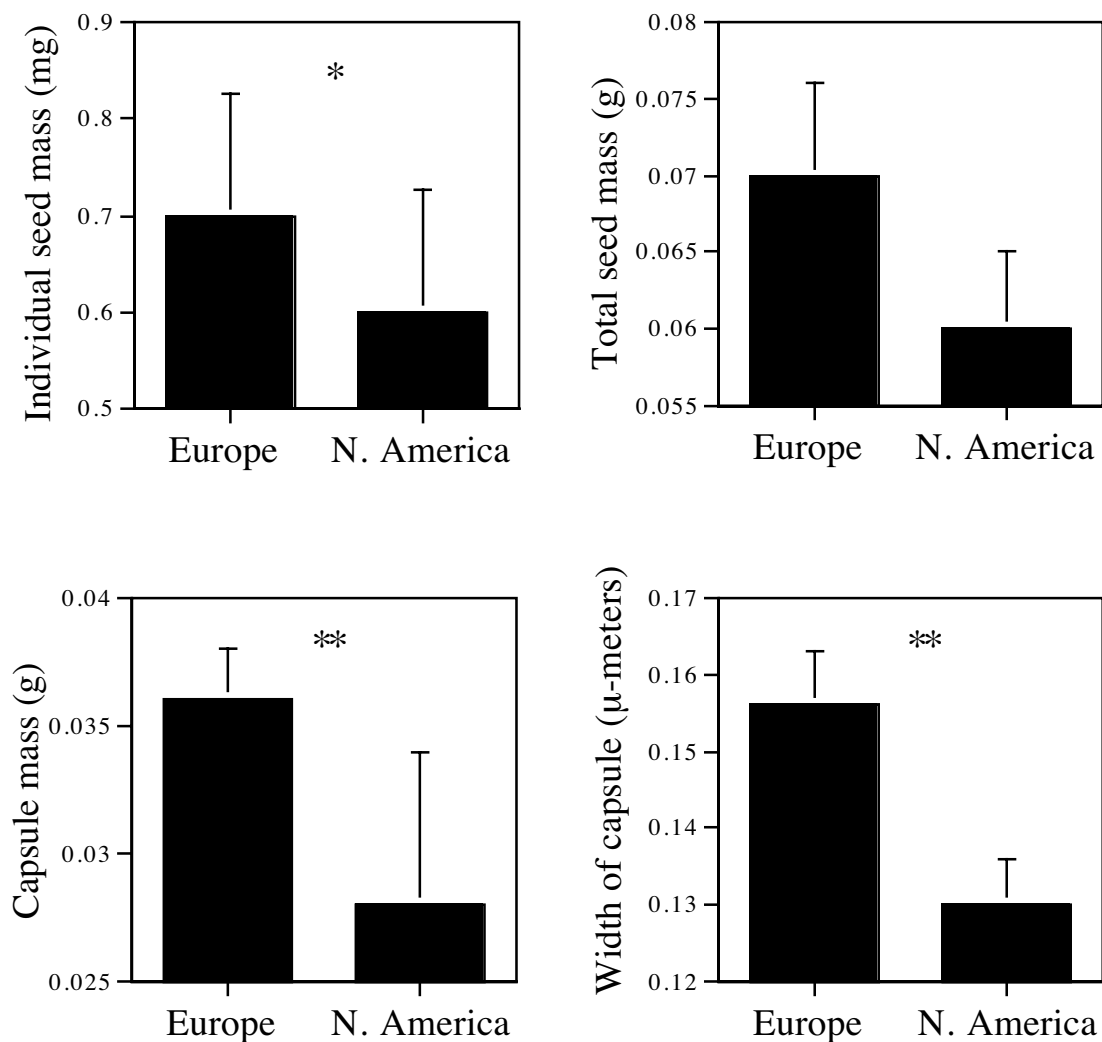


Figure 9. Reproductive traits (mean \pm S.E.) of European and North American *Silene latifolia* grown in Generation I in a greenhouse common garden experiment.

*P < 0.05, **P < 0.01, ***P < 0.001 calculated from the ANOVA model. The values for the graphs in this figure are in Appendix B.

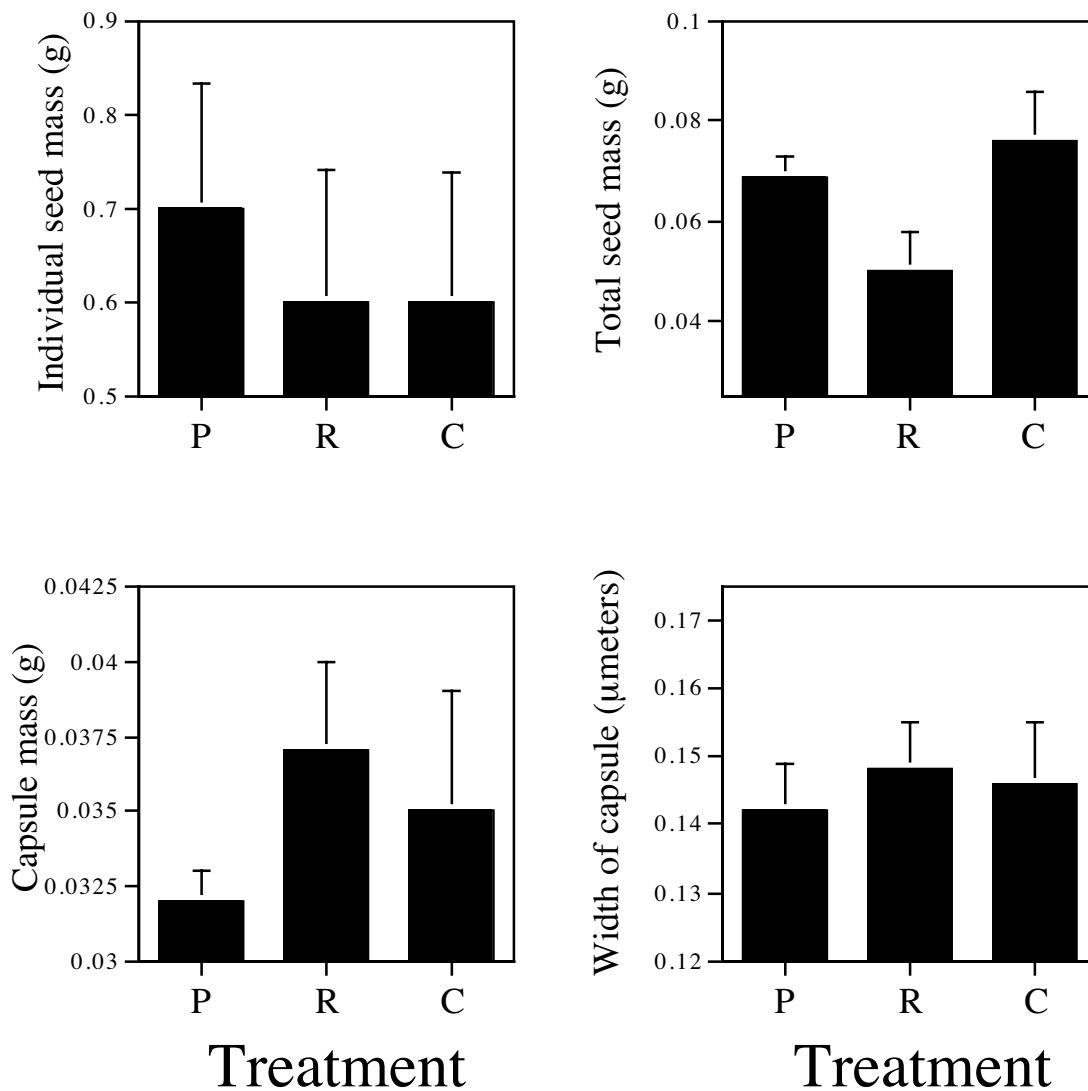


Figure 10. Reproductive traits (mean \pm S.E.) of *Silene latifolia* comparing offspring performance for treatments that vary in their crossing history; P (within-population), R (between-population within continent), and C (between continent). Grown in Generation I in a greenhouse common garden experiment. *P < 0.05, **P < 0.01, ***P < 0.001. The values for the graphs in this figure are in Appendix B.

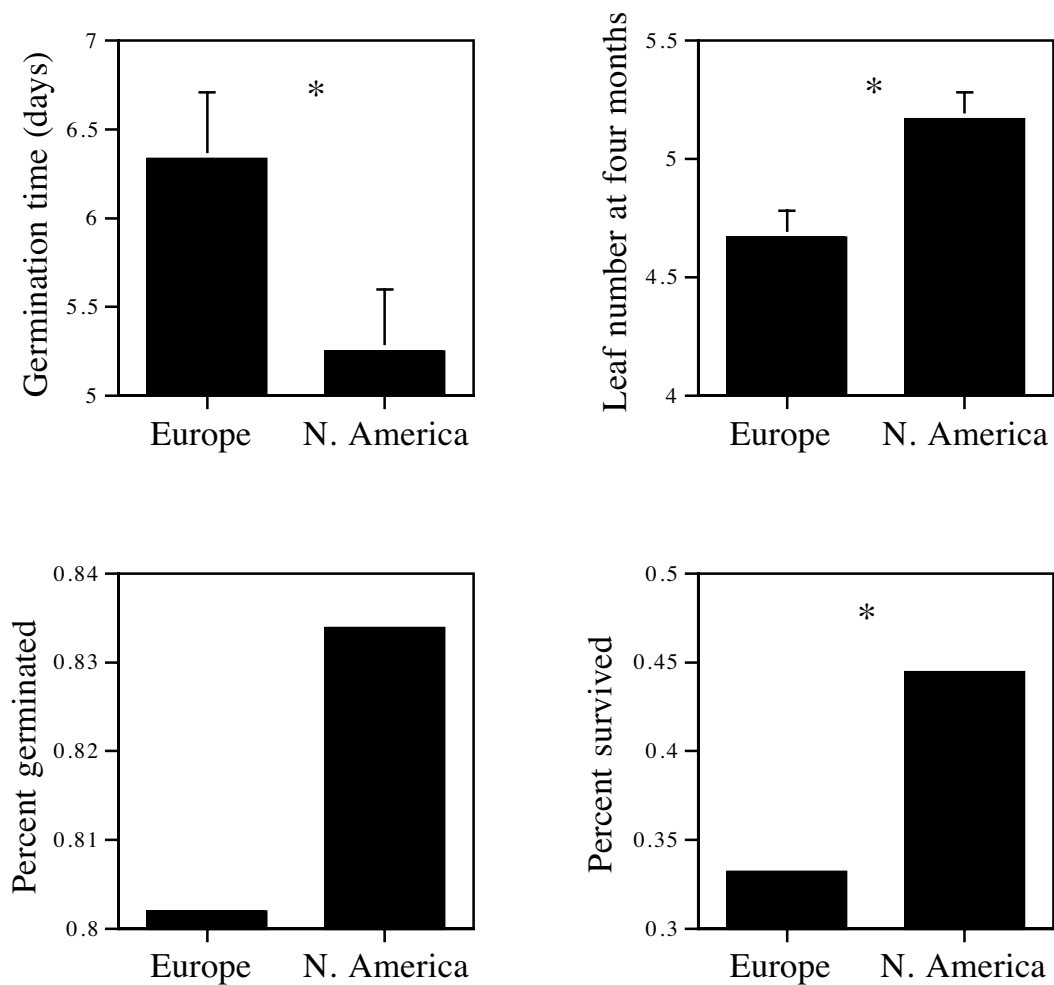


Figure 11. Vegetative traits (means \pm S.E.) and germination and survival probabilities of Generation II European and North American *Silene latifolia* grown in greenhouse common garden experiment. *P < 0.05, **P < 0.01, ***P < 0.001. The values for the graphs in this figure are in Appendix B and C.

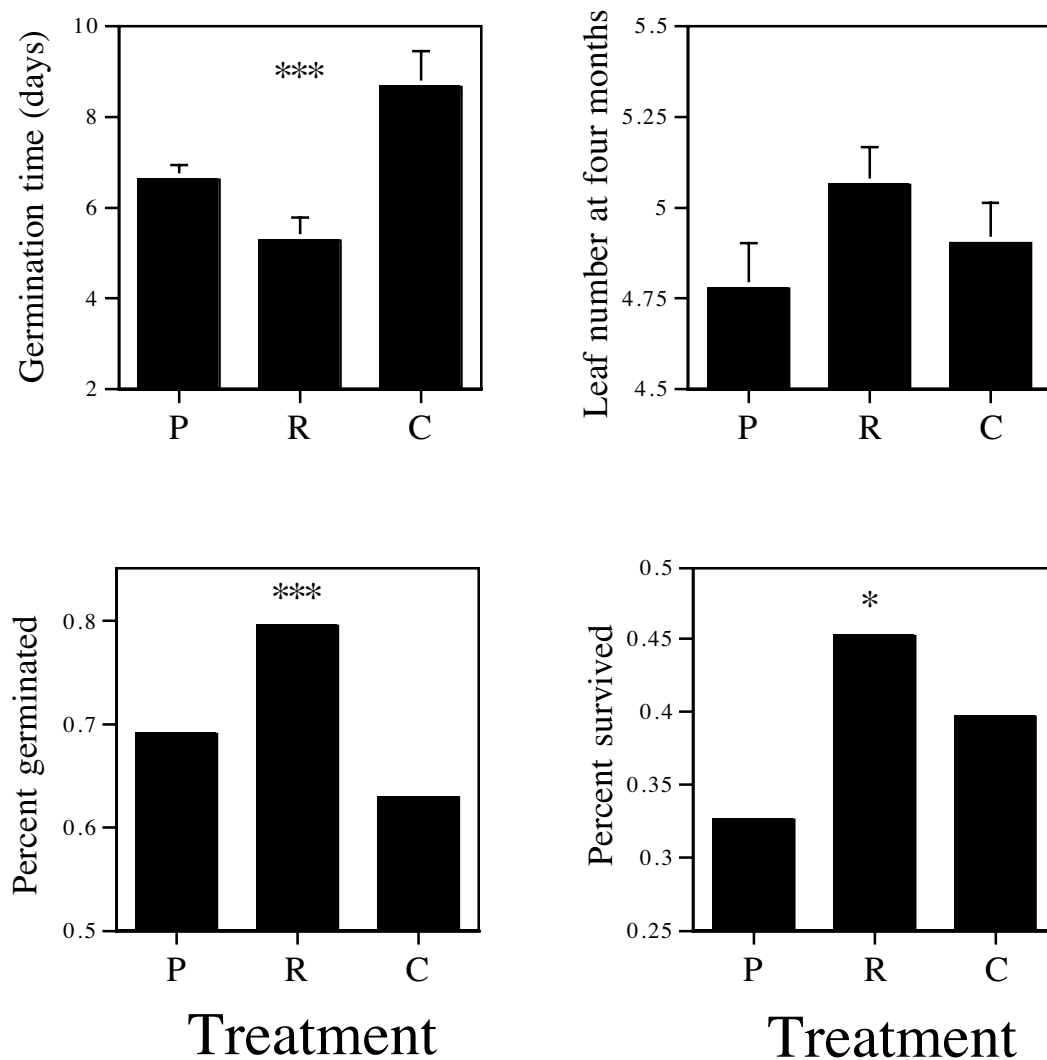


Figure 12. Vegetative traits (mean \pm S.E.) and germination and survival probabilities of *Silene latifolia* comparing offspring performance for treatments that vary in their crossing history; P (within-population), R (between-population within continent), and C (between continent). Grown in Generation II in a greenhouse common garden experiment. *P < 0.05, **P < 0.01, ***P < 0.001. The values for the graphs in this figure are in Appendix B and C.

Appendix A. Plant traits (means \pm SE) for Generation I of *Silene latifolia* in a greenhouse common garden experiment. Each significance column refers to the specific analysis of variation result calculated from the ANOVA. (*P<0.05, **P<0.01, ***P<0.001). P= within-population crosses, R= between-population within-continent crosses, C= between-continent crosses

Plant Trait	<u>Continent</u>			<u>Treatment</u>			
	<u>Europe</u>	<u>N. America</u>	<u>Significance</u>	<u>P</u>	<u>R</u>	<u>C</u>	<u>Significance</u>
Shoot biomass (g)	0.07 \pm 0.006	0.07 \pm 0.006		0.07 \pm 0.006	0.07 \pm 0.005	0.06 \pm 0.006	
Root biomass (g)	0.40 \pm 0.026	0.36 \pm 0.024		0.34 \pm 0.028	0.38 \pm 0.025	0.33 \pm 0.027	
Plant height (cm)	80.24 \pm 0.669	77.69 \pm 0.559		81.92 \pm 0.580	77.52 \pm 0.589	80.87 \pm 0.576	
Petal width (cm)	2.41 \pm 0.026	2.44 \pm 0.021	**	1.56 \pm 0.027	1.57 \pm 0.027	1.56 \pm 0.027	
Petal length (cm)	2.77 \pm 0.022	2.79 \pm 0.018		1.80 \pm 0.023	1.79 \pm 0.024	1.79 \pm 0.023	
Leaf production	30.17 \pm 0.517	29.65 \pm 0.431		29.15 \pm 0.497	29.56 \pm 0.504	29.98 \pm 0.494	
Whitefly damage	2.06 \pm 0.170	2.62 \pm 0.146	*	1.44 \pm 0.166	1.92 \pm 0.149	1.74 \pm 0.141	*
Germination day	6.50 \pm 0.127	5.90 \pm 0.127	**	6.65 \pm 0.165	6.43 \pm 0.164	7.02 \pm 0.171	*
First flower day	108.53 \pm 0.899	96.88 \pm 0.836	***	102.62 \pm 0.833	103.57 \pm 0.833	105.66 \pm 0.846	
Total leaf number	23.80 \pm 0.975	25.61 \pm 0.919		24.28 \pm 0.99	25.22 \pm 0.974	28.76 \pm 1.03	**
Width of capsule (μ m)	0.156 \pm 0.007	0.130 \pm 0.006	**	0.143 \pm 0.007	0.148 \pm 0.007	0.146 \pm 0.009	
Capsule mass (g)	0.036 \pm 0.002	0.028 \pm 0.006	**	0.032 \pm 0.001	0.037 \pm 0.003	0.035 \pm 0.004	
Total flower number	10.39 \pm 0.992	15.53 \pm 0.922	**	12.73 \pm 1.168	11.67 \pm 1.14	14.64 \pm 1.21	
Cumulative success	0.357 \pm 0.036	0.479 \pm 0.036	*	0.388 \pm 0.035	0.434 \pm 0.037	0.450 \pm 0.038	

Appendix B. Percent germination, flowered, and survival of Generation I of *Silene latifolia* in a greenhouse common garden

experiment. Each significance column refers to the F values calculated from the G test analysis. (*P<0.05, **P<0.01, ***P<0.001).

P= within-population crosses, R= between-population within-continent crosses, C= between-continent crosses

<u>Plant Trait</u>	<u>Continent</u>			<u>Treatment</u>			
	<u>Europe</u>	<u>North America</u>	<u>Significance</u>	<u>P</u>	<u>R</u>	<u>C</u>	<u>Significance</u>
Percent germination	0.765	0.812		0.746	0.797	0.813	
Percent flowered	0.703	0.833	**	0.728	0.751	0.750	
Percent survival	0.696	0.776	*	0.720	0.748	0.722	

Appendix C. Plant traits (means \pm SE) for Generation II of *Silene latifolia* in a greenhouse common garden experiment. Each significance column refers to the specific analysis of variance result calculated from the ANOVA. (*P<0.05, **P<0.01, ***P<0.001). P= within-population crosses, R= between-population within-continent crosses, C= between-continent crosses

<u>Plant Trait</u>	<u>Continent</u>		<u>Significance</u>	<u>Treatment</u>			<u>Significance</u>
	<u>Europe</u>	<u>N. America</u>		<u>P</u>	<u>R</u>	<u>C</u>	
Individual seed mass (mg)	0.007 \pm 0.0003	0.006 \pm 0.0003	*	0.7 \pm 0.008	0.6 \pm 0.007	0.6 \pm 0.007	
Total seed mass (g)	0.070 \pm 0.006	0.060 \pm 0.005		0.069 \pm 0.004	0.050 \pm 0.008	0.076 \pm 0.010	
Germination day	6.34 \pm 0.364	5.25 \pm 0.345	*	6.61 \pm 0.516	5.27 \pm 0.481	8.66 \pm 0.770	***
Leaf production	4.67 \pm 0.117	5.17 \pm 0.110	*	4.78 \pm 0.120	5.06 \pm 0.110	4.90 \pm 0.179	

Appendix D. Percent germination and survival of Generation II of *Silene latifolia* in a greenhouse common garden

experiment. Each significance column refers to the F values calculated from the G test analysis. (*P<0.05, **P<0.01, ***P<0.001).

P= within-population crosses, R= between-population within-continent crosses, C= between-continent crosses.

<u>Plant Trait</u>	<u>Continent</u>		<u>Significance</u>	<u>Treatment</u>			<u>Significance</u>
	<u>Europe</u>	<u>North America</u>		<u>P</u>	<u>R</u>	<u>C</u>	
Percent germination	0.802	0.834		0.69	0.795	0.63	***
Percent survival	0.332	0.444	*	0.326	0.453	0.397	*