

LIFE-HISTORY VARIATION AND ADAPTATION IN THE HISTORICALLY MOBILE PLANT *ARABIDOPSIS THALIANA* (BRASSICACEAE) IN NORTH AMERICA¹

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We used field-collected seeds of *Arabidopsis thaliana* (Brassicaceae) to simulate a colonization event of plants from diverse locations into a common environment to compare regionally “local” and “foreign” populations of this historically mobile species. Life history varied among regional groups, but most variation was found among populations within regions. While we found significant differences among populations and regional groups for important life-history characters, we did not find significant differences in performance of plants from different populations or regional groups. Rather, we found evidence that differences in life history contributed to the ability of plants from foreign regions to perform comparably to local Kentucky plants. Had plants from different regions not differed in the timing and size of reproduction, we would have seen that Kentucky (local) plants had higher total fitness via greater reproductive success of individuals that survived to reproduce and that Michigan plants would have had the lowest fitness. The populations are comparably adapted to the environment in Kentucky but through different combinations of life-history characters. Therefore, the life-history variation in this mobile species appears to contribute not to fitness differences among populations but rather to success in colonizing new locations.

Key words: *Arabidopsis thaliana*; Brassicaceae; colonization; flowering time; germination; local adaptation; range expansion; seasonal dormancy.

Many weedy plants are highly mobile through long-distance seed dispersal (Baker, 1974). They frequently expand their geographic range or contribute foreign genotypes to distant locations in this manner. The efficiency of long-distance dispersal to these processes, however, depends on the performance of the dispersing propagules in the new location. If local adaptation to variable microenvironments is prevalent, then dispersing propagules may not perform well in new locations (Jain and Bradshaw, 1966; Antonovics, 1968; Macnair, 1981). Alternatively, if similar microenvironments are available throughout the geographic range of the plants, then dispersing propagules may more easily establish in new locations.

The ability of dispersing propagules to contribute to local genetic variation depends on how foreign genotypes are selected within the new population. Such selection will depend on additive effects of immigrant genes in the new location and also within the background of the new gene pool (Wright, 1932; Tonsor and Goodnight, 1997; Wade, 2002). In highly selfing species, as in many weeds, recombination and mixing of the foreign and native genomes may be low, and adaptive gene combinations may be preserved in new locations. Thus the evolutionary ecology of weedy species depends on how divergent populations are over the geographic range of the species, how particular divergent characters are selected in

new locations, whether combinations of characters and genes contribute to performance, and whether combinations of characters and genes are likely to be preserved in the new location through low recombination.

Arabidopsis thaliana (L.) Heynh. (Brassicaceae) is a highly selfing, weedy annual that has been introduced into North America, most likely from Europe, within the past few hundred years (Sharbel et al., 2000; Vander Zwan et al., 2000; Hoffmann, 2002). It inhabits a broad geographic range within North America, and it is considered to be highly mobile through long-distance dispersal of its tiny seeds. While genetic variation within populations is quite low (Bergelson et al., 1998), ecotypes from different locations have been shown to differ from one another in important life history traits—especially those ecotypes from the European and Central Asian collections available from the *Arabidopsis* seed stock centers (e.g., The Arabidopsis Biological Resource Center and Nottingham Arabidopsis Stock Centre). Several studies have demonstrated ecotypic variation in flowering time as well as in important morphological and physiological characters (e.g., Griffing and Scholl, 1991; Pigliucci and Schlichting, 1996; Pigliucci, 1998; Nordborg and Bergelson, 1999; Mitchell-Olds, 2001; Pigliucci and Marlow, 2001; Kover and Schaal, 2002). Much less is known about patterns of variation among populations in North America, the continent of its more recent introduction, although recent studies have documented differentiation among New England populations in a common greenhouse environment (Dorn et al., 2000).

Arabidopsis thaliana, like many important weeds, typically displays a “winter annual” life history, in which seeds germinate in the autumn, plants overwinter as rosettes, and they grow, flower, set seeds, and die in the spring. In some populations, plants display a “spring annual” life history, in which seeds germinate in the early spring, and they flower, set seeds, and die all during the same season. This basic life history sequence varies among known *A. thaliana* ecotypes worldwide

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(Ratcliffe, 1965; Effmertova, 1967; Evans and Ratcliffe, 1972; Nordborg and Bergelson, 1999), as well as among natural populations in North America (K. Donohue, Harvard University, and L. Dorn, University of Wisconsin, Oshkosh, personal observation). Plants in some populations have even been observed to flower in the autumn (Thompson, 1994), indicating that an "autumn annual" life history is also possible in *A. thaliana* populations. Populations in Kentucky have been characterized as winter annuals that germinate in autumn (Baskin and Baskin, 1983), whereas New England populations have been seen to germinate either in autumn or in spring and to flower in both seasons as well (L. Dorn and K. Donohue, personal observation). Spring germination in New England populations can approach 54% in some locations. The mechanism of "summer annual," "winter annual," and "autumn annual" life-histories in *A. thaliana* is determined both by germination timing and vernalization requirements for flowering (Napp-Zinn, 1976; Nordborg and Bergelson, 1999). The expression of adult life-history characters depends on the timing of germination in natural populations of *A. thaliana*, and this dependency is mediated by the seasonal environment experienced by germinants (Donohue, 2002). Therefore, characterizing basic life-history variation of natural populations of *A. thaliana* requires studies conducted under natural seasonal conditions, beginning with seed germination.

Arabidopsis thaliana is highly suitable for examining the dynamics of the introduction and spread of weedy species because it is fairly recently introduced, has long-distance dispersal, and harbors genetic variation in important life-history characters. In addition, it is a highly selfing species (Abbott and Gomes, 1989), typical of many weeds, and thereby offers the chance to investigate the dynamics of adaptation to new environments in species in which linkage disequilibrium may be pronounced. It has been shown in *A. thaliana* that, while linkage disequilibrium declines within approximately 1 cM among globally distributed collections, it remains substantial within local populations (Nordborg et al., 2002). Therefore, gene combinations, and therefore character combinations, may be important influences on the dynamics of adaptation in this weed. To characterize these dynamics, it is necessary to conduct artificial dispersal events, compare the performance of local and introduced populations, and determine characters and combinations of characters that influence performance of the different populations.

To compare life-history expression and performance of local and newly dispersed foreign seeds of *A. thaliana*, we used field-collected seeds collected from three geographic regions in North America in a common garden experiment conducted in Kentucky. We addressed the following specific questions. (1) Do populations differ in life-history expression, and is life-history variation structured at a regional scale? (2) Which life-history characters, and combinations of life-history characters, contribute most to variation in survival and fecundity? (3) Do local populations perform better than newly introduced populations? (4) What is the contribution of life-history characters to similarities or differences in performance between plants from different populations and regions?

MATERIALS AND METHODS

Experimental design—Seeds of *Arabidopsis thaliana* were collected from five populations in and around Lexington, Kentucky USA (KY hereafter: populations named KYB, KYC, KYD, KYE, KYG), three populations in New

England [NE hereafter: including one from Montague, Massachusetts (MAB), one from Shelburne Massachusetts (MAS), and one from Lincoln Woods State Park in Rhode Island (RI)], and two populations from Michigan [MI hereafter: collected from east New Buffalo (MIA) and Three Oaks (MIC)]. The seeds from Kentucky had been grown in a previous outdoor common garden in Lexington, Kentucky USA, and seeds collected from these field-matured plants were used in this experiment. For the other populations, seeds were collected directly from the field in which the population was found. The use of field-collected seeds more accurately simulates a colonization event from different locations into a common site in Kentucky than would the use of seeds raised in a common environment to remove field-imposed maternal effects. However, field-collected seeds limit our ability to determine whether observed differences between populations are genetically based or due to maternal effects.

The common garden was located at the Ecological Research Facility (ERF) of the T. H. Morgan School of Biological Sciences of the University of Kentucky in Lexington, Kentucky USA. ERF is located at latitude 38°04.834' N, longitude 084°28.397' W, at approximately 305 m above sea level. The plot was located in a grassy field and was mowed, tilled, and raked in late summer. Soil was taken from the experimental plot after tilling for use as the potting medium. The soil was autoclaved for 20 min at 121°C at 103 kPa to kill any naturally occurring seeds. The autoclaved soil was placed in Jiffy Poly-Pak (5 cm) square biodegradable peat pots. Two 0.6 m access strips were made in a 5 × 3 m² plot, giving three 0.6 m wide by 2.8 m long strips in which the pots were planted.

In September 2000, seeds were sprinkled into pots that had been planted into the field. Approximately 20 seeds from a single plant were sprinkled on the soil surface of a pot. Except for the Kentucky populations, in which seeds were pooled over 18 individuals per population, only seeds originating from one individual were planted in each pot.

To accurately assess germination timing and to compare the performance of plants that germinated in the autumn to those that germinated in the spring, 15 pots for each population were randomly assigned to each of two treatments: "autumn" and "spring." In each "autumn" pot, one random autumn germinant was followed as the focal individual, and in each "spring" pot, one random spring germinant was chosen as the focal individual. This gave a total of 720 pots (10 populations × two treatments × 15 replicates per population per treatment). All pots were randomly distributed throughout the plot.

The number of seedlings in each pot was recorded weekly, with 25 censuses from 30 September 2000 until 17 June 2001. No censuses were conducted from 11 December 2000 until 20 February 2001. On average, approximately 80% of all seeds germinated. The focal individual in each pot was chosen as follows. In late October, after most autumn germination, the seedling that was closest to the center of the pot was left in the "autumn" pot as the focal individual while all other seedlings were plucked from the pot. If another germinant emerged later in the autumn and was closer to the center, it was chosen as the replacement focal individual. Few, however, germinated after the thinning. All new germinants were removed from autumn pots after February, as they were then considered to be spring germinants. In spring pots, all seedlings that germinated before February were removed as they germinated, and a focal spring germinant was chosen as the seedling closest to the center of the pot, as described above.

Each pot was covered by an 8-cm high, tent-shaped structure of aluminum window screen to protect the seeds from heavy rains. The effects of aluminum screening on photosynthetically active radiation (PAR) and on the red to far-red ratio (R : FR) were examined on 12 September (before planting) using an Ocean Optics S2000 spectroradiometer (Ocean Optics, Inc., Dunedin, Florida USA) attached to a Dell laptop computer with the Ocean Optics Irrad version 2.00.05 software. The energy flux of light between 400 and 700 nm for light passing through a "tent" had the same spectrum as sunlight, and PAR was reduced by 5% (with tent = 312 mmol, without tent = 328 mmol). The ratio of the energy flux for light between 650 and 670 nm ("red" light) to the energy flux between 720 and 740 nm ("far-red" light) was 1.39, close to the value of 1.37 obtained for sunlight at the same time.

Only spring pots were used to estimate germination timing since rosettes in autumn pots could have suppressed germination of remaining seeds. The

TABLE 1. Results of nested analysis of variance to determine variance within and among geographic groups and populations of *Arabidopsis thaliana*. *F* ratios are given for between-group effects (tested over error plus population) and for between-population effects. Between-population effects are given for each geographic region. KY = Kentucky, MI = Michigan, NE = New England. *df* = 4 for KY, *df* = 1 for MI, *df* = 2 for NE. *N* = 152. *N* ranges from 162 to 181 for post-reproductive characters. *N* = 574 for total fruit production and survivorship to reproduction. * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Trait	Between region	Between population	Between KY populations	Between MI populations	Between NE populations
Germination date in autumn	1.44	8.26***	8.27***	0.51	8.93***
Proportion spring germination ^a	4.08	—	5.63	0.35	3.25
Winter diameter	2.23	3.81***	3.55**	0.11	5.76**
Diameter at bolting	5.38*	1.50	1.06	2.15	2.55
Bolting date ^b	8.17*	4.63***	1.38	2.40	4.96**
Flowering interval	5.74*	1.62	1.05	0.96	2.20
Inflorescence branches	2.32	0.84	0.96	0.65	0.81
Basal branches	2.57	1.16	0.99	2.04	1.02
Total fruit production ^a	2.79	—	3.33	0.73	1.03
Survival to reproduce	1.13	—	1.77	0.00	0.20
Fruit production by reproductive plants	1.53	1.72	1.92	2.93	1.04

^a χ^2 is given based on Kruskal–Wallis tests of non-normal data. *N* = 346 for average germination date and percentage spring germination. *N* = 276 for winter diameter.

^b No significant differences when only spring bolters were analyzed.

mean day of germination of all seedlings in a pot was calculated as the number of new seedlings during each census times the census date (days after seed deposition), divided by the total number of germinants. The germination day of the focal individual was estimated as the average germination date until the autumn thinning date, revised by mortality events that established that the focal seedling germinated after those mortality events. The germination date of the focal plant was then further revised by the probability that a new germinant after that thinning date was closer to the center than the first focal plant. Very few pots actually changed the focal plant, however.

On each focal plant, we recorded the following traits: germination day (described above), rosette diameter in mid December (overwintering diameter), the day on which the plant initiated inflorescence development (bolting date), the number of days between bolting and flowering (flowering interval), the rosette diameter at the time of bolting (diameter), the number of secondary plus tertiary branches produced from the central stem (inflorescence branches), the number of basal branches produced from each rosette (basal branches), and the total number of siliques produced (total fruits) as an estimate of total lifetime fitness. If a plant were recorded as having bolted, it was defined as having survived to reproductive maturity, or having “survived to bolting.”

Statistical methods—All statistical procedures used the Statistical Analysis System (1990). To test whether regions and populations differed in life-history traits, multivariate analysis of variance (MANOVA) was conducted with germination date, overwinter diameter, diameter at bolting, flowering date (combining bolting date and flowering interval), total branches (combining inflorescence and basal branches), and total fruit production as dependent variables, and region (fixed: KY, MI, or NE) and population (random) nested within region as the independent classes. The effect of region was tested over the population plus error variance. Traits were transformed to normality as necessary. Separate analyses of variance (ANOVAs; Proc GLM) using the same model were subsequently conducted to determine which traits varied significantly among regions and populations within regions. Linear discriminant function analysis was used to determine how well plants were classified into geographic regions.

To test whether pre-reproductive traits influenced survival to bolting, logistic regression was used (Liao, 1994; SAS Proc Catmod). First, the effect of season of germination was determined. Next, the effects of overwintering size and germination date in the autumn were determined using autumn germinants only (because only they expressed overwintering size). Population was used as a factor in these analyses.

To measure the strength of natural selection on adult life-history characters, Lande and Arnold's (1983; see also Fairbairn and Reeve, 2001) phenotypic selection analysis was conducted on autumn germinants using individual phe-

notypic values. Only four spring germinants expressed adult life-history characters, so they could not be analyzed. Selection differentials, or the strength of total directional selection, were estimated as the covariance between standardized traits (mean = 0, 1 SD) and relative fitness [total fruits/(mean number of fruits of sample)], and standard errors were calculated from a simple regression of each trait on relative fitness. The selection gradient, or strength of direct selection while controlling for correlated selection acting through other characters, was estimated as the partial regression coefficient of standardized characters on relative fitness. Nonlinear and correlational selection was estimated in a multiple regression that included all two-way interactions among variables.

To test whether the strength of directional selection on characters depended on which region or population the plant was from, analysis of covariance was conducted. An interaction between the trait and region (or population) would indicate that selection on that trait varied among plants from different regions (or populations).

To determine the contribution of life-history characters to similarity or differences in performance of the plants from different regions or populations, logistic regression and ANOVA were conducted, with either survival to bolting or fruit production by those that survived as the dependent variables, respectively. One analysis was conducted with no traits as covariates, and another analysis was conducted with the traits as covariates. The effect of region or population and the least-square means (residual means) of regions and populations were compared across models. If the difference in performance among regions or populations depends on the model, then the measured traits can be interpreted to alter the degree of differences in performance.

RESULTS

Regional and population differences—MANOVA results found significant differences among geographic regions (Wilk's λ *F* = 9.67, *df* = 12, *P* = 0.02) and among populations within geographic regions (Wilk's λ *F* = 1.74, *df* = 42, *P* = 0.003). Individual ANOVAs indicated that germination date in the autumn did not vary across regions, but it did vary among populations within regions (Table 1, Fig. 1a). One population in KY germinated significantly later than the others, and RI germinated earlier than the other NE populations. Surprisingly, the proportion of spring germinants did not differ across regions nor among populations within regions (Fig. 1b). The populations that had later germination in the autumn also had higher proportions of spring germination (Fig. 2), suggesting that spring germination in this sample could be simply

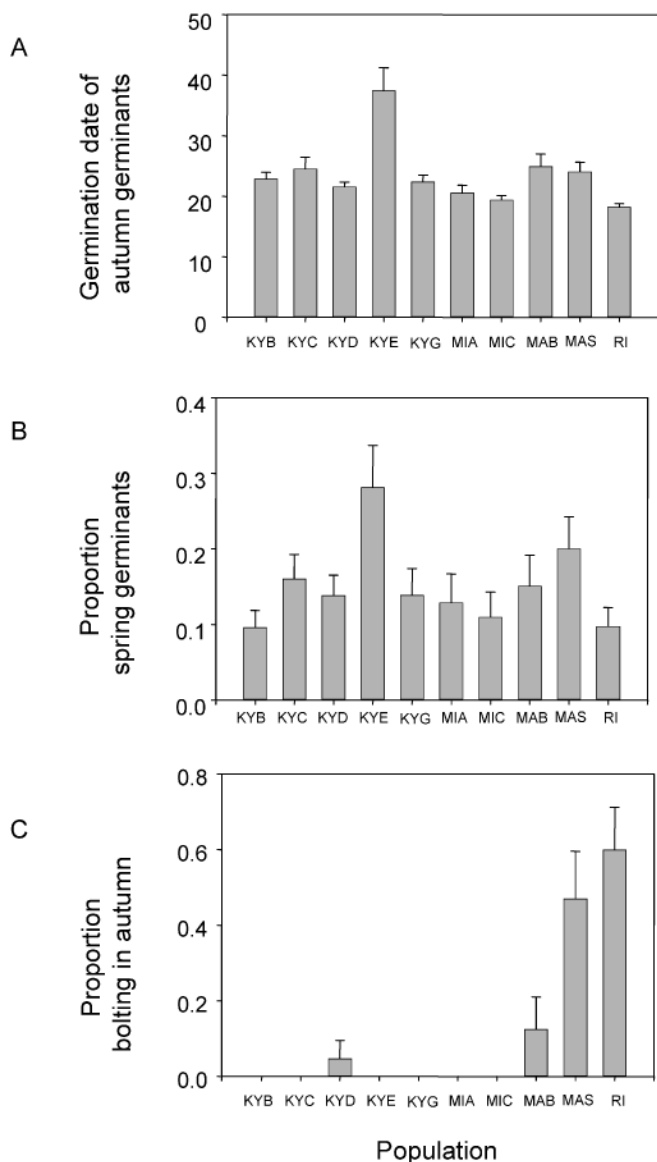


Fig. 1. Population differences in germination and season of bolting (A, germination timing in autumn; B, proportion germinating in spring; C, proportion bolting in autumn) of *Arabidopsis thaliana*. Mean values are presented for each population. Error bars represent standard errors not adjusted for multiple comparisons. Population abbreviations are as described in the Methods section.

the tail end of the distribution of late-autumn germinants. NE populations also tended to bolt in the autumn (Fig. 1c), and this tendency has the potential to alter the seasonal conditions experienced by maturing seeds in a manner that could influence germination (see Discussion).

Populations differed significantly in overwinter size, but this variation did not reflect regional differences (Table 1, Fig. 3a). MI populations were the largest at the time of bolting, and NE populations were the smallest (Fig. 3b). NE plants bolted earlier than plants from the other regions (Table 1, Fig. 3c), and the flowering interval was the longest (Fig. 3d). This was because several individuals in the NE populations (and one individual from a KY population) bolted in the autumn (Fig. 1c), but many did not flower until spring. Branch production

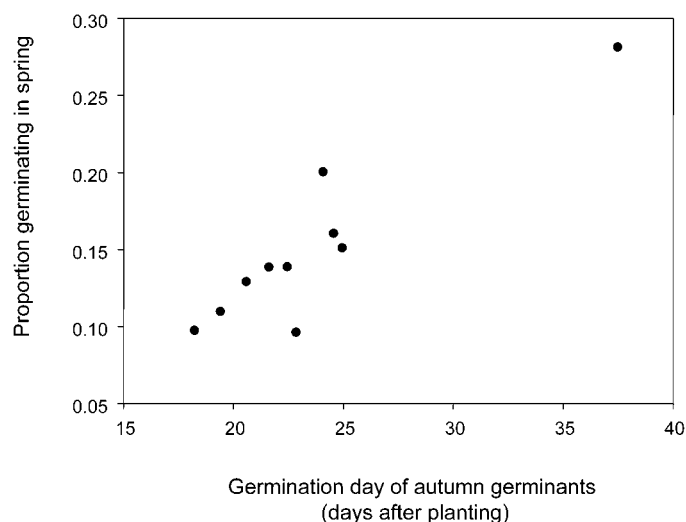


Fig. 2. Relationship between germination timing in the autumn and percentage of spring germinants of *Arabidopsis thaliana*. Each point represents the mean of a population. Spearman correlation = 0.77, $P = 0.01$. Spearman correlation without outlier = 0.68, $P < 0.05$.

did not differ significantly among regions or populations (Fig. 3e, f).

While regional differences were detected for some traits, region of origin was not accurately predicted from an individual's phenotype, as indicated by discriminant function analysis (Table 2). KY populations were classified correctly at a high frequency, but this is partly because the frequency of KY populations was greater than 50%. Therefore, the geographic structure of the phenotypic variation, while present, is not especially pronounced. Bolting date appears to be the most diagnostic character that we measured.

Local adaptation—The regions or populations did not differ significantly in their performance (Table 1, Fig. 4). Neither survival to reproductive maturity nor fruit production by reproductive individuals differed significantly among populations or regions. Therefore, we detected no evidence for local adaptation of KY populations to KY. While most KY populations did have higher than average fitness, a MI population had the highest, and a KY population had one of the lowest. Given the level of variance in performance within populations, our sample had low power to detect significant differences among populations. The difference in performance that could be detected with this sample and nested design, given the observed variance, was 200 fruits. This is greater than the mean number of fruits produced by plants from any population, so variation in performance within populations overwhelmed population differences in performance.

Natural selection on life history—The season in which a seed germinated significantly influenced total lifetime fitness by influencing both survivorship to bolting and fruit production of reproductive individuals (Fig. 5). Only four individuals that germinated in the spring actually survived to produce fruits, and those that did produced few fruits.

For autumn germinants, those that germinated earlier and overwintered at a larger size had a higher probability of surviving to reproduce (Fig. 6). Results of logistic regression indicated no effect of population ($\chi^2 = 11.64$, $P = 0.23$, $N =$

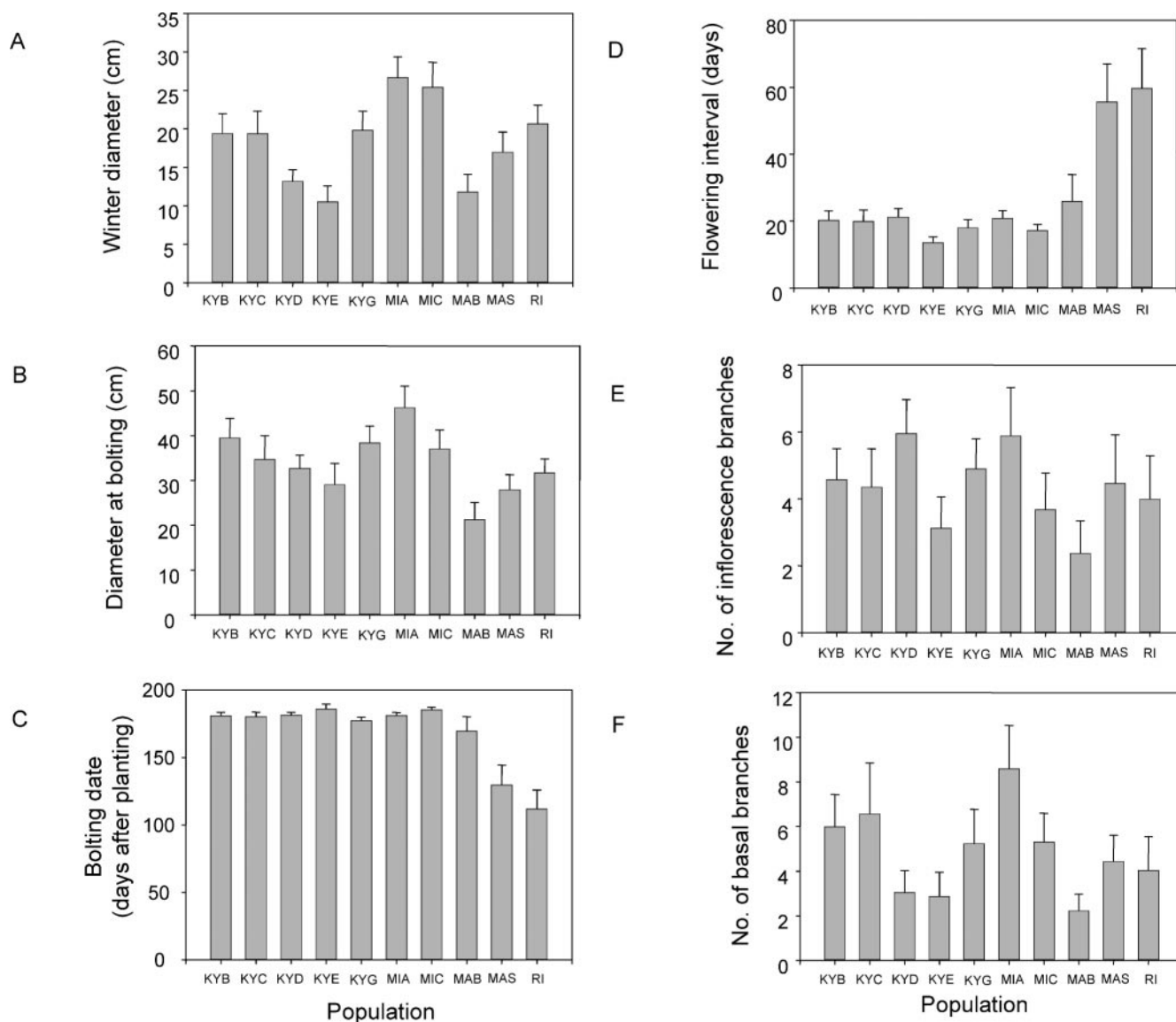


Fig. 3. Population differences in life history characters (A–F) of reproductive plants of *Arabidopsis thaliana*. Mean values are presented for each population. Error bars as in Fig. 1.

TABLE 2. Discriminant function analysis to determine the ability of phenotypes of *Arabidopsis thaliana* to predict geographic region of origin. Standardized variables were used. Prior probabilities were proportional to the frequencies within each region. The linear discriminant function of the parameters is given in the upper portion of the table. $N = 152$.

Trait	KY	MI	NE
Germination date	-3.54	-4.66	-3.15
Winter diameter	0.48	1.12	-0.22
Diameter at bolting	-0.14	-0.21	-1.15
Bolting date	1.10	1.83	-1.57
Flowering interval	-0.12	0.03	-0.47
Inflorescence branches	0.11	-0.04	-0.01
Basal branches	0.05	0.53	0.56
Prior probability	0.54	0.21	0.25
Percent correctly classified	95.12	34.38	39.47

272), no interaction between germination timing and overwinter diameter ($\chi^2 = 0.56$, $P = 0.46$, $N = 272$), but a significant effect of germination timing ($\chi^2 = 11.06$, $P = 0.001$) and overwintering diameter ($\chi^2 = 28.41$, $P = 0.0001$; marginally significant when the non-significant interaction was included in the model) on survivorship to reproduction. Overwinter mortality was substantial. Of those seedlings that survived until the onset of winter, 35% of them died before they could reproduce in the spring. Twenty-nine percent of the plants that bolted in the autumn died over the winter, and 45% of the plants that did not bolt in the autumn died.

Of those plants that survived to bolting, those that were larger at the time of bolting, those that bolted earlier, and those that had more inflorescence and basal branches had higher fitness (Table 3). Significant total selection was also observed on overwintering size (favoring larger individuals) and flowering interval (favoring longer intervals). Selection on overwintering size and flowering interval was caused by correlated

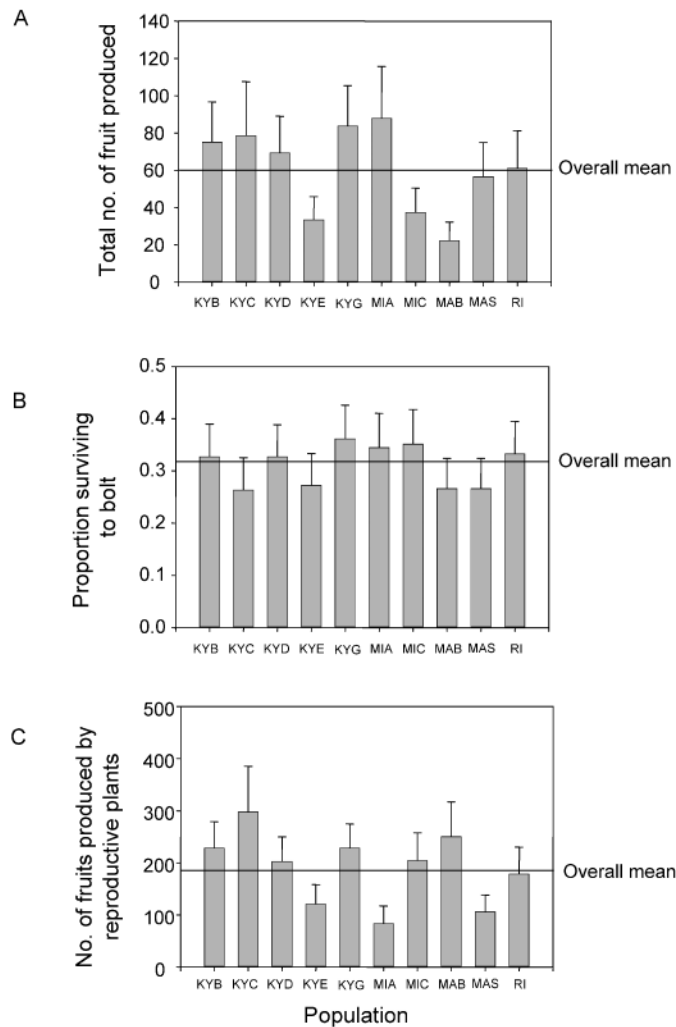


Fig. 4. Performance measures (A–C) of each population of *Arabidopsis thaliana*. Mean values are presented for each population. Error bars represent standard errors not adjusted for multiple comparisons.

selection acting through other characters, because no direct selection on these characters was detected. We also found evidence (after removal of one outlier with extremely high fruit production) that those that germinated later in the autumn produced more fruits if they survived to bolt.

Directional selection on branch production differed significantly among regions and populations, with the strongest selection on inflorescence branches in MI populations and the strongest selection on basal branches in KY populations [KY: β (inflorescence branches) = 0.19, $P < 0.05$; β (basal branches) = 0.71, $P < 0.001$. MI: β (inflorescence branches) = 0.65, $P < 0.001$; β (basal branches) = -0.09, $P > 0.05$. NE: β (inflorescence branches) = 0.32, $P < 0.01$; β (basal branches) = 0.49, $P < 0.001$]. There is also evidence that directional selection on overwintering diameter varied among populations, being positive in most populations but negative in one NE population [MAB β (overwinter diameter) = -0.21, $P < 0.05$], and that directional selection on bolting date was significant only in NE populations [KY: β (bolting date) = 0.31, $P > 0.05$. MI: β (bolting date) = 1.14, $P > 0.05$. NE: β (bolting date) = -0.37, $P < 0.01$]. Selection on flowering

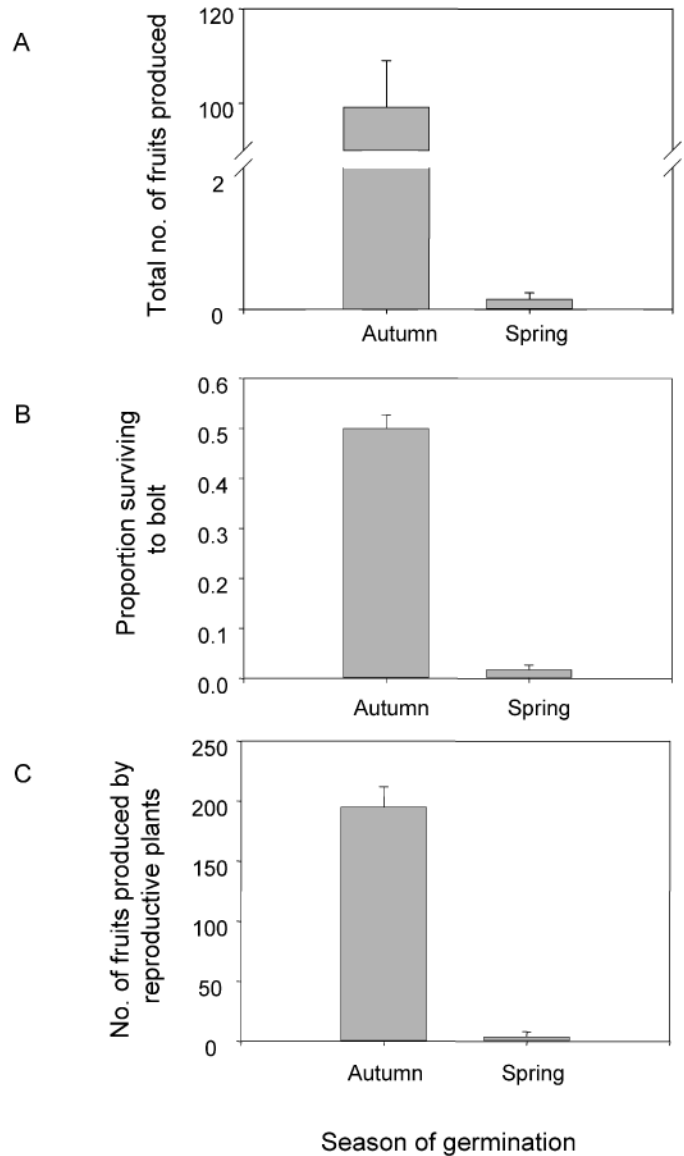


Fig. 5. Fitness differences (A–C) between autumn and spring germinants of *Arabidopsis thaliana*. A. Total lifetime fitness (Kruskal Wallis $\chi^2 = 125.71$, $P < 0.001$, $N = 574$). B. Survivorship to reproduction (Logistic regression $\chi^2 = 60.38$, $P < 0.001$, $N = 574$). C. Fruit production of reproductive plants (ANOVA $F = 9.87$, $P = 0.002$, $N = 179$). Mean values and standard errors are presented.

interval varied marginally among populations, with non-significant selection gradients being negative in NE ($\beta = -0.23$), close to zero in KY ($\beta = 0.02$), and positive in MI ($\beta = 0.75$).

Significant disruptive selection was detected for inflorescence branch production, such that those plants that made an intermediate number of branches had the lowest fitness. In addition, significant correlational selection was detected. Plants with larger diameters at bolting had higher fitness if they also made more basal branches (Fig. 7). Basal branch production had a larger positive effect on fruit production in larger plants than in smaller plants (coefficient = 0.28, SE = 0.14, $P < 0.05$). Also, those plants that had early bolting had

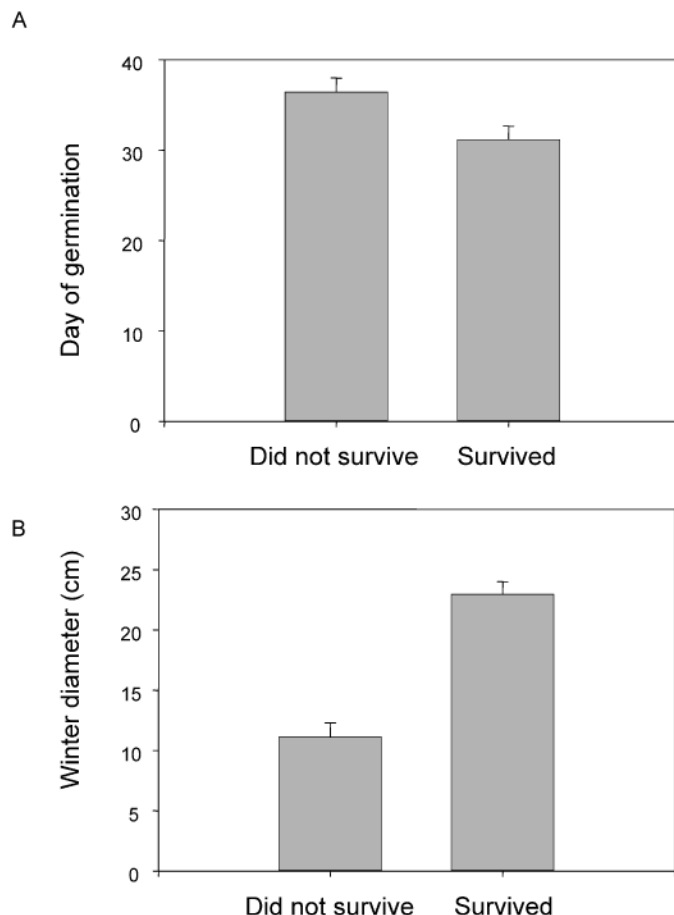


Fig. 6. Differences between reproductive and nonreproductive plants of *Arabidopsis thaliana* in germination timing and overwintering diameter. Germination timing ($F = 6.70$, $P = 0.01$, $N = 350$) and overwintering diameter ($F = 80.84$, $P < 0.0001$, $N = 272$) differed significantly between reproductive and nonreproductive plants. Mean values and standard errors are presented.

higher fitness if they also had shorter flowering intervals (coefficient = 0.65, SE = 0.31, $P < 0.05$; Fig. 8).

Contribution of traits to fitness patterns among regions—As seen earlier (Table 1, Fig. 4), plants from different populations or regions did not differ significantly in performance when grown in this common garden in KY. However, when

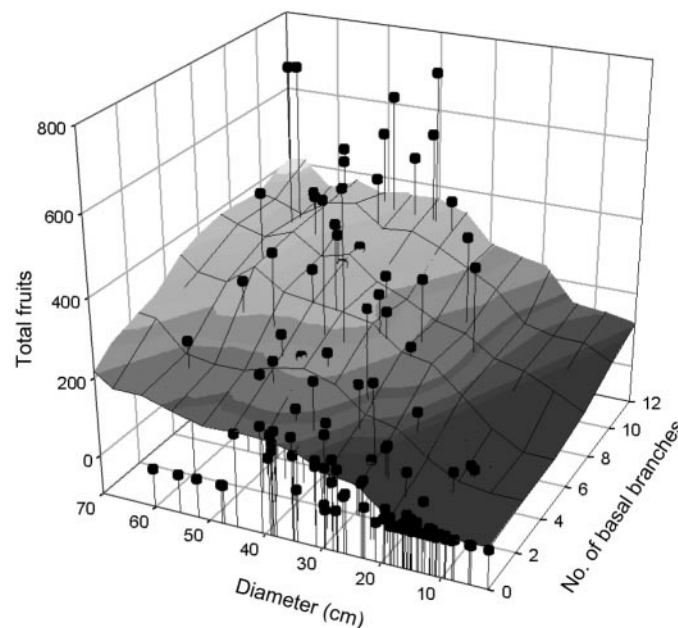


Fig. 7. Correlational selection on diameter and branch production in *Arabidopsis thaliana*. Data are smoothed by a running average of nearest neighbors. Points represent individual observations.

differences in the measured life-history characters were controlled for, significant differences among populations and regions were detected for fruit production by reproductive plants (Table 4, Fig. 9). When life-history differences were controlled for, KY populations had the highest fruit production, and MI populations had the lowest. Differences in size and timing of reproduction and differences in basal branch production all contributed to this pattern (Table 4). The observed higher significance of population differences in performance is partially due to the fact that inclusion of the variables increased the power to detect small differences in reproduction by decreasing the residual variance. With traits included, the experiment had the power to detect differences of two fruits with 97% power, but without traits the power was $<50\%$. While the mean square for the population effect did increase when traits were included, the increase was slight (4.5 vs. 4.7). Thus individual differences in life-history expression appear to have caused variation in performance within populations, leading to large overlap in the performance of populations. At the re-

TABLE 3. Results of phenotypic selection analysis of reproductive plants of *Arabidopsis thaliana*. Only autumn germinants were used since only four spring germinants expressed the phenotypes. Selection differentials, or total selection (S), and selection gradients, or direct selection (β), are shown. Nonlinear selection coefficients estimate the strength of stabilizing (negative coefficients) or disruptive (positive coefficients) selection. F ratios test for significant differences in the strength of selection acting on members of different populations [$F(\text{trait} \times \text{population})$] and different regions [$F(\text{trait} \times \text{region})$]. $N = 152$. Results did not differ when population was included in the model. + $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Trait	S (SE)	β (SE)	Nonlinear (SE)	$F(\text{trait} \times \text{population})$	$F(\text{trait} \times \text{region})$
Germination day	-0.05 (0.08)	0.11 + ^a (0.06)	-0.03 (0.09)	0.88	1.37
Winter diameter	0.32*** (0.08)	0.00 (0.07)	-0.11 (0.07)	1.38 ^a	1.62
Diameter at bolting	0.65*** (0.07)	0.30*** (0.08)	0.06 (0.11)	0.67	2.06
Bolting date	-0.21* (0.08)	-0.18* (0.08)	0.36 (0.23)	0.96	2.44 + ^a
Flowering interval	0.21* (0.08)	-0.08 (0.09)	0.11 (0.08)	0.61	2.59 +
Inflorescence branches	0.44*** (0.08)	0.32*** (0.06)	0.26** (0.10)	3.19**	5.73***
Basal branches	0.66*** (0.07)	0.43*** (0.08)	0.02 (0.12)	1.81 +	7.20***

^a Significant after deletion of one outlier.

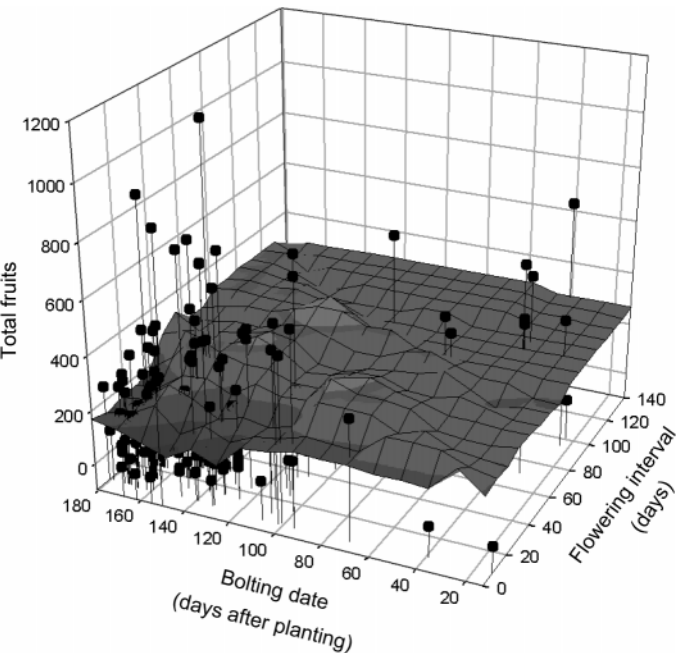


Fig. 8. Correlational selection on bolting time and flowering interval in *Arabidopsis thaliana*. Data are smoothed by a running mean of nearest neighbors. Points represent individual observations.

gional level, however, the difference in power between the two models was not extreme; a difference of two fruits could have been detected among regions at nearly 100% with and without traits included. The mean squares increased substantially in the model that included traits (MS without traits = 1.55; MS with traits = 4.51). This increase in regional differences in performance when traits are included, in addition to decreased variance within regions, indicates that if the regions had not differed in these characters, the local KY populations would have had detectably highest fitness. Therefore, regional differences in timing and size of reproduction apparently compensated for other characters that would have caused plants from foreign locations to perform relatively poorly in KY.

DISCUSSION

We found that North American *Arabidopsis thaliana* harbors significant variation in fundamental life-history traits such as the timing of germination and reproductive initiation. Sev-

eral life-history characters altered the probability of survival to reproductive age and the amount of reproduction of those that survived. No population showed evidence of being optimally adapted to the KY location, because no stabilizing selection was detected. Rather, some populations had favorable phenotypes for some traits but unfavorable phenotypes for others. Surprisingly, we found that the life-history variation did not contribute to differences in performance between populations and regions but rather caused the newly introduced plants to perform as well as plants from the local KY populations. This unusual result suggests that populations from different regions are comparably adapted to the KY environment but through different mechanisms; by compensating for deficiencies in other traits, life-history variation appears to contribute to the ability to colonize new areas rather than limit that ability through specialized adaptation to specific local environmental conditions.

Life-history variation—Life-history characters varied among populations, but the geographic structure of the variation, while detectable, was not especially pronounced. Much variation was found among populations within regions, indicating that *A. thaliana* can express local variation even within a larger geographic pattern of life-history variation. Traits that varied regionally included size and timing of reproduction. The pre-reproductive characters of germination date and overwintering size varied substantially at the local scale.

In contrast to field observations of local populations in situ, we found no significant variation among populations in the proportion of spring germinants. In natural populations in their native location, spring germination has been seen to be between 2% to less than 10% in most KY locations, but it has been documented to be up to 54% in some locations in New England (K. Donohue, unpublished data). Therefore a lower proportion of spring germination was seen in this study than is typically observed in the field in New England.

The results of this study indicate that two different mechanisms may contribute to spring germination and the “spring annual” life history. First, we found a strong positive association between germination timing in the autumn and the proportion of spring germination. The spring germination observed in this study therefore may simply be a continuation of severely postponed autumn germination. Seeds may require a certain number of days of cold to germinate (Baskin and Baskin, 1998; Nordborg and Bergelson, 1999), and this cumulative cold requirement may cause some seeds to postpone germination until they experience prohibitive temperatures for

TABLE 4. Contribution of traits of *Arabidopsis thaliana* to fitness similarities between members of different populations and regions. Analysis of covariance compared differences between populations with (“All traits”) and without (“No traits”) traits as covariates and with each trait as a covariate. *N* = 152. + *P* < 0.10, * *P* < 0.05, ** *P* < 0.01.

Trait	Fruit production		Survival	
	<i>F</i> (Population)	<i>F</i> (Region)	<i>F</i> (Population)	<i>F</i> (Region)
No traits	1.48	0.49	3.72	1.13
All traits	1.97*	5.67**	11.66	3.82
Germination day	1.75	0.48	4.55	0.46
Winter diameter	1.12	1.35	8.62	2.05
Diameter at bolting	1.36 +	2.56 +	—	—
Bolting day	1.71	3.88*	—	—
Flowering interval	1.35	2.03	—	—
Inflorescence branches	1.26	0.10	—	—
Basal branches	1.15	2.98 +	—	—

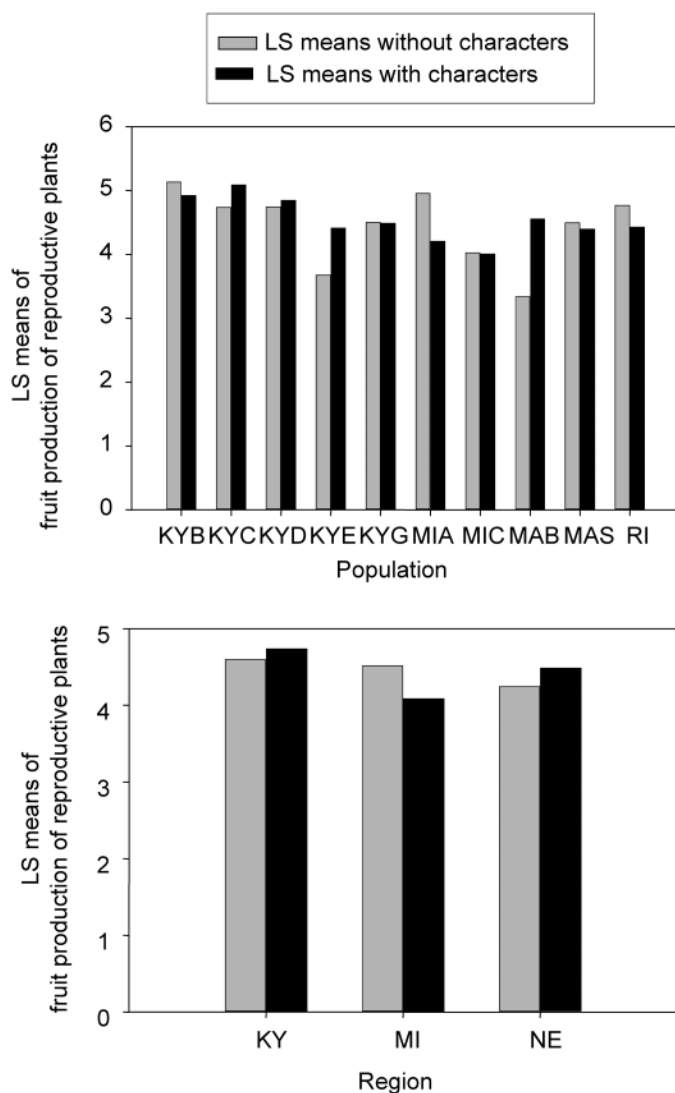


Fig. 9. Least-square (LS) (residual) means of fruit production of reproductive plants of *Arabidopsis thaliana* from different populations (upper; not nested in region) and regions (lower) without and with life-history character differences controlled for.

germination in the winter. Germination would then occur only after temperatures become permissive again in the spring.

Interestingly, we found significant variation among populations in their timing of germination in the autumn even though we did not detect variation in the proportion of spring germination. This indicates that populations may differ genetically in their cold requirement for germination. This interpretation is supported by subsequent studies of germination of seeds matured in a common environment in which the populations differed significantly in the proportion of seeds that germinated without cold stratification (up to 72% difference; $F = 11.80$, $P < 0.0001$; C. Griffith, C. Polisetty, K. Donohue, unpublished results). These results suggest that if populations were dispersed into more northerly latitudes in which prohibitive winter temperatures arrived earlier, populations may exhibit higher proportions of spring germination, and variation in the proportion of spring germination may then vary genetically among populations. Counterintuitively, it may actually

be those populations that have responded to selection for delayed autumn germination (due perhaps to protracted summer drought conditions associated with warmer climates) that would exhibit a greater proportion of spring germination if they happened to be dispersed to more northerly latitudes. Rather than being an adaptive mechanism to escape overwinter mortality during conditions of harsh winters, spring germination may be simply a correlated response to selection for delayed autumn germination.

The second possible mechanism for spring germination includes maternal effects on germination. The season of seed maturation and dispersal determines the seasonal cues that seeds are exposed to and can influence the morphology and behavior of the seeds (Junttila, 1971; Gutterman, 1978, 1994; Pourrat and Jacques, 1978; Lacey and Pace, 1983; Lacey, 1991, 1996). As mentioned previously, spring germination in New England is more prevalent in the field than was observed in this study conducted in KY. In this study, only seeds collected in the spring were used. However, New England populations have also been observed to flower and set seeds in autumn (K. Donohue and L. Dorn, personal observation). Even when grown in KY, the New England populations exhibited a pronounced tendency to initiate reproduction in the autumn. This habit is genetically based to some degree, because subsequent studies, conducted under growth chamber conditions and controlling for maternal effects, detected significant differences among these populations in the proportion of plants flowering with no rosette vernalization (up to 75% difference), or the proportion of plants flowering with only one month of rosette vernalization (up to 64% difference; $\chi^2 = 91.68$, $P < 0.001$). Therefore, New England populations are more likely to mature seeds in the autumn. A previous study of germination in *A. thaliana* conducted on recombinant inbred lines under controlled conditions (Munir et al., 2001) demonstrated that seeds matured under autumn-like seasonal conditions—namely seeds matured under short days which subsequently receive cold stratification as they would during winter—germinate to high percentages. Thus, autumn seasonal conditions of seed maturation can promote spring germination, even without the typical summer warm afterripening period required by many winter annuals (Baskin and Baskin, 1972, 1974, 1983, 1990). The high proportion of spring germination in New England may therefore not be caused by genetic differences in germination requirements per se, but rather by genetic differences in the probability of experiencing the seasonal maternal effects that induce spring germination, through genetic variation in flowering time.

Spring germination and the “spring annual” life history can therefore be caused by (a) a cumulative cold requirement for germination, followed by the early onset of prohibitive winter temperatures that results in the postponement of germination until permissive temperatures are experienced in the spring, or (b) seasonal maternal effects accompanying autumn seed maturation that promote germination in the spring. The degree to which these two mechanisms account for variation in spring germination observed in the field requires further study of populations grown under New England seasonal conditions. Because of the importance of germination timing to subsequent life-history expression (Donohue, 2002), such studies of mechanisms of seasonal dormancy would contribute to our understanding of life-history variation expressed at all life stages.

In summary, the life-history variation observed among *A. thaliana* populations in situ cannot be explained entirely by

genetic differences among regions or populations in life history characters. Rather, genetically based differences interact with local seasonal conditions to determine the life history that is expressed in the field.

Natural selection on life-history characters—Several life-history traits that we measured influenced survival or fruit production. Plants that germinated earlier in the autumn and overwintered at a larger size had a higher probability of surviving to initiate reproduction. Postponing germination until spring caused an extreme reduction in the probability of survival, indicating that the spring annual life history that is frequently observed in New England was not adaptive in KY, at least during that year, despite overwinter mortality (see also Donohue, 2002). We found evidence that, of those that did survive the winter, later germination in the autumn was associated with somewhat higher fruit production. Therefore, selection on germination timing might act differently at different life stages.

Earlier bolting and bolting at a larger size was associated with the highest fruit production, as has frequently been observed in *A. thaliana* (Clauss and Aarssen, 1994; Mitchell-Olds, 1996; Dorn et al., 2000). Early bolting permits fruit maturation before the summer drought, while bolting at a larger size could insure that more resources are available for reproduction. Total selection was stronger than direct selection on both characters, indicating that selection on correlated characters reinforced direct selection on these characters. In particular, selection favoring increased branch production would reinforce selection favoring larger diameters, because the two were positively correlated ($r = 0.68$, $P < 0.05$ for inflorescence branches; $r = 0.87$, $P < 0.01$ for basal branches).

Selection on bolting time depended on the interval between bolting and flowering, as indicated by significant correlational selection between the two traits. The positive correlational selection between bolting time and flowering interval is most likely because most of the variance in the relationship between bolting and flowering interval within this sample was due to those plants, primarily from New England, that bolted in the autumn but did not flower until spring. Earlier bolting was favored most strongly in New England populations, a result which could be interpreted as selection favoring autumn bolting. Autumn bolters did in fact produce more fruits than spring bolters on average (213 ± 228 for autumn bolters vs. 187 ± 220 for spring bolters). The pattern of correlational selection suggests that those autumn bolters that flowered the earliest in spring had higher fitness. Indeed, delayed flowering would not give any reproductive advantage to those plants that bolted early since allocation to vegetative meristems stops at the time of bolting.

Plants that produced many branches also produced more fruits, although those that produced the fewest inflorescence branches did not have the lowest fitness, as indicated by significant disruptive selection. The smallest plants therefore appeared to set more fruits if they did not allocate resources to branches. No tradeoff was observed between inflorescence branch and basal branch production ($r = 0.49$, $P > 0.05$), so larger plants overall produced more fruits. Increased basal branch production had particularly strong positive effects on plants that were larger at the time of bolting, and these plants were able to make the largest number of basal branches. Smaller bolters did not gain as much by making more basal

branches, in part because they were able to make fewer of them.

The strength of natural selection sometimes depended on the population or region the plant was from. In particular, selection on inflorescence branches was strongest in MI populations, and selection on basal branches was strongest in KY populations. The differences in the strength of selection among populations can be attributed in part to differences in the opportunity for selection caused by higher phenotypic variance in some regional samples than in others. The strong selection for basal branch production in KY populations appears to be attributable to the fact that they inhabit a region on the adaptive landscape in which increased branch production has a strong effect on fitness (that is, they have larger diameters), and they have a large variance in branch number. The marginally significant difference among regions in the direction of selection on flowering interval is due to the fact that NE populations bolted in the autumn, and autumn bolting tended to induce selection for shorter flowering intervals (as indicated by the pattern of correlational selection). The other populations flowered in the spring, and selection on flowering interval was negligible (in KY) or was in the opposite direction (in MI). Thus when bolting differs among individuals from different regions, selection on flowering interval can differ among individuals from different regions as a consequence.

Local adaptation—If the KY populations had been exposed to and responded to past natural selection that was specific to conditions in KY, then one would expect that plants from the KY populations would perform better in an experiment conducted in KY. However, we found no significant variation among populations in either survival or fecundity. All populations performed variably but equally well when grown in a common environment in KY. This suggests either that all populations have been exposed to similar selective influences across a broad geographic range, or that no population, including those from KY, is locally adapted to KY conditions due to lack of adequate response to natural selection after introduction.

The similarity in performance of all populations may reflect a similarity in the past natural selection experienced by the ancestors of all the populations. Selection may act in similar directions in different populations because the habitat of *A. thaliana* may be fairly similar over a wide geographic area. *Arabidopsis thaliana* frequently occurs in open areas such as fields, yards, roadsides, or agricultural field margins (Fernald, 1950; Radford et al., 1968; Strausbaugh and Core, 1977; Correll and Johnson, 1979; Gleason and Cronquist, 1991). Such open areas could experience similar microclimates, regardless of their geographic locations. On a broader geographical scale, in contrast, the locations of the seed sources are under different climatic regimes, as defined by the Koppen–Geiger climatic classification. Kentucky and Rhode Island are described as mild, moist and warm climates, the Michigan locations as severe, moist and warm, and the Massachusetts locations as severe, moist, and cold (maps in Howarth et al., 1998). The difference in climate may not be as important to the performance of *A. thaliana* as the similarity in microenvironment experienced by all populations.

The lack of evidence for local adaptation may also be because even the KY populations are not especially adapted to KY conditions. That is, instead of all populations displaying a comparable degree of adaptation to KY, all populations could

be displaying a comparable degree of maladaptation to KY. The lack of stabilizing selection indicates that no population is optimally adapted. Populations that had favorable phenotypes for some characters had unfavorable ones for others. For example, MI populations were the largest at the time of bolting, which was favorable, but they bolted later, which was unfavorable. The opposite was true of NE populations. Stabilizing selection is much less frequently documented than directional selection in most systems (Kingsolver et al., 2001), and this result, when statistically substantiated, is often interpreted as evidence for genetic constraints on achieving optimal phenotypes (Lande and Arnold, 1983; Arnold and Wade, 1984). The well-known tradeoff between size and timing of reproduction in *A. thaliana* (Mitchell-Olds, 1996) does appear to have constrained performance in these plants. In historically mobile species such as *A. thaliana*, however, the lack of adaptation is also likely to be due to the non-equilibrium status of many introduced populations that simply haven't had time to adapt to new conditions.

We still do not know whether the observed regional and population differentiation of life history traits represents historical processes of relatedness and colonization patterns or adaptation to local or regional conditions. For example, the lack of autumn flowering plants in KY and MI populations could be because autumn-flowering genotypes never dispersed into those regions or because they have been selected against in those regions. While our results did not find evidence of stronger selection against life-history strategies exhibited by foreign populations, this experiment measured selection in only one year and under one set of experimental conditions. Longer-term selection studies under different experimental conditions would provide more information on the quality of natural selection on life history traits that vary among populations. In addition, genetic information on the structure of relatedness among populations would provide valuable information on the importance of historical processes in creating geographic patterns of life histories.

Even if the lack of evidence for local adaptation is due to purely historical factors in populations not in adaptive equilibrium, we nevertheless found evidence that life-history differences among populations do in fact influence the relative performance of populations. All populations performed comparably despite natural selection on life histories and despite population differentiation in life-history traits. This result and the significant correlational selection imply the fitness of a plant depends on the particular combinations of characters that the plant expresses. While variable life histories can be under natural selection, different combinations of life-history and other characters can lead to similar fitness of different populations.

In fact, we found that differences in life-history expression actually contributed to the similarity of performance of plants from different regions. That is, life-history characters compensated for deficiencies in other characters that were not included in the study. Variation among regions in the timing of bolting, size at bolting, and basal branch production all contributed to similarity of performance. For example, the ability of plants from NE to bolt in the autumn (which was associated with higher fitness) was able to compensate for deficiencies in other traits that would have decreased their fitness. One such trait may be slower growth rates in the spring. NE plants that did not bolt in the autumn were smaller at bolting than the other populations (24 cm compared to 42 cm for MI plants and 35 cm for KY plants). Because larger plants had higher fitness,

NE spring bolters had lower fitness than the other plants, but NE autumn bolters had higher fitness. Thus bolting in the autumn could have compensated for slower growth rates in the spring, although spring growth rate was not measured in this study. Similarly, MI plants had the largest diameters and produced the most basal branches (7.0 compared to 4.7 for KY and 3.6 for NE), yet they did not have higher fitness than the others. MI plants therefore appear to have some unmeasured traits that were disadvantageous in KY, and their size advantage compensated for those deficiencies. These observations indicate that, while all *A. thaliana* populations performed similarly, they did so because they expressed different combinations of characters. These combinations of characters can act in an additive manner to preserve fitness, as is the case of autumn bolting apparently compensating for slower growth rates, or in a nonadditive manner, as in the case of the observed correlational selection. In particular, basic life-history traits appear to compensate for deficiencies in other traits.

Character combinations therefore appear to be important determinants of performance in novel locations within the range of this highly mobile species. *Arabidopsis thaliana* is highly selfing (Abbott and Gomes, 1989). Rare outcrossing events followed by many generations of selfing would effectively create suites of recombinant inbred lines that contain many different combinations of traits from the hybridizing parental lines. The results from this study suggest that such patterns in mating system result in populations with different viable combinations of characters that are comparably adapted to environments that are distributed over a broad geographic range. Such a mating system pattern may be a particularly effective manner of adaptation to broad geographic ranges while maintaining genetic variation among populations.

Conclusion—We found evidence for genetic differences among populations in fundamental life-history traits, but life-history expression in situ is likely to be mediated by local environmental conditions as well. Despite differences in life history, and despite selection on life-history traits, we found no significant differences in the performance of different populations from many locations in a common environment in KY. The lack of local adaptation and stabilizing selection suggests that these populations may not be in adaptive equilibrium, a result that accords with the suspected historical mobility of the populations. Different populations expressed different combinations of life-history characters, and life-history traits apparently compensated for deficiencies in other traits. Thus different combinations of characters caused plants from different populations to perform equally well. In highly inbreeding and mobile species such as *A. thaliana*, variation in life-history expression may contribute to its ability to expand into novel locations while maintaining genetic variation at local and regional scales.

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