Lagging adaptation to warming climate in *Arabidopsis thaliana*

Amity M. Wilczek*,b, Martha D. Cooper*, Tonia M. Korves*,c, and Johanna Schmitt*d,1

*Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912; bDepartment of Natural Sciences, Deep Springs College, Big Pine, CA 93513; cData Analytics Department, The MITRE Corporation, Bedford, MA 01730-1420; and dDepartment of Evolution and Ecology, University of California, Davis, CA 95616

This contribution is part of the special series of Inaugural Articles by members of the National Academy of Sciences elected in 2008.

Contributed by Johanna Schmitt, April 8, 2014 (sent for review June 14, 2013; reviewed by Steven J. Franks and Julie R. Etterson)

If climate change outpaces the rate of adaptive evolution within a site, populations previously well adapted to local conditions may decline or disappear, and banked seeds from those populations will be unsuitable for restoring them. However, if such adaptational lag has occurred, immigrants from historically warmer climates will outperform natives and may provide genetic potential for evolutionary rescue. We tested for lagging adaptation to warming climate using banked seeds of the annual weed *Arabidopsis thaliana* in common garden experiments in four sites across the species’ native European range: Valencia, Spain; Norwich, United Kingdom; Halle, Germany; and Oulu, Finland. Genotypes originating from geographic regions near the planting site had high relative fitness in each site, direct evidence for broad-scale geographic adaptation in this model species. However, genotypes originating in sites historically warmer than the planting site had higher average relative fitness than local genotypes in every site, especially at the northern range limit in Finland. This result suggests that local adaptive optima have shifted rapidly with recent warming across the species’ native range. Climatic optima also differed among seasonal germination cohorts within the Norwich site, suggesting that populations occurring where summer germination is common may have greater evolutionary potential to persist under future warming. If adaptational lag has occurred over just a few decades in banked seeds of an annual species, it may be an important consideration for managing longer-lived species, as well as for attempts to conserve threatened populations through ex situ preservation.

**Significance**

If adaptive evolution cannot keep up with rapid climate change, populations and even species may decline or go extinct. Such adaptational lag is predicted, but evidence is scarce. We tested for lagging adaptation to warming climate in banked seeds of the annual weed *Arabidopsis thaliana* in common garden experiments in four sites across the species’ native European climate range. Genotypes originating in climates historically warmer than the planting site had higher relative fitness than native genotypes in every site. This result suggests that local adaptive optima have shifted rapidly with recent warming across the species’ native range, and that the potential for adaptational lag deserves consideration in conservation and management decisions for many species.

Rapid climate change has already caused species range shifts and local extinctions (1) and is predicted to have greater future impacts (2). As the suitable climate space for a species shifts poleward (3), populations previously well adapted to the historical climate in a particular region may experience strong selection to adapt to rapidly warming local temperatures (4–10). Rapid evolutionary response to climate change has already been observed (11, 12), but it remains unclear whether evolutionary response can keep pace with rapidly changing local adaptive optima (6, 8, 13–15). If local adaptation is slower than the rate of climate change, the average fitness of local populations may decline over time (7, 14, 16, 17), possibly resulting in local extinctions and range collapse at the warmer margin. Where such lag exists, we expect that local seeds banked for conservation may no longer be well adapted to their sites of origin (18). However, such adaptational lag may be mitigated by migration or gene flow from populations in historically warmer sites if those populations are better adapted to current conditions in a site than local populations (8, 13, 19, 20). Although adaptational lag has been predicted (4–6, 8, 14, 15, 19, 21, 22), the distinctive signature of mismatch between local population performance and current climate optima has not yet been explicitly demonstrated in nature.

Despite evidence for local adaptation in many organisms (23), there have been few explicit tests for the role of specific climate factors in shaping local fitness optima (4, 9, 13). Such tests require growing many genotypes from populations spanning a range of climates in common gardens across a species’ range to decouple climate of origin from geographic variation in other selective factors (4, 6, 14). If adaptation to local climate has occurred, then genotypes from climates similar to each planting site are expected to have high fitness in that site relative to genotypes from dissimilar climates (6). However, if local adaptive optima have shifted with rapid warming trends over the last 50 y, we expect that banked genotypes from historically warmer climates will have higher fitness within a site than banked genotypes of local origin (6, 21, 22).

We tested for lagging adaptation to climate using *Arabidopsis thaliana*, a naturally inbreeding annual species that inhabits a broad climate space across its native Eurasian range (24). *A. thaliana* exhibits strong circumstantial evidence of climate adaptation, including geographic clines in ecologically important life-history traits (25–28) and in candidate genes associated with these traits (29, 30), as well as genome-wide associations of single nucleotide polymorphisms with climatic factors (31–34). To test explicitly for local adaptation to climate we measured the lifetime fitness of more than 230 accessions from banked seeds originating from a broad range of climates in replicated field experiments in four sites across the species’ native climate range.
Results

Absolute fitness varied dramatically across our field sites in Spain, England, Germany, and Finland, and among spring, summer, and autumn cohorts in our English site. Average fecundity was highest in our Halle, Germany site and lowest in Oulu, Finland (Dataset S1 and Table S1). Differences in absolute fitness among sites may reflect differences in edaphic factors, environmental stresses, or biotic factors as well as climate and growing season length. To test for evidence of regional adaptation, we therefore examined genotype relative fitness within each planting. Relative fitness is the basis for selection among accessions within any particular growth environment (35) and is a good predictor of the outcome of selection across heterogeneous environments (36). Accessions from different regions differed significantly in relative fitness within each planting site (Fig. 2). Iberian accessions performed well in Spain, UK accessions in England, and German accessions in Germany, suggesting broad-scale regional adaptation (Fig. 2). However, although Nordic accessions achieved their highest relative fitness in our most northern, Finnish planting location, their relative fitness in Oulu was still lower than that of German accessions (Fig. 2 and Fig. S1). Relative fitness of accessions declined significantly and monotonically with increasing physical distance of the site of origin from each common garden site except in Finland, where accessions with the highest average fitness came from locations on average ~1,000 km distant from the garden site (Fig. S2).

Fitness was significantly heritable within each of the experimental plantings, providing evidence of genetic variation among accessions (Table S2). However, the genetic basis of fitness varied among planting locations. Genetic correlations in fitness between plantings in Spain, England, and Germany were weakly positive or nonsignificant. Accession mean fitness in Finland was not significantly correlated with fitness in any other site, except for a negative correlation with fitness in Spain (Table S2), suggesting a genetic tradeoff in performance between the northern and southern range limits. Correlations in accession mean fitness across years were moderate but significant ($P < 0.05$) for winter annual cohorts in Spain ($r = 0.43$) and Germany ($r = 0.48$), where a subset of accessions was planted in both 2006 and 2007.

To test whether regional differences in relative fitness were associated with climate, we regressed relative fitness within each experimental planting on absolute climatic distance of an accession’s site of origin from the planting site. In Valencia, Norwich, and Halle, relative fitness declined significantly with climatic distance of an accession’s site of origin from the planting site (Fig. 3 and Tables S3 and S4), suggesting a role for climate in regional adaptation. In Finland, however, a significant quadratic term indicated that genotypes from climates most similar to the historical climate for the planting site did not have the highest relative fitness (Fig. S3).

Absolute climate distance cannot distinguish asymmetries in fitness between accessions derived from areas colder and warmer than the growth climate, although such asymmetries are predicted under adaptational lag to warming temperature. To test for such lag, we regressed relative fitness in each planting against mean annual and seasonal temperatures in the site of origin. Relative fitness was significantly associated with mean annual and seasonal temperatures in the site of origin in all four planting sites, and in all three seasonal plantings within England (Fig. 3, Figs. S4 and S5, Table 1, and Table S3). However, the optimal native temperature varied across sites and seasons and was in every case warmer than the estimated historical climate of the common garden site. In the autumn plantings in Finland and Germany (2006), as well as the spring planting in England, there was a significant quadratic relationship between fitness and mean annual, April, and October temperature in the site of origin, with accessions originating in sites with intermediate temperatures having higher relative fitness than accessions from warmer or cooler sites. In Spain, at the southern range limit, as well as in the Norwich autumn and summer plantings, relative fitness increased linearly with mean temperature in the site of origin, such that the “optimum” native temperature was at or beyond the warmest values in our sampled population range (Table 1, Table S4, Fig. 3, and Figs. S4 and S5). In Spain in 2007, accessions from warmer climates of origin had higher fitness, as observed for the larger sample in 2006 (Tables S3 and S4). In Germany, we saw similar estimated effect sizes of temperature for the 2 y (Table S4), although our reduced sample size in 2007 provided little power to detect the quadratic effects on fitness observed at this site with the larger 2006 accession sample.

Across the four sites, the optimal native temperature for the autumn cohort was lowest in Finland, followed by Germany, then
England and Spain, as expected if there is a history of local adaptation to climate across the species range. However, in each case the optimal native temperature was higher than the historic temperature in the planting site, but similar to the actual April and October temperatures recorded on site during the experiment (Table 1, Fig. 3, and Fig. S5) (37). We observed a similar mismatch between the latitude of common garden sites and the optimum native latitude of origin estimated from the accessions in all of the plantings. The optimal latitude of origin decreased from Finland to Germany and England, but was always south of the actual latitude in each planting site in both 2006 and 2007 (Table 1 and Table S3). Thus, genotypes from southern populations in historically warmer climates had higher average fitness than genotypes from the local latitude in every planting site.

We also observed differences in optimal mean native temperatures and latitudes among seasonal cohorts in England, demonstrating that for annual plants adaptation to climate can depend on the growth season. In the Norwich summer and autumn plantings, where seedlings experienced warm temperatures for several months, selection monotonically favored accessions originating in warmer climates. In contrast, in the cooler spring planting, accessions originating in sites with a mean April temperature of 11.4 °C had higher relative fitness than accessions from warmer or cooler climates. This optimal native temperature was warmer than the historical mean for the site, but very similar to the actual April temperature recorded during the experiment (Table 1). Thus, selection can favor adaptation to different thermal environments in different seasonal cohorts within a site.

The accessions in this study were banked in the stock center over a period of nearly 70 y. If these collections were collected uniformly in space and time across that period, we might expect that accessions collected earlier would show greater adaptational lag than more recently collected populations from the same region. Unfortunately it was not possible to test this prediction using our entire sample, because different geographic regions were largely sampled in different decades, with early collections concentrated in western and central Europe and more recent collections concentrated in other parts of the species range (Dataset S1). We found no association between date of collection and fitness in a core set of 56 accessions from Germany, the region that spanned that largest range of collection dates (1939–1993).

Discussion
Our results provide evidence for broad-scale adaptation to regional climate across *A. thaliana*’s native European range as well as for adaptational lag. In all of our experimental plantings, southern “immigrants” from historically warmer climates had higher relative fitness on average than local genotypes, particularly at the northern range margin in Finland. These results suggest that climatic optima for *A. thaliana* populations have shifted rapidly since the collection of the accessions used in our experiment. The observation of adaptational lag over a few decades in banked seeds of a short-lived annual plant suggests that such lag should be considered in planning for conservation and management of many species.

On a broad regional scale, local genotypes on average had higher relative fitness than genotypes from other regions in every planting site except Finland, at the northern range limit (Fig. 2). Nevertheless, the relative fitness of Nordic genotypes was higher in Finland than in any other site, suggesting that they were best adapted to northern conditions (Fig. S1). For example, in the summer planting in Norwich, many Nordic accessions grew
vegetatively but failed to flower, possibly because they did not receive sufficient chilling to satisfy their vernalization requirements (38). Conversely, accessions from the Iberian peninsula had low survival in Finland, possibly due to low cold tolerance (29). Thus, different selective mechanisms may contribute to adaptation in different geographic regions (31, 32, 39–41). These results are consistent with evidence for adaptation on a broad geographic scale in a wide range of species (23, 42–45). However, the wide geographic diversity of accessions available for *A. thaliana* also permitted us to test explicitly for a signature of adaptation to climate (4, 13, 14) and explore the genetic basis of local adaptation.

The weak genetic correlations we observed between different planting sites suggest regional differences in the genetic basis of fitness in *A. thaliana*. In particular, fitness in Finland was weakly correlated with fitness in the other sites and displayed a negative genetic correlation with fitness in Spain. Local adaptation in our most northern site may thus have a distinct genetic basis and contribute to a tradeoff between adaptation to local environments at the northern and southern climatic range limits of *A. thaliana*. This quantitative genetic evidence for local adaptation is corroborated by results from a genome-wide scan showing that SNP alleles associated with fitness differed among these same sites, and that alleles conferring greater fitness within a site were locally abundant and climatically differentiated relative to genomic controls (31).

This study provides, to our knowledge, the first direct field test of regional climate adaptation in *A. thaliana*, although several previous studies have measured the fitness of natural accessions in the field in this species (26, 28, 39, 41, 46–51). Reciprocal transplant experiments between northern and southern sites show evidence of local adaptation but were not designed to distinguish the role of climate (41). We tested for adaptation to climate by deploying a large geographically diverse sample in the future (67), suggesting that warm years like those of our experiment will be increasingly common in the future. If so, continued directional shifts of local fitness optima are likely, and gene flow or migration from historically warmer regions could increase mean population fitness (14, 16, 19, 22). Short-term climatic variation may help to maintain standing genetic variation in climatic tolerance within populations and allow introgression of warm-adapted traits from southern migrants during warm years or seasons. However, genetic potential for adaptation to track warming temperatures at the southern range limit may be limited (4, 14, 16).

Climatic optima also shifted among seasonal cohorts within the Norwich site. Such seasonal variation in selection may help to maintain genetic variation in climatic tolerance in populations with multiple generations per year. Thus, populations occurring where summer germination is common may have greater potential for adaptation to future warming. Germination timing in itself is likely to contribute to climate adaptation, as suggested by observations of clinal variation (26, 30, 68). However, because our experimental design required us to synchronize germination,

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Table 1. Patterns of selection on climate of accession origin demonstrate geographic variation in selection and lagging adaptation to temperature

<table>
<thead>
<tr>
<th>Location and season</th>
<th>United Kingdom</th>
<th>Germany</th>
<th>Spain</th>
<th>Finland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature, °C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historic mean annual</td>
<td>10.0</td>
<td>10.0</td>
<td>10.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Optimal mean annual</td>
<td>&gt;16</td>
<td>13.9</td>
<td>&gt;16</td>
<td>12.5</td>
</tr>
<tr>
<td>Historic April</td>
<td>7.7</td>
<td>7.7</td>
<td>7.7</td>
<td>8.1</td>
</tr>
<tr>
<td>Growth April</td>
<td>11.4</td>
<td>11.4</td>
<td>11.4</td>
<td>11.8</td>
</tr>
<tr>
<td>Optimal April</td>
<td>&gt;15</td>
<td>11.4</td>
<td>&gt;15</td>
<td>11.2</td>
</tr>
<tr>
<td>Historic October</td>
<td>11.0</td>
<td>11.0</td>
<td>11.0</td>
<td>9.6</td>
</tr>
<tr>
<td>Growth October</td>
<td>13.7</td>
<td>13.7</td>
<td>13.7</td>
<td>13</td>
</tr>
<tr>
<td>Optimal October</td>
<td>&gt;17</td>
<td>14.8</td>
<td>&gt;17</td>
<td>13.7</td>
</tr>
<tr>
<td>Latitude, ° N</td>
<td>52.6</td>
<td>52.6</td>
<td>52.6</td>
<td>51.5</td>
</tr>
<tr>
<td>Optimal latitude, ° N</td>
<td>43.7</td>
<td>46</td>
<td>&lt;37</td>
<td>46.8</td>
</tr>
</tbody>
</table>

Historic temperature data are based on 30-y climate normals, and temperatures from the year of growth are based on hourly air temperature averages made at on-site weather stations. Optimal values of temperature and latitude of accession origin were determined from selection analyses of field-measured fitness (Tables S3 and S4).

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we could not assess the contribution of this life stage to the adaptational lag we observed.

Whether evolution can drive adaptation in the face of future climate change will depend upon the heritability, genetic covariance structure, and plasticity of adaptive traits within populations, as well as migration rates (4–7, 10, 21). Our results suggest that high standing genetic variation and/or substantial gene flow from more southern A. thaliana populations will not be necessary for adaptive evolution to keep pace with predicted rates of future warming. The lagging adaptation to warming temperatures that we observed for A. thaliana occurred over just a few decades, suggesting that similar lags may be likely for other plant species conserved in ex situ seed banks. Studies designed to measure rates of adaptation (e.g., ref. 69), and to compare measured evolutionary rates with rates of climate change (15, 70), will be vital to a fuller understanding of the importance of adaptational lag (4–7, 10, 19, 21). Nonetheless, the rapidly shifting climate optima observed for this annual species suggest that adaptational lag is likely to occur within individual lifetimes for some longer-lived species. The possibility that climatic optima of local populations may not keep pace with rapid climate change deserves consideration in future forestry and conservation management decisions.

**Methods**

**Common Garden Experiments.** During the years 2006–2008, we measured real-time fitness in the field with a geographically diverse panel of A. thaliana accessions in four common garden sites spanning the species’ native European climate range: Oulu, Finland; Norwich, United Kingdom; Halle, Germany; and Valencia, Spain (Fig. 1). We grew a panel of A. thaliana accessions (ecotypes) derived from the US and European stock centers as well as recently collected and bulked seed from Central Asian populations contributed by K. J. Schmid (University of Hohenheim, Stuttgart, Germany) (71, 72) (Dataset S1 and Fig. 1). Accessions used in this experiment were collected from wild populations between the late 1930s and 2002, with most ecotypes having been sampled from 1939 to 1991 (http://arabidopsis.org) (73) and (Dataset S1). Using these banked seeds from stock center-derived inbred lines (accessions or “ecotypes”), originally collected from natural populations, it is possible to measure lifetime fitness of replicated individuals in multiple locations. Seeds for the field experiment were taken from a common bulking generation in which all accessions were grown at 20 °C with 14-h days.

We planted between 15 and 20 replicates of each accession in a randomizod block design in four common garden sites spanning the climate range of A. thaliana: an ex situ active distribution (Oulu, Finland; Norwich, United Kingdom; Halle, Germany; and Valencia, Spain) (Fig. 1). We grew a panel of A. thaliana accessions (ecotypes) derived from the US and European stock centers as well as recently collected and bulked seed from Central Asian populations contributed by K. J. Schmid (University of Hohenheim, Stuttgart, Germany) (71, 72) (Dataset S1 and Fig. 1). Accessions used in this experiment were collected from wild populations between the late 1930s and 2002, with most ecotypes having been sampled from 1939 to 1991 (http://arabidopsis.org) (73) and (Dataset S1). Using these banked seeds from stock center-derived inbred lines (accessions or “ecotypes”), originally collected from natural populations, it is possible to measure lifetime fitness of replicated individuals in multiple locations. Seeds for the field experiment were taken from a common bulking generation in which all accessions were grown at 20 °C with 14-h days.

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that demonstrated that accessions from each of these four regions differed in relative fitness (at $\alpha = 0.05$).

To determine the extent of local adaptation, we calculated both physical distance and an index of climate distance of each accession site of origin from each planting site. To generate estimates of the native climate niche, we obtained occurrence records of *A. thaliana* from within the native range from the Global Biodiversity Information Facility Web portal (www.gbif.org). We supplemented these records with data from recent collections in underrepresented areas (71, 83) to generate a better estimate of the complete species’ distribution in climate space. We reduced overlapping records to one occurrence per 10-min grid cell. Our final sample of *A. thaliana* occurrence consisted of 4,980 unique grid cell records in the native range for which we were able to obtain climate data (data available upon request). Using data from the CRU CL 2.0 (77), we calculated separately the first four principal component (PC) axes (using correlation matrices) for the climate envelope space as characterized by monthly temperature (mean and number of frost days) and precipitation (mean amount and number of rainy days) variables. These first four PC axes accounted for 97.0% and 95.4% of the variation in monthly temperature and precipitation, respectively (Table S5). After calculating the position of each common garden location in climate space along these PC axes, we calculated climate distance between each accession and each common garden location as the Euclidian distance along the eight PC axes. Just as for physical distance, each accession was therefore closer in climate distance to some growth sites (common gardens) than to others.

Climate and physical distance to a given field site were significantly positively correlated in all cases. For the sample of accessions grown within a given site, physical distance explained 44–84% of the variation in climate distance (83). Physically proximate accessions were often among the most similar to the growth site in climate space, but the most distant accessions were never furthest in climate space.

**Performance Relative to Climate and Location.** To determine whether individual climate variables were associated with local adaptation, we determined the relationship between fitness and selected biometric, temperature, and precipitation estimates that had been identified a priori as potential candidate indicators of adaptation to climate. For each climate variable considered, we calculated linear and quadratic fit of the climatic variable versus accession relative fitness in that planting (Tables S3 and S4). We explicitly tested for adaptation to temperature in October and April because temperatures in these months have been implicated as determining factors for the climatic range limits for *A. thaliana* (29) and because one or both of these months fall within the growing season for the majority of natural annual cohorts in European locations. An earlier study of *A. thaliana* found a strong relationship between estimates of diurnal temperature range (dtr) [CRU variable dtr (77)] at the site of origin and accession performance in the field in Maryland (47); however, we found that these temperature range variables explained less of the variance in fitness than corresponding monthly average temperatures.

Our final analysis of local adaptation considered three location variables (latitude, longitude, and physical distance to planting site) and five climatic variable estimates (mean annual temperature (BIO1), mean annual precipitation (BIO12), October mean temperature, April mean temperature, and climate distance to planting site (Tables S3 and S4)). Many individual climate variables (monthly values of average temperature, frost days, precipitation and rainy days; see above) were included in our metric of climate distance between each accession and each common garden location. To determine whether or not local adaptation in fitness was associated with the distance from the closest planting site, we regressed fitness on year of collection and to test whether adaptational lag and also introduced a potential bias. Using German accessions, for which we have good representation from many collection dates, we also regressed fitness on year of collection and to test whether adaptational lag was greater in accessions collected earlier.

**Genetic Components of Fitness.** Broad sense heritabilities ($V_c/V_T$) were estimated from restricted maximum likelihood (REML) variance components by taking the variance attributed to (inbred homozygous) accession divided by the total phenotypic variance (accession plus block and error). The heritability of relative fitness was significant at $\alpha = 0.05$ in all plantings (Table S2). Cross-environment genetic correlations in fitness were calculated using two methods. First, we used family mean (as the accessions were collected in a time-restricted subset. Unfortunately, year of collection was strongly confounded with geographic region of origin, which both reduced our power to detect adaptational lag and also introduced a potential bias. Using German accessions, for which we have good representation from many collection dates, we also regressed fitness on year of collection and to test whether adaptational lag was greater in accessions collected earlier.


