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## Local Adaptation for Life-History Traits in *Silene Latifolia*

Brandy May Penna

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# **LOCAL ADAPTATION FOR LIFE-HISTORY TRAITS IN *SILENE LATIFOLIA***

by

**BRANDY M. PENNA**

**(Under the Direction of Lorne M. Wolfe)**

## **ABSTRACT**

A fundamental question in evolutionary ecology is how species adjust post colonization. The plant *Silene latifolia* was introduced to North America (NA) from Europe (EU) in the 1800s. The goal of this thesis was to test if *Silene latifolia* has become locally adapted across its range. My first experiment tested local adaptation of germination success to three temperatures across three latitudinal regions in a growth chamber using seeds from nine EU and NA populations. Germination success or speed was similar among latitudinal regions across continents. My second experiment examined local adaptation at a continental scale; I grew plants from 15 EU and NA populations in four common gardens across continents. Growth and survival for the first year revealed that plants grew larger in their respective continents. My results demonstrate while germination does not appear to be locally adapted, but continental factors have selected for differential juvenile growth.

INDEX WORDS: Local adaptation, Life-history traits, *Silene latifolia*, Plant growth chamber, Common garden.

LOCAL ADAPTATION FOR LIFE-HISTORY TRAITS IN *SILENE LATIFOLIA*

by

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B.S., University of Maine at Machias, 2004

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2006



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by

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May 2006

## **DEDICATION**

I would like to dedicate this thesis to my parents, Richard and Michele, for all of their constructive advice in regards to my education. They have always encouraged me to keep working hard and to become a better person; I could not have gotten this far without their love and support. To my brother, Brandon, who had to put up with me his entire life and who has become one of my greatest friends. To my grandparents, Richard and Alicia, who have always stood behind me in everything that I have done. Finally, to my fiancé, Corey, who has been there for me every moment even when he is 1500 miles away. He has been my inspiration and I cannot thank him enough for believing in me. Thank you all for supporting me in every way and for giving me the strength to keep working towards my hopes and dreams.

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## CHAPTER I

### INTRODUCTION

A fundamental question in evolutionary ecology is how species respond to changing environmental conditions. This is particularly relevant when a species encounters novel environments following dispersal and colonization events. Range expansions have increased dramatically over the past 100 years with the development of long-distance trading, agriculture, and increased movements of humans throughout the globe (Williams and Meffe 1998). There are essentially two mechanisms that allow species to adjust to new or changing habitats. Species with broad distributions may be able to cope with a wide variety of environments if individuals are phenotypically plastic and genotypes can then adjust to variable environmental conditions (Antonovics 1968, van Tienderen and van der Toorn 1991, Joshi et al. 2001, Volis et al. 2002, Parker et al. 2003, Kolbe et al. 2004). The other possibility is that species respond to natural selection and specialize by adapting to specific environmental conditions (Antonovics 1968). Species specialized to their environment are often characterized by enhanced performance in their native habitat than in any other part of their range (Miller and Fowler 1994).

If a species possesses the potential for adaptation to novel and heterogeneous environments, what process creates specialist genotypes? Many studies have examined populations throughout a species' range to determine the effects that heterogeneous habitats have on the forces promoting adaptation to local environmental conditions (Antonovics 1968, Antonovics and Bradshaw 1970, van Tienderen and van der Toorn 1991, Miller and Fowler 1994, Kindell et al. 1996, Weber and Schmid 1998, Joshi et al.

2001). Plants that occur over a wide geographic distribution may experience varying conditions such as day length, temperature, soil type, and rainfall. These can then produce novel selection pressures that can promote evolution of a specialist genotype (Antonovics 1968, Antonovics and Bradshaw 1970, Schemske 1984, Schluter and McPhail 1992, Kindell et al. 1996).

The traits that evolve to become locally adapted will depend on the specific environmental variables that change. Given their fitness consequences we may expect natural selection to operate on target traits that enhance growth and survival in particular habitats. In many species it is known that there are adult traits highly correlated with events that occur early in the life cycle. Thus, the developmental trajectory of adult traits may be determined by germination. Plant size (total diameter, height, and leaf number), survival, germination success can all increase fitness, competitive ability, and total reproductive output of an individual (Baskin and Baskin 1971, Wolfe 1992, Conner et al. 1996, Dyer et al. 2000, Donohue 2002). Germination time is the first major life-history event to be expressed in plants and one that may ultimately explain patterns of success at adulthood (Schemske 1984). If plants produce seeds that germinate faster and have a higher percent germination, their offspring may be larger and have greater survival than other individuals within the population (Purrington 1993, Sakai and Sakai 1995, Mathias and Kisdi 2002, Leger and Rice 2003).

Specialization to local environmental conditions has been found in several experimental studies. David and Bocquet (1975) discovered that invasive populations of *Drosophila* have evolved prominent and recurring clines with latitude for many traits, indicating evolution of adaptive qualities for different regions across its distribution.

When Kindell et al. (1996) performed a reciprocal transplant experiment for the plant *Aristida stricta*, they found increased survival and biomass for populations planted in their home range relative to the transplanted individuals. Additionally, Joshi et al. (2001) discovered that three plant species (*Trifolium pretense*, *Dactylis glomerata*, *Plantago lanceolata*) showed consistent home advantage in survival and plant size for a reciprocal transplant experiment across Europe. They suggested that local specialization might be the rule rather than the exception in these species.

Invasive species make excellent study organisms for the study of local adaptation because they occur over a broad area and have recently encountered new habitats (Parker et al. 2003). *Silene latifolia* was introduced to North America from Europe approximately 200 years ago (Baker 1948), and recent studies have revealed differences in critical life-history traits between the native (Europe) and invasive (North America) ranges (Wolfe 2002, Blair and Wolfe 2004, Wolfe et al. 2004). Yet, it is not known whether these differences represent local adaptation. The overall goal of this thesis was to examine the potential for local adaptation in *S. latifolia* under field and laboratory conditions. Specifically, I addressed the following questions. 1) Is germination behavior of distinctive populations adapted to temperatures corresponding to their respective home environmental conditions? In other words, are speed and success of germination highest in experimental temperatures that correspond to the population's home environmental conditions? I addressed this objective by manipulating temperature in a growth chamber in the laboratory. 2) Is early plant growth and survival locally adapted to the conditions of the home continent? I addressed this objective by growing plants from multiple populations in common gardens in Europe and North America. 3) A third objective was

to evaluate statistically the level of phenotypic variation in traits between Europe and North America. Because of founder events, I expected to detect less genetic variation in the introduced range than in the native range. I therefore used the coefficient of variation of germination and plant size to evaluate phenotypic variation in these traits between the two continents.

## CHAPTER II

### METHODS

#### Study Species

*Silene latifolia* Poiret (= *S. alba* (Mill.)(Caryophyllaceae) is a dioecious, short-lived perennial plant native to Europe (McNeill 1977) where it is a common species in fields and along roadsides (Baker 1948). This plant was accidentally introduced to North America in the 1800s through impure clover seed and rubbish from grain ships (Baker 1948, Prentice 1979). Since its introduction, *S. latifolia* has become a problematic weed in crop fields and disturbed habitats in Canada and the United States (McNeill 1977). There is a great deal known about various aspects of the species' biology including population genetic structure, sex ratios, pollination biology, metapopulation structure, and colonization history (Baker 1948, Prentice et al. 1984, Prentice 1987, Antonovics et al. 1994, Altizer et al. 1998, Taylor 1999, McCauley and Turner 2002, Taylor and Keller in review). *Silene latifolia* was pushed to the southern reaches of Europe during the last glaciation period, and studies have shown that as the glaciers receded, populations gradually moved northward creating different clades across the continent (Prentice 1987, Taylor and Keller in review).

#### Local Adaptation to Germination Temperature

In order to test for local adaptation of early life-history traits to temperature, germination times need to be tested under different experimental temperatures to determine if populations are adapted to specific latitudinal temperatures. There were three latitudinal regions for each continent and these were derived by examining previously determined germination times (Blair and Wolfe 2004) and by phylogeographic

studies (Prentice 1987, Vellekoop et al. 1996, Taylor and Keller in review). North American regions were partitioned into the following latitudes: north ( $>45^\circ$ ), intermediate ( $35^\circ - 45^\circ$ ), and south ( $<35^\circ$ ). European regions were partitioned into the following latitudes: north ( $>50^\circ$ ), intermediate ( $50^\circ$  - Alps, in the western portion of the continent –  $40^\circ$ , in the eastern portion of the continent), and south (below the Alps -  $<40^\circ$ ) (Figure 1). Since relatively little is known about germination time in *S. latifolia*, temperatures were determined based on weather census data from Europe and North America, and was only available in monthly averages. Temperatures for each region were derived from the monthly average temperatures for the growing season (May through September). I conducted three temperature trials in a plant growth chamber ( $21.1^\circ$ ,  $26.7^\circ$ , and  $32.2^\circ$  C) to simulate latitudinal conditions. If populations within each latitudinal region were locally adapted to temperature conditions, then the fastest germination time for each region would occur under its predicted temperature: North =  $21.1^\circ$  C, Intermediate =  $26.7^\circ$  C, and South =  $32.2^\circ$  C.

I used a hierarchical design in the plant growth chamber to test local adaptation in germination time. Three populations were selected from each region. Each population was selected based on a compromise between seed availability and its geographic range in either Europe or North America ( $n = 18$  populations, Table 1). There were three maternal families per population ( $n = 54$  maternal families) and three replicates per maternal family. The experimental unit was a petri dish divided into four sections and each was filled with five mL sterile agar (15 grams of agar per L of distilled water and sterilized for 45 minutes). One seed was placed in each of the four sections ( $n = 648$ ). The growth chamber was kept dark, and the petri dishes were monitored daily. For each



seed I recorded the date of radicle emergence and cotyledon emergence. Radicle emergence was recorded when  $> 2$  mm of the radicle emerged through the seed coat. Cotyledon emergence was recorded when the cotyledons were fully expanded. Percent germination was calculated for each population at each temperature. Each temperature trial lasted approximately four weeks and ended when no germination had occurred for approximately five days.

### **Field Common Garden Experiment**

The goal of this experiment was to quantify whether early growth and survival varied geographically and appeared to be locally adapted. I predicted that populations would perform better in their home continent compared to their exotic habitat if they have become locally adapted to prevailing environmental conditions. In September 2004, 15 populations from both Europe and North America were grown in a greenhouse at the University of Virginia. Each population was selected based on a compromise between seed availability and its geographic range in either Europe or North America ( $n = 30$  populations, Table 2). Seeds were grown in standard *Silene*-mix (perlite, pinebark, peatmoss, and potting soil) in 2.5 cm containers©. Plants flowered and their sex was determined and then their aboveground biomass was clipped prior to shipping plants to the four common garden sites. I used a hierarchical design that included replication at all levels.

The North American sites were located at Mountain Lake Biological Station in Pembroke, Virginia and Queens' University Biological Station in Ontario, Canada. European sites were located at Wytham Woods in Oxford, England and at Grancy, Switzerland. Transplanting for these common gardens was completed July (North

America) and August (Europe) 2005. At each site, I constructed 30 plots (3 m by 3 m) that were separated by 50 m; each contained 20 plants (10 male and 10 female) from a single population ( $n = 600$  plants/site). Plots were mowed with a weed whacker prior to planting and a motorized auger was used to dig holes. The 20 individuals in each plot were planted directly into the soil in randomly selected locations on a 3 by 3 m grid. Plots were surrounded by 1.8 m fencing to protect the plants from deer herbivory (except in Switzerland where deer are not abundant). At Wytham Woods, plots were also surrounded by barbed wire to protect the plants from sheep grazing.

I censused all plants in North America during October 2005 and censused all plants in Europe during November 2005. For each plant, I recorded whether they were alive or dead, number of leaves, and plant rosette diameter.

### **Statistical Analysis**

Statistical analyses were conducted with JMP-IN version 5.1 (SAS Institute, INC, 2004). Each variable was tested for homogeneity of variance and normality by examining the distributions of the residuals. Plant size and germination time were approximately normal. When I log transformed and re-analyzed the data, there was no difference between the effects in the analysis of variance. Therefore, the data in this thesis were not transformed for the analysis of variance for all traits.

Data for the test of local adaptation in germination time were analyzed with a hierarchical nested analysis of variance with the following effects: seed origin (Europe or North America), region nested within seed origin, population nested within region (random), and maternal family nested within population (random). I calculated the

coefficient of variation to compare the level of phenotypic variation between continents by using the population means of germination time.

I analyzed the field common garden experiments with a model I analysis of variance. The sources of variation were partitioned into the following effects: seed origin (Europe or North America), and site. The mean value for each plot provided a population estimate that was used as the replication unit in the analysis of variance.

## CHAPTER III

### RESULTS

#### Local Adaptation to Germination Temperature

Germination percentage varied with temperature. Germination percentage was highest at 26.7° C (67%) and was lowest at 32.2° C (40%) (Figure 2). Germination percentage was not significantly different between continents (Figure 3). North American regions had the highest percent germination for all temperature trials except for the intermediate region in the 21.1° C trial (Figure 3), but this pattern was not significant. There was no significant interaction between temperature and region, which is the test that determines if germination percentage is locally adapted (Table 3).

Both measures of germination time were correlated, as there was a significant relationship between radicle and cotyledon emergence ( $r = 0.45$ ,  $P = 0.0001$ ). Germination time was significantly different among temperature treatments (Tables 4 and 5). Most populations had the fastest germination time for the 21.1° C trial ( $5.3 \pm 2.8$  to  $9.4 \pm 2.2$  days; mean  $\pm$  standard deviation) and the slowest germination time occurred in the 32.2° C trial ( $10.9 \pm 6.2$  to  $21.5 \pm 7.3$  days) (Figures 4 and 5). There was no difference between continents for either measure of germination time (Tables 4 and 5). Both measures of germination time showed a significant interaction between temperature and region, indicating that plants from different continental regions varied in germination time under different temperature regimes (Tables 4 and 5). European populations showed more variation among populations (coefficient of variation = 34) than North American populations (coefficient of variation = 19).

Although there were differences in seed age (Table 1), there was no difference in percent germination or germination time based on this characteristic. All populations and maternal families germinated under each temperature treatment.

### **Field Common Garden Experiment**

I found little evidence of local adaptation at the continental level for plant survival in the field common garden experiment. Survival was similar across Europe (92%) and North America (90%) (Table 6, Figure 6), indicating that the continent of seed origin had no impact on survival for populations of *S. latifolia*. There was also no difference in survival rates between the continents where plants were raised (plant destination) for European (91%) and North American (90%) individuals (Table 6). However, there were differences among populations from each continent (Figure 7), with populations ranging from 68% to 100% survival.

I found evidence of local adaptation at the continental level for both measures of plant size. A significant relationship was found between leaf number and plant diameter of *S. latifolia* ( $r = 0.44$ ,  $P = 0.0001$ ). Leaf number and plant diameter were significantly different between continents (seed origin)(Tables 7 and 8). *Silene latifolia* populations from North America had more leaves ( $13.2 \pm 11.2$ , mean  $\pm$  standard deviation) than European plants ( $11.8 \pm 8.6$ ) when planted in North America (Table 7). I found a similar trend for European populations; European plants had more leaves ( $18.5 \pm 10.7$ ) and were larger ( $14.5 \pm 6.9$  cm) than North American plants ( $12.2 \pm 8.0$  and  $11.3 \pm 5.0$  cm, respectively) when planted in Europe (Tables 7 and 8). Interestingly, North American plants in Europe were larger ( $11.3 \pm 5.0$  cm) than North American plants grown in North America ( $10.6 \pm 5.4$  cm). Overall, there was a significant site by continent (seed origin)

interaction for both leaf number and diameter (Tables 7 and 8; Figures 7 and 8; respectively).

## CHAPTER IV

### DISCUSSION

The overall goal of this thesis was to determine if *Silene latifolia* exhibits adaptation to local environmental conditions throughout its European and North American range. Because of its relatively recent colonization and subsequent dispersal across a wide geographic range, it represents a model organism to study local adaptation. Based on the observation that plants tended to be larger in their native habitat, my results support the conclusion that early plant growth (measured as size) is adapted locally to home continents in both Europe and North America. However, I found no evidence to support the conclusion that germination success is locally adapted to latitudinal regions when grown under three different temperatures.

This study revealed that germination time was different for each latitudinal temperature treatment. Germination time was not consistent with the expected pattern across latitudinal temperatures. The observed pattern of germination resulted in all regions germinating faster under the cooler temperature treatment. North American and European regions fluctuated between having the fastest germination for a particular temperature and neither continent had the fastest germination for all regions.

*Silene latifolia* did exhibit local adaptation in the field common gardens. Plants grown within their native habitat grew larger than their foreign counterparts. European populations had more leaves and larger diameter than North American populations. North American plants exhibited a similar trend when grown in their home range. However, when the interactions between continent and site for leaf number and diameter were investigated further, North American plants in Virginia did not express greater plant

size than European populations. This indicates that North American populations had poorer performance in Virginia, and this could be attributed to the site being at a higher elevation (1160 m) than the Canada site (approximately 49 m) and therefore North American populations could be maladapted to higher elevations.

There could be several explanations for the differences in local adaptation for the traits examined in this thesis. First, because temperature treatments were determined by averaging daily temperatures across a region during *S. latifolia*'s entire growing season, they could have been overestimated because *S. latifolia* seeds are thought to germinate in the early spring or fall months. Second, it is possible that *Silene latifolia* does not exhibit local adaptation for germination in any region on any continent, but has a general-purpose genotype that performs better under lower temperature conditions. Baker (1965) described colonizing species that thrive in a wide range of environmental conditions through phenotypic plasticity as having a general-purpose genotype. Recently, Parker et al. (2003) hypothesized that some successful colonizing species may be general-purpose genotypes rather than rapidly adapting species (i.e. species that locally adapt to environmental conditions). For example, they found little evidence that populations of *Verbascum thapsus* were locally adapted to temperature when grown at different elevations. *Verbascum thapsus* populations exhibited similar performance across all elevations for many traits, which conforms to Baker's concept of general-purpose genotypes rather than to adaptation to local conditions (Parker et al. 2003).

Third, it is possible that there was insufficient genetic variation in the germination trait to allow a response to natural selection. Local adaptation is a genetic response, and the amount of genetic variation can affect the way an organism responds to selection



(Parker et al. 2003). Populations of invasive species may be further influenced by founder effects (i.e., low genetic diversity) during range expansion (Carroll and Dingle 1996). Previous work has revealed that certain life-history traits in *S. latifolia* have evolved since its introduction to North America. However, these studies were conducted at the continental level and did not examine fine-scale local adaptation. On the other hand, there were significant differences among populations and maternal families for plant size and survival in the field common garden experiment, which suggests that there is genetic variation among populations on each continent. Blair and Wolfe (2004) found evidence of evolution in *S. latifolia* since its introduction to North America, and Wolfe et al. (2004) found differences among populations of this species from both North America and Europe when grown in Europe. Local adaptation may have more opportunity to occur if multiple introductions take place in the expanded range, which could increase the amount of genetic variation in a species (Ellstrand and Schierenbeck 2000). Taylor and Keller (in review) have found evidence that *S. latifolia* has been introduced multiple times into North America. Overall, there is genetic variation in North America, but it is unclear how it is distributed. Therefore, *Silene latifolia* could likely have greater responses to natural selection, increasing the instances of populations adapting to local conditions.

Finally, germination time may be regulated more by influences from the maternal plant than by genetic attributes of the seed. The seed coat and size of the seed are critical determinants of germination time and these attributes are a direct result of the maternal resources provisioned to the offspring (Baskin and Baskin 1971, 1973, Schutz and Milberg 1997, Vaughton and Ramsey 1997). Thus, habitat differences mediated through

the maternal plant may have a disproportionate influence on progeny, and may outweigh contributions from its own genetic makeup.

At first glance my results from the two experiments may appear to be contradictory. However, the observed outcome may be explained by the influence of the maternal plant (Linnington et al. 1979, Wulff 1984, Hume 1994, Bell et al. 1995, Limbach and Call 1996, Klos and Brummer 2000). Therefore, this study could indicate that maternal effects have a strong influence on early traits expressed (germination), but the maternal impact decreases in magnitude as the plants age, allowing the plant to express higher fitness in its local environment (Wolfe 1993). Early traits may be expressing maternal effects because seeds were obtained directly from the field. It is also possible that some populations exhibit local adaptation some years but not others due to temporal and spatial environmental variation that can affect the direction and intensity of natural selection (Kindell et al. 1996).

### **Summary**

In general, the results of this study found no adaptation in germination success to latitudinal temperature regions but did find evidence of local adaptation in life-history traits in juvenile plants. While few studies have examined local adaptation in colonizing species (Parker et al. 2003, Genton et al. 2005), those that have found no evidence of local adaptation for invasive species in the new range. This study provides evidence that plant size traits may be expressing adaptation to local conditions while germination traits do not. Further studies should include multi-generational experiments that would eliminate many of the maternal effects that could influence germination time.

Table 1. *Silene latifolia* populations used in the test of local adaptation in germination time.

**Europe**

Figure ID	Region	Population	Year Collected
1	North	United Kingdom	2005
2	North	Netherlands	2002
3	North	Denmark	
4	Intermediate	Austria	2005
5	Intermediate	Czech Republic	2005
6	Intermediate	Germany	
7	South	Portugal	2000
8	South	Italy	2000
9	South	Spain	2001

**North America**

Figure ID	Region	Population	Year Collected
10	North	Maine	2005
11	North	Saskatchewan	2000
12	North	Michigan	2000
13	Intermediate	Virginia	2001
14	Intermediate	Iowa	2001
15	Intermediate	Illinois	2001
16	South	Tennessee	2001
17	South	North Carolina 1	
18	South	North Carolina 2	

Table 2. *Silene latifolia* populations used in the field common garden experiment.**Europe**

Figure ID	Population	Location	Year Collected
1	BER	la Bernerie en Retz, France	1999
2	CDR	Croix-de-Rozon, France	1999
3	CRE2	Creon, France	2004
4	GAP	Gap, France	1999
5	KIS	Kiskunfelegyhaza, Hungary	1999
6	MON	France	1999
7	OSE1	Oseja de Sajambre, Spain	2004
8	PRG	Prague, Czech Republic	2004
9	PRT	Porto, Portugal	2004
10	ROD	Rodomouls, France	1999
11	ROS	Rosia, Italy	1999
12	SAL	Salhouse, England	2004
13	SG	San Gimignano, Italy	1999
14	SVL1	St. Valentin, Austria	1999
15	DK5	Denmark	

**North America**

Figure ID	Population	Location	Year Collected
16	23s	N. Carolina/Tennessee border	2000
17	CHELD2	Chelmsford, Massachusetts	2004
18	CQQ	Chillisquaque, Pennsylvania	1999
19	FMN	Freeburg, Minnesota	2001
20	JNS	Jones, Co., Iowa	2001
21	MLBS	Pembroke, Virginia	2001
22	NAS	Nashville, Tennessee	2004
23	PDRV	Ft. Collins, Colorado	2004
24	RDGP	Reeds Gap, Virginia	2004
25	RNKE	Roanoke, Virginia	2004
26	SASA	Saskatoon, Canada	2000
27	SCR	Ontario, Canada	2000
28	WEB	Webster, Wisconsin	
29	WHS	Whiteside, Illinois	2001
30	RVVW	Colorado	

Table 3. Nested ANOVA results for percent germination in *Silene latifolia* for all temperature trials in the test of local adaptation in germination time. Seed origin = Europe and North America; Region = North, Intermediate, and South. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed origin	1	5051.8	$F_{(1, 4)} = 6.5$
Temperature	2	7536.7	$F_{(2, 36)} = 9.8^{***}$
Region(seed origin)	4	3109.5	$F_{(4, 36)} = 2.0$
Temperature x Seed origin	2	1882.8	$F_{(2, 36)} = 2.4$
Temperature x Region	8	1194.6	$F_{(8, 36)} = 0.4$
Error	36	13904.2	
Total	53	32679.6	

Table 4. Mixed-model nested ANOVA results for radicle emergence days in *Silene latifolia* for all temperature trials for the test of local adaptation in germination time. Seed origin = Europe and North America; Region = North, Intermediate, and South. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed Origin	1	41.6	$F_{(1, 1074)} = 1.8$
Temperature	2	3910.1	$F_{(2, 1074)} = 84.1^{***}$
Region(seed origin)	4	1158.7	$F_{(4, 1074)} = 12.5^{***}$
Temperature x Seed origin	2	180.5	$F_{(2, 1074)} = 3.9^*$
Temperature x Region	8	490.0	$F_{(8, 1074)} = 2.6^*$
Error	1074	24964.4	
Total	1091	32390.3	

Table 5. Mixed-model nested ANOVA results for cotyledon emergence days in *Silene latifolia* for all temperature trials for the test of local adaptation in germination time.

Seed origin = Europe and North America; Region = North, Intermediate, and South. \* P < 0.05, \*\* P < 0.005, \*\*\*P < 0.001.

Source	DF	SS	F
Seed origin	1	1.1	$F_{(1, 791)} = 0.1$
Temperature	2	8908.6	$F_{(2, 791)} = 176.3^{***}$
Region(seed origin)	4	1368.8	$F_{(4, 791)} = 13.5^{***}$
Temperature x Seed origin	2	118.2	$F_{(2, 791)} = 2.3$
Temperature x Region	8	627.2	$F_{(8, 791)} = 3.1^{**}$
Error	791	19989.9	
Total	808	39224.4	

Table 6. Mixed-model nested ANOVA on percent survival rates for *Silene latifolia* across continents (seed origin) and populations within a continent after four months in the field common gardens. Seed origin = Europe and North America; Site = Canada, Virginia, Switzerland, and England. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed origin	1	20.8	$F_{(1, 28)} = 0.1$
Population(seed origin)	28	8336.7	$F_{(29, 84)} = 1.6^*$
Site	3	840.8	$F_{(3, 84)} = 1.5$
Site x Seed origin	3	14.2	$F_{(3, 84)} = 0.1$
Error	84	15320.0	
Total	119	24532.5	



Table 7. Mixed-model nested ANOVA for number of leaves of *Silene latifolia* after four months in the field common garden experiment. Seed origin = Europe and North America; Plant destination = Europe and North America; Site = Canada, Virginia, Switzerland, and England. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed origin	1	183.4	$F_{(1,112)} = 7.4^{***}$
Site	3	3227.1	$F_{(3, 112)} = 43.4^{***}$
Seed origin x Site	3	533.8	$F_{(3, 112)} = 7.2^{***}$
Error	112	2774.2	
Total	119	6718.5	

Table 8. Mixed-model nested ANOVA for plant diameter of *Silene latifolia* after four months in the field common garden experiment. Seed origin = Europe and North America; Plant destination = Europe and North America; Site = Canada, Virginia, Switzerland, and England. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed origin	1	82.1	$F_{(1,112)} = 6.3^{**}$
Site	3	631.7	$F_{(3, 112)} = 16.0^{***}$
Seed origin x Site	3	107.4	$F_{(3, 112)} = 2.7^*$
Error	112	1471.3	
Total	119	2292.6	

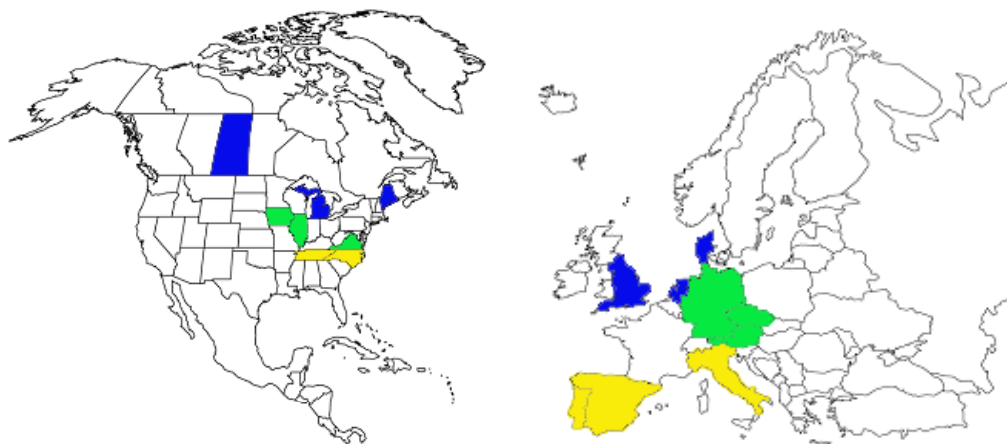


Figure 1. Populations within latitudinal regions. Blue = north ( $21.1^{\circ}\text{C}$ ), green = intermediate ( $26.7^{\circ}\text{C}$ ), and yellow = south ( $32.2^{\circ}\text{C}$ ).

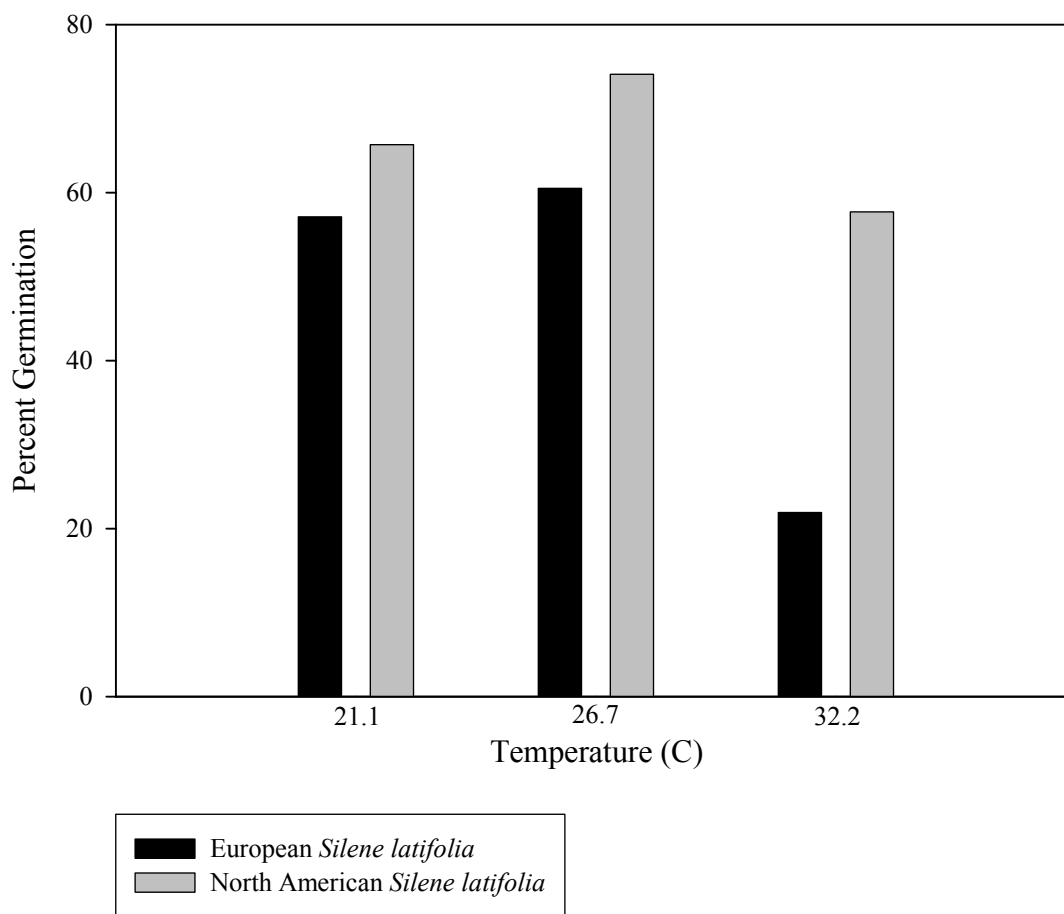


Figure 2. Germination percent for Europe and North America *Silene latifolia* seeds at three different temperatures in the growth chamber temperature experiment. See Table 3 for analysis.

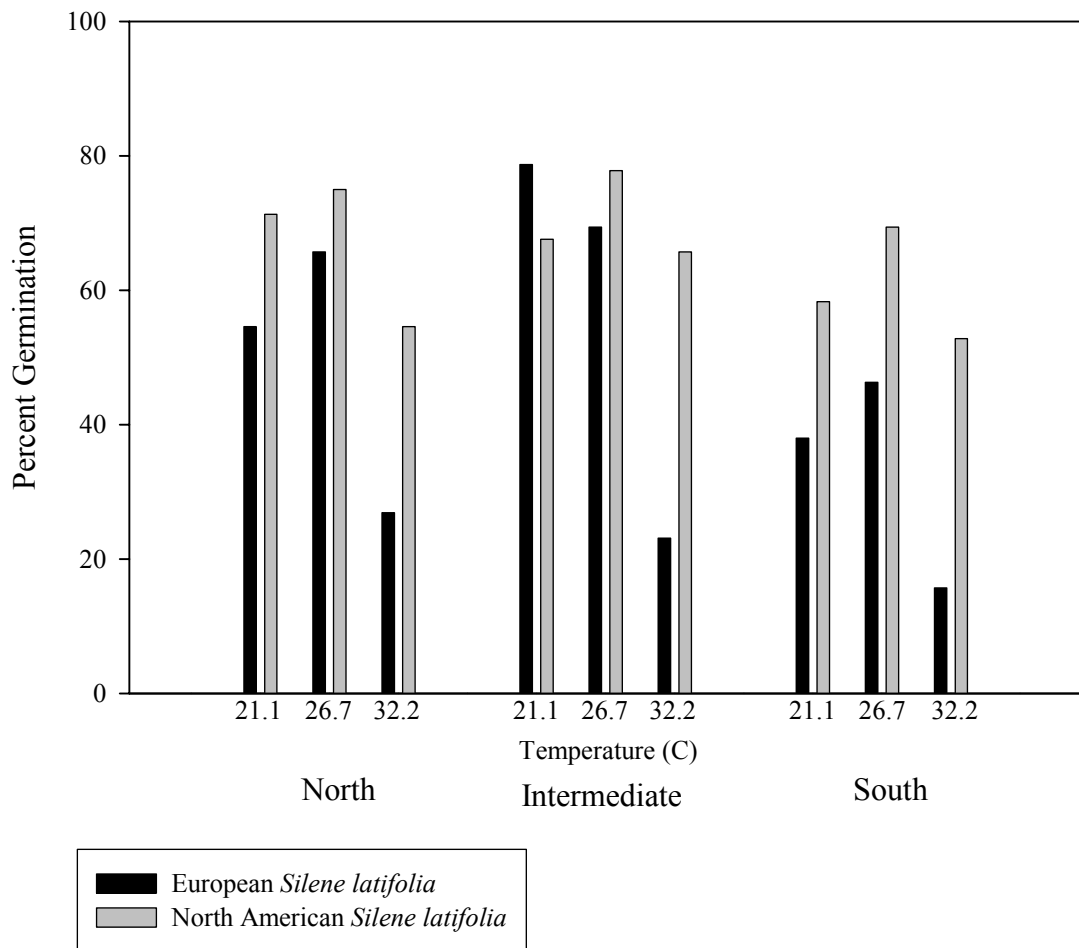


Figure 3. Germination percent for *Silene latifolia* seeds from different latitudinal regions in Europe and North America at three temperatures in the growth chamber temperature experiment. See Table 3 for analysis.

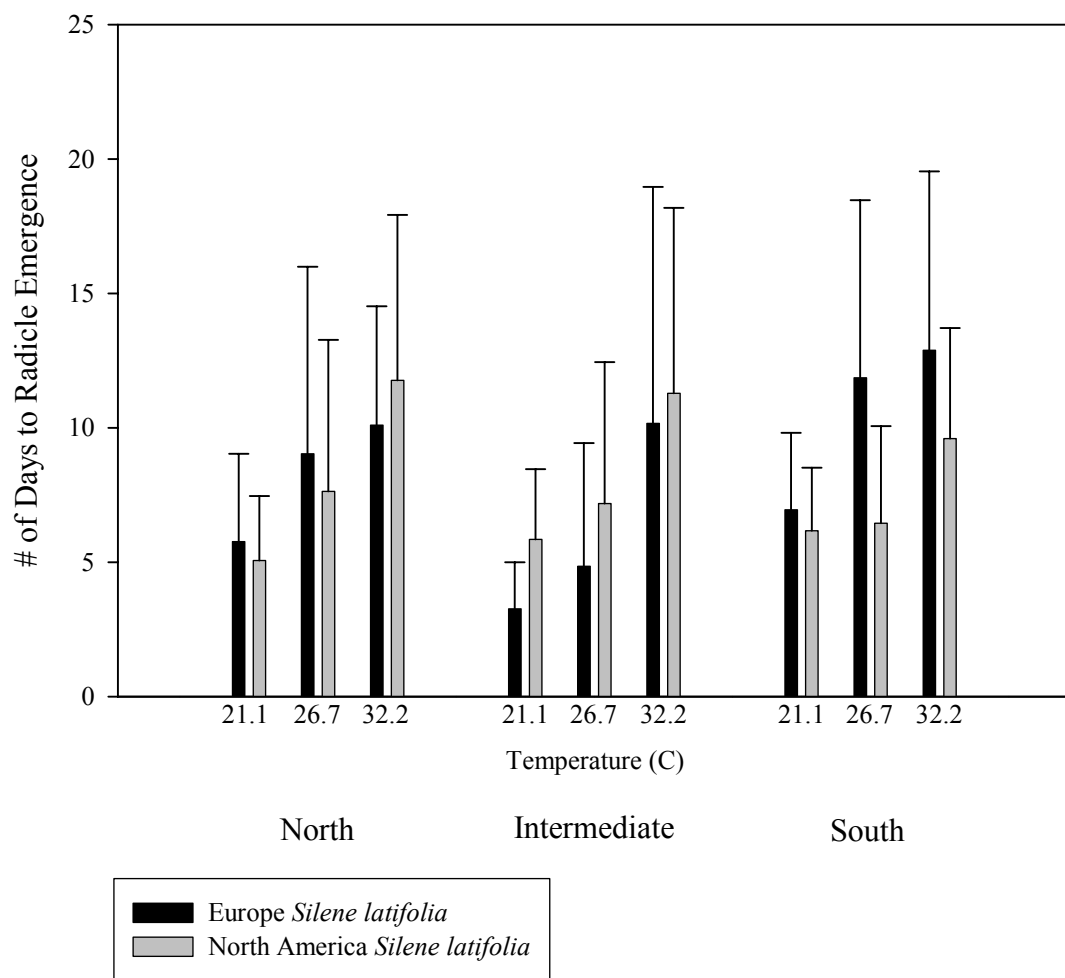


Figure 4. Germination time (radicle emergence) for European and North American *Silene latifolia* seeds in the growth chamber temperature experiment. Values are mean  $\pm$  standard deviation. See Table 4 for analysis.

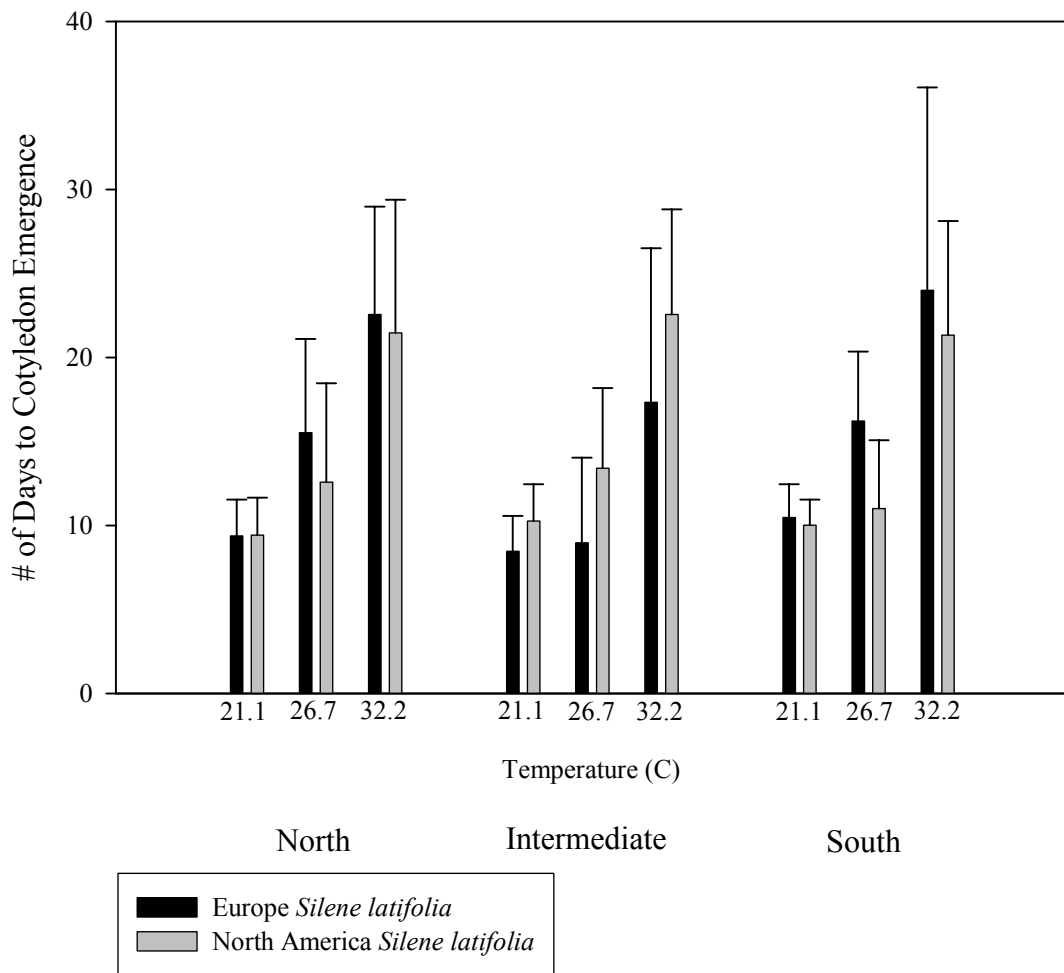


Figure 5. Germination time (cotyledon emergence) for European and North American *Silene latifolia* seeds in the growth chamber temperature experiment. Values are mean  $\pm$  standard deviation. See Table 5 for analysis.

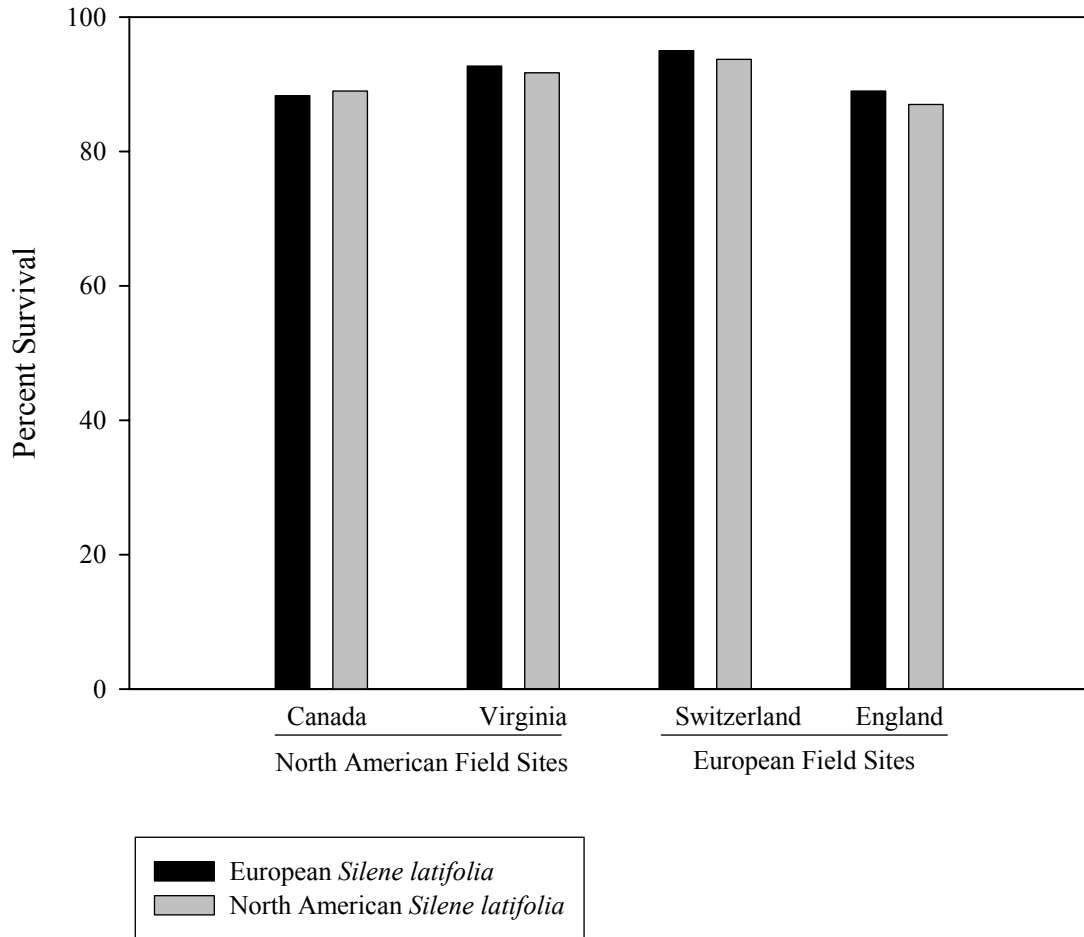


Figure 6. Survival percent after four months for European and North American *Silene latifolia* at sites in the field common garden experiments. See Table 6 for analysis.



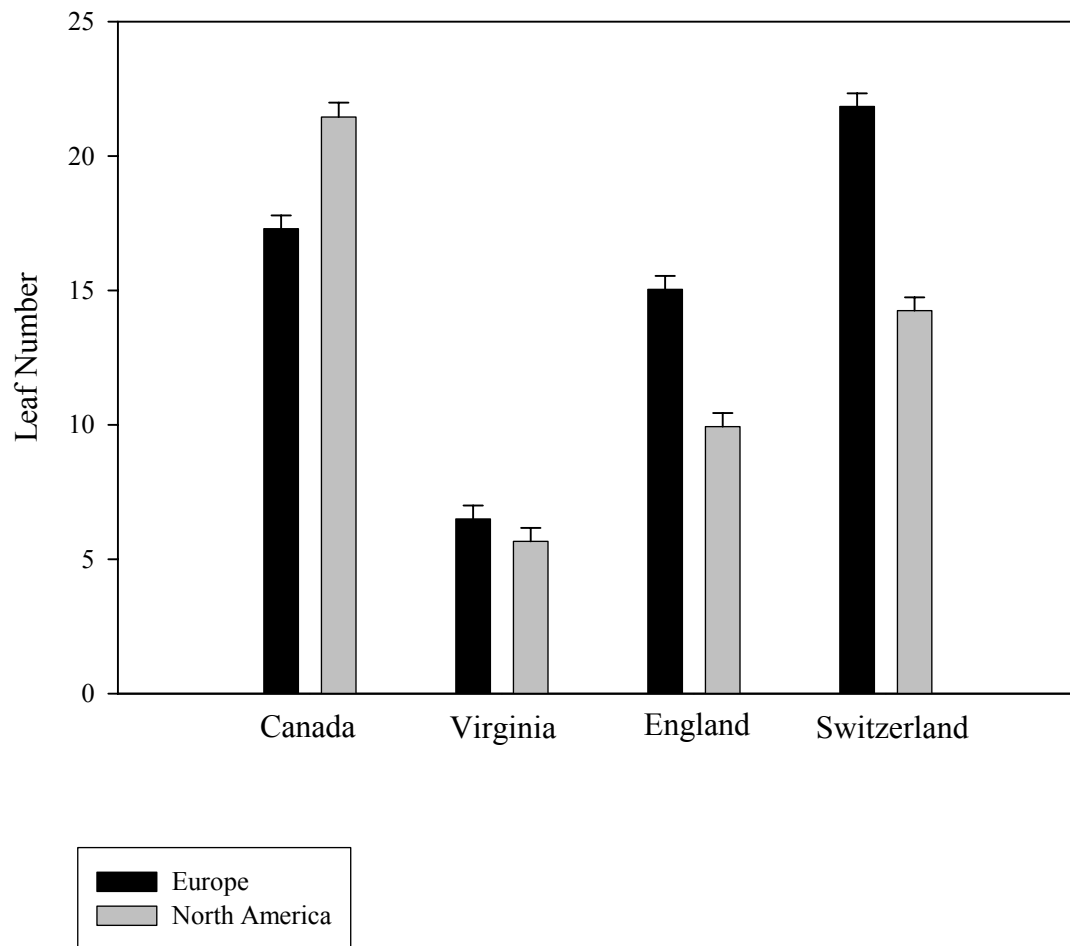


Figure 7. Plant size measured as the number of leaves per plant of *Silene latifolia* across sites in the field common garden experiment. Values are mean  $\pm$  standard deviation. See Table 7 for analysis.

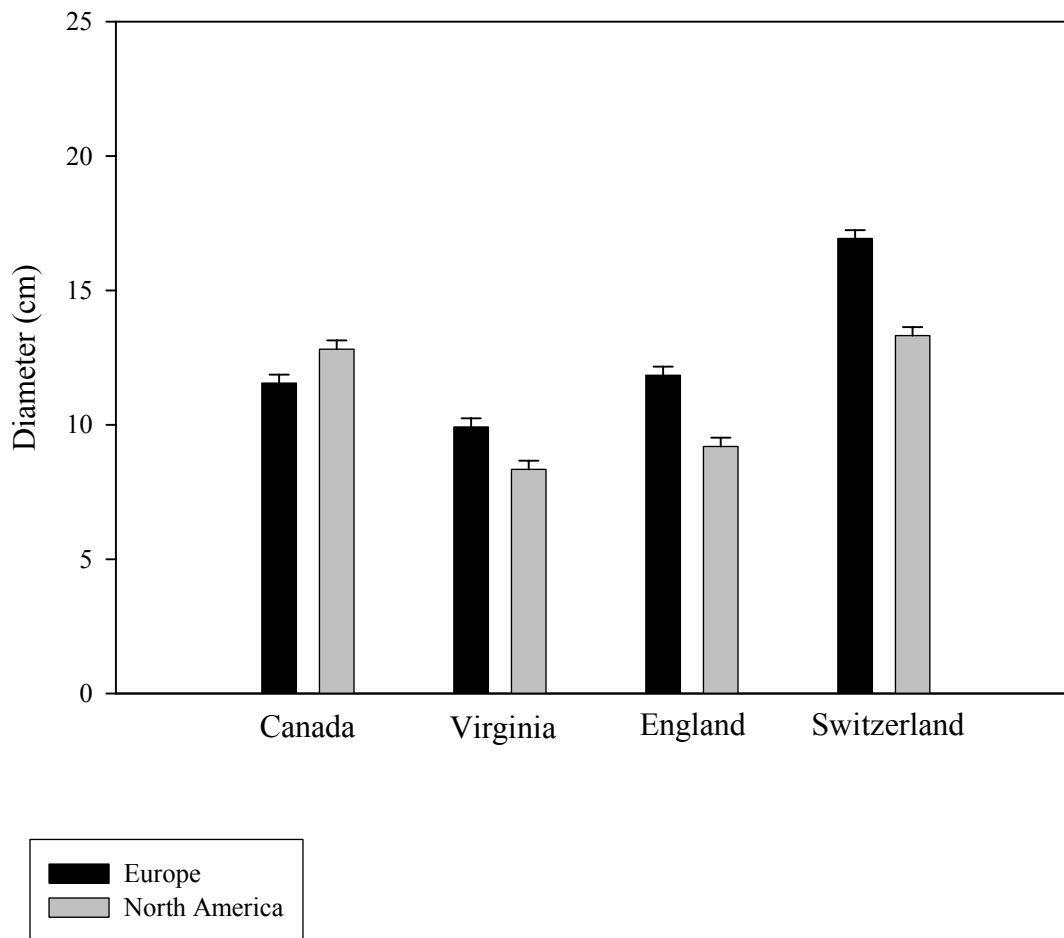


Figure 8. Plant size measured as diameter (cm) per plant for *Silene latifolia* across sites in the field common garden experiment. Values are mean  $\pm$  standard deviation. See Table 8 for results.

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## APPENDICES

APPENDIX A. Mixed-model nested ANOVA for number of leaves of *Silene latifolia* after four months in the field common garden experiment. Seed origin = Europe and North America; Plant destination = Europe and North America; Site = Canada, Virginia, Switzerland, and England. Population and Family are random. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed origin	1	2378.7	$F_{(1,28)} = 5.4^*$
Plant destination	1	3190.0	$F_{(1,2000)} = 51.1^{***}$
Seed origin x Plant destination	1	7690.4	$F_{(1,2000)} = 123.2^{***}$
Site(plant destination)	2	48461.0	$F_{(2, 2000)} = 388.0^{***}$
Seed origin x Site(plant destination)	2	1734.4	$F_{(2, 2000)} = 13.9^{***}$
Sex	2	59.2	$F_{(2, 2000)} = 0.5$
Population(seed origin)	28	12339.6	$F_{(28, 141)} = 6.0^{***}$
Family(population)	141	10247.2	$F_{(141, 2000)} = 1.2^{***}$
Error	2000	124886.7	
Total	2178	221893.8	

APPENDIX B. Mixed-model nested ANOVA for plant diameter of *Silene latifolia* after four months in the field common garden experiment. Seed origin = Europe and North America; Plant destination = Europe and North America; Site = Canada, Virginia, Switzerland, and England. Population and Family are random. \*  $P < 0.05$ , \*\*  $P < 0.005$ , \*\*\* $P < 0.001$ .

Source	DF	SS	F
Seed origin	1	1148.2	$F_{(1,28)} = 4.2^*$
Plant destination	1	1642.3	$F_{(1,2000)} = 69.4^{***}$
Seed origin x Plant destination	1	902.3	$F_{(1,2000)} = 38.1^{***}$
Site(plant destination)	2	6775.0	$F_{(2, 2000)} = 143.1^{***}$
Seed origin x Site(plant destination)	2	712.4	$F_{(2, 2000)} = 15.0^{***}$
Sex	2	167.4	$F_{(2, 2000)} = 3.5^*$
Population(seed origin)	28	7695.1	$F_{(28, 141)} = 7.6^{***}$
Family(population)	141	5091.0	$F_{(141, 2000)} = 1.5^{***}$
Error	2000	47345.6	
Total	2178	74571.3	