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Differential patterns of plasticity to water availability along native and naturalized latitudinal gradients

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ABSTRACT

Questions: Does plasticity to water availability differ between native and naturalized and laboratory plant accessions? Is there a relationship between morphological plasticity and a fitness measure? Can we account for latitudinal patterns of plasticity with rainfall data from the seed source location?

Organism: We examined an array of 23 native, 14 naturalized, and 5 laboratory accessions of *Arabidopsis thaliana*.

Methods: We employed a split-plot experimental design in the greenhouse with two water treatments. We measured morphological and fitness-related traits at various developmental stages. We utilized a published dataset representing 30-year average precipitation trends for each accession origin.

Results: We detected evidence of differential patterns of plasticity between native, naturalized, and laboratory populations for several morphological traits. Native, laboratory, and naturalized populations also differed in which traits were positively associated with fitness, and did not follow the Jack-of-all-trades or Master-of-some scenarios. Significant negative relationships were detected for plasticity in morphological traits with latitude. We found modest evidence that rainfall may play a role in this latitudinal trend.

Keywords: *Arabidopsis thaliana*, cline, phenotypic plasticity, water availability.

INTRODUCTION

Many plant genotypes are able to respond to variation in abiotic conditions through phenotypic plasticity, the capacity of a given genotype to produce different phenotypes in varying environments (Bradshaw, 1965; Schlichting, 1986; Sultan, 1995; Pigliucci, 2001; Kurashige and Callahan,

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2007). Plastic responses in plants, both on short- and long-term scales, have been shown to facilitate the expansion of a plant's ecological breadth across latitudes and into non-native environments (e.g. Sultan *et al.*, 1998; Richards *et al.*, 2006; Maron *et al.*, 2007). Baker (1965), in his work on the general-purpose genotype concept, initiated the modern idea that plasticity is an important mechanism that contributes to success of weeds. In recent years, researchers have examined the role of plasticity in invasive taxa versus non-invasive taxa or other native taxa. Results from these studies largely demonstrate the importance of plasticity in invasive or other naturalized non-native taxa (e.g. Richards *et al.*, 2006; Muth and Pigliucci, 2007; McAlpine *et al.*, 2008). Examination of populations within species that differ in their ecological or evolutionary histories also provides insight into how plasticity may contribute to establishment outside the native range or performance along native and naturalized latitudinal gradients.

Studies comparing plasticity between populations of the same species from the native and non-native ranges are growing (e.g. Kaufman and Smouse, 2001; DeWalt *et al.*, 2004; Maron *et al.*, 2007) and these studies have detected differences in patterns of plasticity depending on origin. Recently, close examination of environmental contributions predicting success outside of the native range (e.g. Rutter and Fenster, 2007) and variation across latitudes (e.g. Wilczek *et al.*, 2009) has demonstrated the importance of broad-scale ecological factors (both potentially favourable and stressful) and ecological history in adaptation. These insights come from a taxon with a widespread naturalized distribution yet is non-invasive, and provides important evolutionary ecology understanding of range expansion. If a relationship between plasticity and fitness exists in the new non-native environment, a favourable reaction norm may be maintained or evolve depending on the genetic variation present within the non-native range.

A framework described by Richards and colleagues (2006) outlines three scenarios comparing invasive with native or non-invasive groups that can be applied at the taxa or population level. This framework specifically examines invasive species in response to favourable resource gradients, and examines how species in the non-native range might be characterized by different patterns of fitness reaction norms than those populations in the native range. The first scenario, the Jack-of-all-trades, describes when an invader is able to maintain fitness across environments via plasticity of other morphological or physiological traits to increased or more favourable resources. The second scenario is the Master-of-some, when an invader takes advantage of favourable environments and is able to increase fitness via plasticity of morphological or physiological traits. The final scenario is the Jack-and-master, which combines characteristics of both of the first two scenarios such that the plant maintains fitness across most (including low-resource) environments, but can also take advantage of favourable environments and increase fitness accordingly.

While the Jack-of-all-trades and Master-of-some perspectives were proposed to help explain the success of invasive species, elements of this broad framework may also be applied to evaluate plasticity as a mechanism for successful establishment and persistence outside of their native range for taxa that are not considered invasive. Geographic expansion can both be an extension of the native range [e.g. northward due to climate change (Thomas, 2010)] or on a new continent, and both may include opportunistic plasticity for success in the new habitat (Dudash *et al.*, 2005). Naturalized species are often found in disturbed areas and while they may have locally large population sizes, have not yet made the transition to becoming invasive (e.g. Phillips *et al.*, 2010). Naturalized species are large components of the flora worldwide (e.g. van Kleunen and Fischer, 2009), yet unlike invasive species may not outperform native

populations of the same taxon. For example, *Arabidopsis thaliana*, a naturalized species with a unique and broad latitudinal distribution in Eurasia and North America, allows for simultaneous examination of native and non-native accessions for clinal variation in plasticity to water availability. This type of plasticity experiment can facilitate a broader understanding of which traits vary in plasticity among populations of different evolutionary origins (Dudash *et al.*, 2005), and shed light on which of the fitness plasticity scenarios may contribute to range expansion under climate change, or naturalization processes.

Clinal variation in morphological, physiological, and developmental traits among plant populations has often been documented along latitudinal gradients (Chapin, 1974; Chapin and Chapin, 1981; Reinartz, 1984; Pilon *et al.*, 2002; Kollmann and Banuelos, 2004). Latitude corresponds not only to variation in important abiotic aspects of the environment including temperature and photoperiod, but also to patterns of seasonal rainfall for many parts of the world (New *et al.*, 2002). High latitudes generally have smaller plant populations (Clausen *et al.*, 1948; Chapin and Chapin, 1981) with lower relative growth rates (Li *et al.*, 1998), longer lifespan (Kudo, 1995), and greater leaf nitrogen content (Kudo, 1995). Several studies have investigated latitudinal patterns of non-native plant populations for either morphological traits or plasticity (see, for example, Reinartz, 1984; Weber and Schmid, 1998; Kollmann and Banuelos, 2004; Maron *et al.*, 2007; Colautti *et al.*, 2009; Moloney *et al.*, 2009). Colautti and colleagues (2009) demonstrate that latitude should be taken into account when considering comparisons between native and non-native populations. In some cases, clinal variation may account for phenotypic differences detected between ranges (Colautti *et al.*, 2009). Examining latitudinal variation in plasticity in non-native populations could tell us more about the mode of range expansion in exotic species.

A critical environmental characteristic that varies within and between habitats as well as across latitudes is water. Water is integral to the growth, development, and reproduction of all terrestrial life. While seasonal rainfall is a relatively predictable characteristic of major parts of the world's geography and often associated with latitude (New *et al.*, 2002), short-term variability within rainfall regimes can produce heterogeneous conditions (Barry and Chorley, 1992). Developmental plasticity to water in plants has been reported in both coarse-grained (i.e. constant availability over the plant's lifetime) and fine-grained (i.e. variation in water over a short time scale) experiments (Pigliucci *et al.*, 1995; Engelmann and Schlichting, 2005; Nicotra and Davidson, 2010; O'Halloran and Carr, 2010). Depending upon the taxon, water stress can be experienced at both the high and low end of the spectrum of water availability. As plasticity increases the options for response to variation in available water, genotypes that have greater plasticity might be more able to colonize (Dudash *et al.*, 2005). Taken together, these ideas suggest that genotypes with plastic responses to water likely contribute to success outside the native range.

The model plant *Arabidopsis thaliana* (Brassicaceae) is an ideal test organism for investigating patterns of plasticity to water across latitudes, and certain accessions have been employed for the study of plasticity and water responses (e.g. Pigliucci and Kolodynska, 2002). In addition to the vast amount of information available on its physiological, molecular, and developmental biology, *A. thaliana* accessions from an extensive range of latitudes and climates are accessible from the seed stock centre (www.arabidopsis.org) for native European and central Asian populations, as well as naturalized populations from North America and Japan (Al-Shehbaz and O'Kane, 2002; Hoffmann, 2002), and widely employed laboratory accessions with which to compare. Such a wealth of natural genetic variation makes *A. thaliana* suitable for comparative studies of plasticity between native, non-native, and

laboratory populations. Recent studies with an array of native and non-native *Arabidopsis* accessions have documented differences among populations in drought (Meyre *et al.*, 2001; McKay *et al.*, 2003) and flood tolerance (Pigliucci and Kolodynska, 2002), as well as differences in characters such as flowering time that vary across non-native populations (Callahan and Pigliucci, 2002). Thus we can examine the influence of latitudinal responses and evaluate in the Jack-of-all-trades and Master-of-some framework for a naturalized species (Richards *et al.*, 2006), and compare results to prior studies with laboratory accessions. In this study, we used native, naturalized, and laboratory accessions of *A. thaliana* to answer the following questions:

1. Is there evidence for plasticity of traits to variation in water availability? Do these patterns of plasticity differ between native, naturalized, and laboratory accessions, or among accessions within these origin categories? Do patterns of performance and plasticity of fitness traits across environments differ between native, naturalized, and laboratory accessions? Can we differentiate between the Jack-of-all-trades and Master-of-some concepts for a naturalized non-invasive alien?
2. Is there latitudinal variation in plasticities or mean trait values of populations from native and non-native regions? Can we account for these relationships by broad-scale patterns in average rainfall or variation in rainfall?

MATERIALS AND METHODS

Experimental design and data collection

A set of 219 accessions from personal collections and the ABRC (the Arabidopsis Biological Resource Center, The Ohio State University, Columbus, Ohio, USA) were sown on Sunshine #3 soilless potting mix and cold treated for 7 days at 5°C to synchronize germination of accessions. Two replicate pots of at least 30 seeds were originally sown. After 7 days in the cold, pots were transferred to the greenhouse. Of this original set, most accessions did not germinate with sufficient replication to be included in this study. We selected seeds from 42 accessions of *Arabidopsis thaliana* (L.) Heynh (native = 23; naturalized = 14; standard laboratory lines = 5 to serve as control) from the set that germinated with sufficient replication ($n > 12$ per accession) (Table 1). Latitudinal coordinates and localities for each accession were established based on details provided by ABRC through The Arabidopsis Information Resource website (www.arabidopsis.org; Table 1). Following germination and a 2-week growth period in the College of Charleston greenhouse, seedlings were randomly selected and transplanted into 3-inch (7.62-cm) pots containing Sunshine Mix 3 growing medium (Sun Gro Horticulture). Plants were arranged using a randomized split-plot design to control for the influence of micro-environmental heterogeneity on growth. We planted one replicate per treatment per block of each of 42 accessions. We employed a total of six blocks for a total of 504 plants. Each high-water treatment plant was given 60 mL of water three times weekly; thus together the whole tray of plants received 1260 mL per watering. Standing water was removed before each watering to minimize hypoxic conditions. The low-water treatment groups received 20 mL of water individually administered to each plant three times a week, such that the whole tray received 400 mL of water each period. We employed a pair of plants per accession per block to obtain six replicate plasticity measurements per accession (replicate plasticity measures per accession were calculated as: plasticity = a differential performance measure calculated

Table 1. Populations included in this study and information from TAIR on collection site and stock number

Stock number	Origin	Collection site	Latitude	Longitude
22642	Native	Martuba, Libya	33° N	23° E
22639	Native	Catania, Italy	37.5° N	15° E
22647	Native	Tossa del Mar, Spain	41.5° N	3° E
22524	Native	Rome, Italy	41.9° N	12.5° E
22518	Native	Tsagguns, Austria	47.1° N	9.9° E
22622	Native	Weiningen, Switzerland	47.3° N	8.26° E
1106	Native	Dijon, France	47.5° N	5° E
22589	Native	Zdarec, Czech Republic	49.2° N	16.2° E
22606	Native	Karagundy, Kazakhstan	50° N	59.3° E
22617	Native	Glueckingen, Germany	50.5° N	8° E
6603	Native	Antwerpen, Belgium	51.5° N	4.5° E
22643	Native	Noordwijk, Netherlands	52° N	4° E
22644	Native	Warsaw, Poland	52.5° N	21° E
22656	Native	Burren, Ireland	53° N	8° W
Crosby[a]	Native	Crosby, England	53.4° N	0.4° W
1287	Native	Kaunas, Lithuania	54.5° N	23.5° E
3109	Native	Copenhagen, Denmark	55° N	12° E
22585	Native	Ostra Mocklo, Sweden	55.5° N	14.1° E
1144	Native	Espoo, Finland	60° N	25° E
1643	Native	Oystese, Norway	60.2° N	6.1° E
22621	Native	Konchezero, Russia	61.5° N	34° E
22573	Native	Eden, Sweden	63.4° N	17.0° E
P[a]	Naturalized	Porcher, South Carolina	33° N	79.5° W
E[a]	Naturalized	Eutaw Springs, South Carolina	33.2° N	80.2° W
6874	Naturalized	Tsu, Japan	34.5° N	136.5° E
22641	Naturalized	Tsu, Japan	34.5° N	136.5° E
8069	Naturalized	Santa Clara County, California	37° N	121.1° W
8068	Naturalized	Berkeley, California	37.5° N	122.2° W
22624	Naturalized	Yosemite Nat. Park, USA	37.5° N	119.5° W
8070	Naturalized	Friedensville, Pennsylvania	40.3° N	75.2° W
22420	Naturalized	Long Island, New York	40.5° N	73.6° W
1387	Naturalized	Martha's Vineyard, Massachusetts	41.2° N	70.3° W
8023	Naturalized	Toledo, Ohio	41.4° N	83.3° W
8141	Naturalized	Hartford, Connecticut	41.5° N	72.4° W
22571	Naturalized	Benton Harbor, Michigan	42.1° N	86.3° W
22353	Naturalized	Cambridge, Massachusetts	42.2° N	71.1° W
22391	Naturalized	Ithaca, New York	42.3° N	76.3° W
907	Laboratory	Columbia line	–	–
22625	Laboratory	Columbia line	–	–
11564	Laboratory	Wassilewskija line	–	–
11651	Laboratory	Wassilewskija line	–	–
22618	Laboratory	Landsberg line	–	–

Note: Mean coordinate values are reported where a range was given. Coordinates were taken from Google Earth software when not provided by individual researchers or the ABRC website. Accessions from Japan are classified as non-native following Beck *et al.* (2008).

[a] Accessions are from sources outside of the Arabidopsis Biological Resource Center collection.

as the trait value of the i^{th} individual in the low-water treatment minus the trait value of the i^{th} individual in the high-water treatment); this is a measure of absolute performance differences across environments. This plasticity measure allows us to evaluate if there is a difference among origins in cross-environment performance.

Rosette diameter was measured for all plants after about one month of growth, while stem diameter (taken 2.5 cm above the rosette), bolt height, petiole and blade length of the longest leaf, and aborted and viable fruit counts were determined 5 weeks later for all individuals that had successfully bolted and had completed fruit production. These plants were then harvested. Plants that failed to bolt after 3 months underwent a one-month vernalization period in a cold incubator at 5°C ($N = 96$), following which they were restored to the greenhouse for a 2-month growth period, bolted, and were included in the analyses described below. The same trait measurements as above were then taken for this second group of individuals and the plants harvested.

Statistical analyses

To assess plasticity, differences between native, naturalized, and laboratory accessions, genetic variation of accessions within these origins, and how accessions (i.e. populations) and origins varied in their patterns of plasticity (genetic variation for plasticity), we used a restricted maximum likelihood (REML) approach in a mixed model analysis of variance (ANOVA) with a covariance structure based on variance components (Littell *et al.*, 1996). We considered block (to account for micro-environmental variation), population nested within origin (a measure of genetic variation), block × treatment, and population within origin × treatment (a measure of genetic variation for plasticity) to be random effects with a covariance structure based on variance components (covtest option in the mixed procedure). The significance of the random effects was examined using a likelihood ratio statistic and evaluated using a chi-square test (Littell *et al.*, 1996, p. 44; also employed by Murren *et al.*, 2009). Origin (native, naturalized or laboratory strain) and treatment (a measure of plasticity), as well as their interaction (a measure of genetic variation for plasticity across origins), were treated as fixed effects. Response variables in this set of analyses were the morphological and fruit set traits. Appropriate transformations were conducted to meet the assumptions of ANOVA that included homogeneity of variances of residuals and normality of residuals. These included log transformations of rosette diameter, petiole, blade length, stem diameter, aborted fruit number, viable fruit number, and total fruit number. Reaction norms allow for a graphical visualization of plasticity (variation in trait response to environmental level) and variation in plasticity among populations. Plotting reaction norms allows for general comparison of patterns of plasticity (patterns of slopes and crossing reaction norms) across traits and among laboratory, native, and non-native accessions.

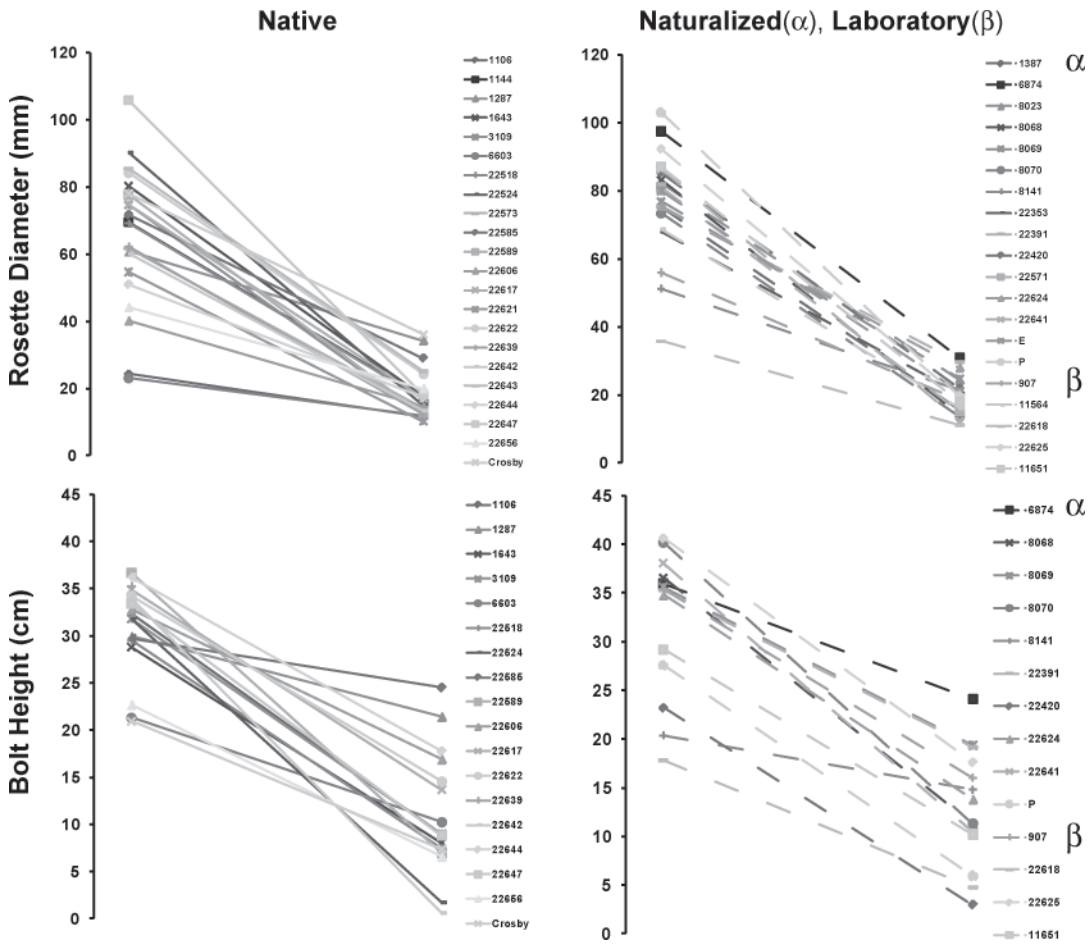
In a second analysis to examine patterns of plasticity, we calculated plasticity as a performance differential between paired plants in the high- and low-water treatments. Six plasticity measures per accession of our morphological and fitness-related traits were calculated as the trait value of the low-water treatment replicate minus the trait value of the high-water treatment replicate plant of the same accession in the same block. This resulted in a total of 252 plasticity measures per trait across all accessions. We performed a mixed model ANOVA to assess differences for our measure of plasticity (difference in accession performance across environments, our dependent variable) among origins (native,

naturalized or laboratory strain – considered a fixed effect) and among populations nested within origin (considered a random effect, to examine genetic variation among accessions within a particular origin). As above, we tested for and confirmed that assumptions of ANOVA including homogeneity of variances were met. If the origin effect was significant, we performed a Tukey *post-hoc* test to specifically compare native and naturalized populations.

Using a regression approach, we examined the relationship between plasticity (trait differences between treatments) and relative fitness across treatments (response variable), separately for the three origin categories. We examined total fruit production as our measure of fitness, as this measure has been widely employed in related studies (e.g. Rutter and Fenster, 2007). To obtain cross-environment relative fitness measures by accession, we summed fruit production of high and low replicates within a block, and divided by the average across-environment fruit production. Thus we obtained a fitness measure scaled to overall accession performance. This regression approach allowed us to examine whether plasticity maximizes fitness across environments in a heterogeneous landscape.

To examine the scenarios described in Richards *et al.* (2006), we used ANOVA to determine if there was a difference between native, naturalized, and laboratory lines in the plasticity in total fruit production (difference in fruit production of the i^{th} individual in the high treatment and the i^{th} individual of the low treatments, such that we had six replicate plasticity measures for fruit production per accession). In an additional analysis with the plasticity of fruit production as the response variable, we focused specifically on native and naturalized lines (eliminating laboratory lines from this particular analysis) and included latitude as a covariate. Previous analyses employing the approach of Richards *et al.* (2006) had not included latitude as advocated by Colautti *et al.* (2009). We log-transformed fruit production plasticity to meet the assumptions of ANOVA. We also examined the means of the native and non-native populations in the high- and low-water environments, and examined the slopes of the reaction norms to evaluate if they fit the Jack-of-all-trades or the Master-of-some scenarios. The Jack-and-master scenario was indistinguishable from the Jack-of-all-trades or the Master-of-some as described by Richards *et al.* (2006) in our experiment, in part because we examined plasticity across only two environments. Also, water levels represent part of the resource gradient from favourable (low water) to stressful (high water).

Relationships between trait plasticities and latitude, trait plasticities and rainfall parameters (including yearly total rainfall, average monthly precipitation, standard deviation of yearly precipitation), and trait means and latitude were examined using a regression model approach. We examined if there were latitudinal clines in plasticity of morphological traits to water and if precipitation patterns were a predictor of performance. All global climate data were obtained from New *et al.* (2002), who provide totals, averages, and variance parameters across 30 years of data (see also Rutter and Fenster, 2007). For the trait plasticities, data were analysed separately between native and naturalized accessions to address whether clines exist in both continents and if environmental data from these continents relate to plasticity patterns. East Coast North America accessions were also analysed separately. For the trait means, analyses were conducted separately for the high- and low-water conditions, and by origin. All statistical analyses were conducted using SAS v.9.1.3 (SAS Institute, 2003).


Native
Naturalized(α), Laboratory(β)
Rosette Diameter (mm)
Bolt Height (cm)
0
5
10
15
20
25
30
35
40
45
60
80
100
120
1106
1144
1287
1643
3109
6603
22518
22524
22573
22585
22589
22606
22617
22621
22622
22639
22642
22643
22644
22647
22656
Crosby
1387
6874
8023
8068
8069
8070
8141
22353
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22420
22571
22624
22641
E
P
907
11564
22618
22625
11651
α
β

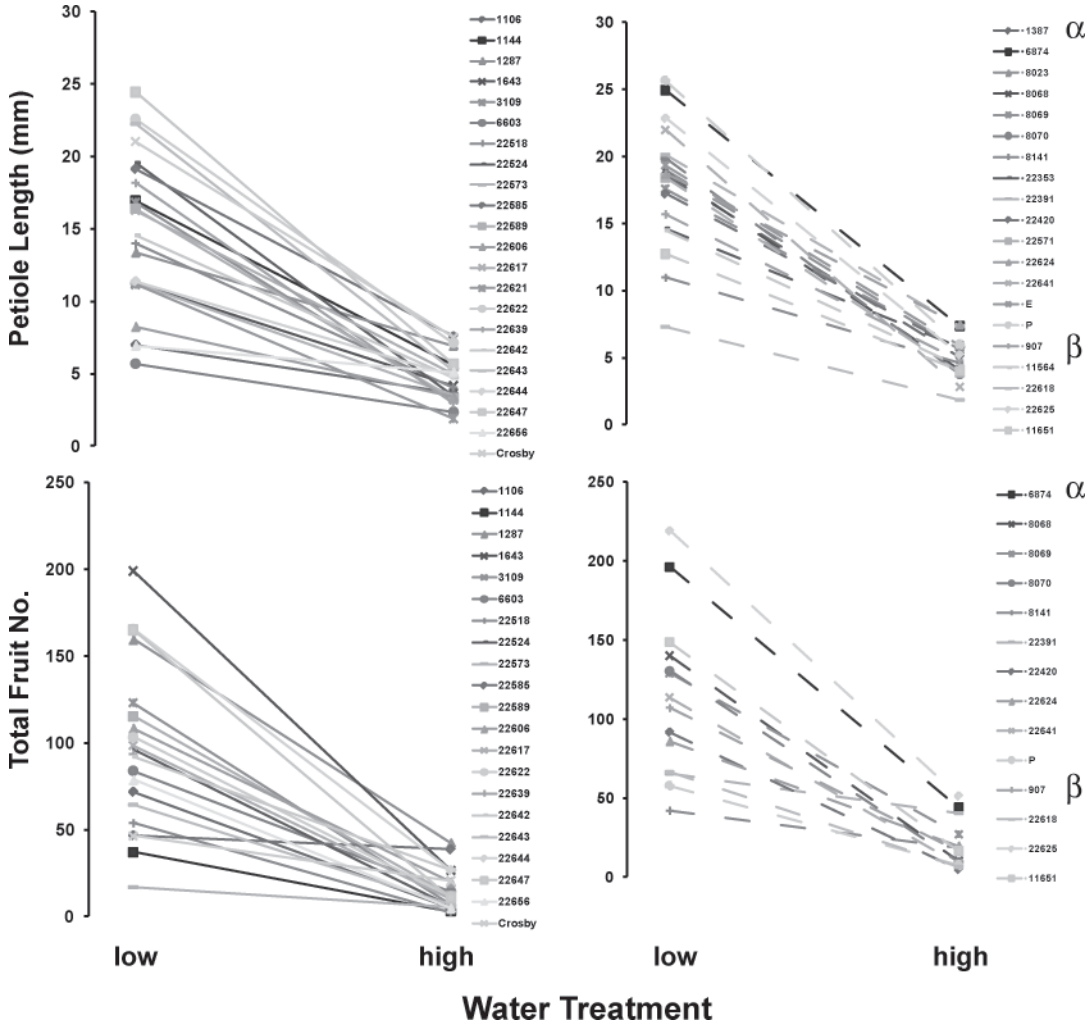

Fig. 1. Reaction norms for all traits with significant population × treatment interactions. Each data point corresponds to the trait mean for that population. Fitness measure is total fruit production.

Table 2. Restricted maximum likelihood analysis of a variety of morphological and fitness-related traits

Trait	Origin	Treatment	Population (Origin)	Origin* Treatment	Population (Origin)* Treatment	Block	Block* Treatment
Rosette diameter	1.84	**389.95**	**0.033**	0.38	**0.04**	**0.0099**	0
Petiole length	2.7	**314.6**	**0.05**	1.53	**0.02**	*0.01*	*0.0003*
Blade length	0.057	**480.9**	*0.015*	0.23	**0.03**	**0.005**	0
Bolt height	1.51	**113.47**	**22.89**	0.28	**17.6**	1.18	0.48
Stem diameter	1.82	**196.56**	0.0009	0.40	*0.002*	*0.0003*	0
Aborted fruit	1.39	**90.57**	0.02	*2.97*	**0.21**	0	0
Viable fruit	**5.26**	**176.99**	**0.38**	0.22	**0.14**	0	0
Total fruit	2.26	**156.66**	*0.16*	0.66	**0.16**	0	0

Note: Populations are nested within native or naturalized origin categories. Block, Population(Origin), Block*Treatment, Population(Origin*Treatment) are all random effects, evaluated using a chi-square of the log likelihood. Treatments are two levels of watering. For the random effects, parameter estimates are reported. For the fixed effects, Origin (numerator d.f. = 2, denominator d.f. = 26.9), Treatment (numerator d.f. = 2, denominator d.f. = 37.6), and Origin*Treatment (numerator d.f. = 2, denominator d.f. = 37.8) *F*-values are presented. **Bold font** indicates values that are significant at $P < 0.05$, and *italic font* is for $0.1 < P > 0.05$.

RESULTS

Treatment, origin, and population effects

We found a significant treatment effect for all traits that we examined (Table 2), with larger trait values observed in the low-water treatment (Fig. 1). We detected a significant origin effect for fruit number ($N = 504$; Table 2). Petiole length plasticity, rosette diameter plasticity, and stem diameter plasticity differed between native, laboratory, and non-native populations (Table 3). We found significant differences between origins in plasticity for all fruit measures (Table 3), as well as significant differences among populations nested within origins in this measure of plasticity.

Mixed model ANOVA (and log-likelihood ratio tests) revealed a significant population (nested within origin) effect for rosette diameter, petiole length, bolt height, and viable fruit number. We also found significant genotype × environment interactions (evaluated by population × treatment effect) for all traits measured excluding stem diameter (Tables 2 and 3). Patterns of plasticity varied among populations, including variation in *both* crossing reaction norms and changes in slopes among populations (Fig. 1). Some populations showed steep decreasing slopes (high plasticity: e.g. CS22647 for rosette diameter and E for petiole length), and others nearly flat slopes (little or no plasticity: e.g. CS8141 for bolt height and CS22391 for fruit production). Figure 1 demonstrates that patterns of crossing reaction norms and changes in slope among populations are both detected as patterns of genetic variation for plasticity to water level. There were accessions that were outliers in performance for fruit number in low water (at the high end CS1106 a native accession, CS907 a laboratory accession, and CS6874 a naturalized accession, and at the low end CS22573 a native accession and CS8141 a naturalized accession).

In examining the relationship between trait plasticity and fitness across environments, different patterns emerged across origins. We found significant positive relationships

Table 3. Analysis of variance examining patterns of plasticity (difference between the low and high treatments) among native, naturalized, and laboratory lines.

Trait plasticities	Origin	Population(Origin)
Petiole length	**11.04******	**4.29******
Blade length	0.95	**3.77******
Rosette diameter	**5.00*****	**4.42******
Bolt height	0.45	**2.08*****
Stem diameter	**3.10***	**1.59***
Aborted fruit	**6.26****	**1.91****
Viable fruit	**2.95***	**1.90***
Total fruit	**4.57****	**2.03****

Note: *F*-values are presented, with ****$P < 0.0001$, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. All *F*-values with $P < 0.05$ are in **bold font**. Degrees of freedom for origin was 2, whereas those for population depended on whether it was a rosette trait (d.f. = 39) or a post-bolting trait (d.f. = 32). Overall model d.f. was 182 for rosette traits and 109 for post-bolting traits.

between plasticity and average fitness across treatments in naturalized populations for blade length ($t = 1.99$, $P < 0.05$). In native populations, the positive relationships were found between fitness and rosette diameter ($t = 2.05$, $P < 0.04$). In the laboratory lines, a significant relationship was found between fruit set and plant height ($t = 2.26$, $P < 0.03$). The results of Tukey *post-hoc* tests to compare native and naturalized populations specifically, indicate that while naturalized (non-native) populations had higher plasticities to water for petiole length and rosette diameter, there were no significant differences in plasticity of fitness (measured as fruit count) between origins. However, we detected a significant difference between native and non-native origins ($F_{1,78} = 4.44$, $P < 0.04$) in plasticity of fruit production in a model that accounted for latitude. Thus, in evaluating the Jack-of-all-trades and Master-of-some scenarios, we found significant differences among origin accessions (native, non-native, and laboratory) population means and plasticities of our fitness measures. However, on average, the total fruit means of non-native populations were lower than those of native origin in both treatments (high water native 16.9 ± 2.1; high water naturalized 15.8 ± 3; low water native 102.4 ± 6.7; low water naturalized 72.2 ± 6.8) and plasticities (differences in performance between treatments) of native populations were slightly higher than those of non-natives. Although plasticity in fruit production is distinguishable statistically between natives and non-natives, our results do not support the idea that the non-native accessions are more able to maintain fitness across treatments (Jack-of-all-trades) or that they are more able to take advantage of increased water resources (Master-of-some).

Latitudinal trends in plasticity and mean trait values

Plasticities of petiole length, rosette diameter, bolt height, and stem diameter were negatively associated with latitude in the native accessions (Table 4). Similarly, plasticities of petiole length, blade length, and rosette diameter were negatively associated with latitude in

Table 4. Regression relationship between latitude and plasticity of morphological and fitness-related traits

	Native		Naturalized		Naturalized (East Coast USA)	
Trait plasticities	Coefficient	*P*	Coefficient	*P*	Coefficient	*P*
Petiole length	**−0.29**	**0.0015**	**−0.55**	**0.02**	**−2.46**	**0.02**
Blade length	−0.14	0.17	**−0.62**	**0.004**	**−3.00**	**0.004**
Rosette diameter	**−0.82**	**0.02**	**−2.42**	**0.008**	**−2.67**	**0.01**
Bolt height	**−0.56**	**0.006**	−0.76	0.50	−0.65	0.52
Stem diameter	**−0.01**	**0.03**	0.59	0.64	−0.42	0.68
Aborted fruit	0.11	0.76	0.02	0.98	0.48	0.63
Viable fruit	−0.18	0.89	0.72	0.83	0.25	0.81
Total fruit	−0.28	0.87	−0.32	0.93	−0.08	0.93

Note: Coefficients of the linear relationship between latitude and plasticity and *P*-values are presented. **Bold font**: $P < 0.05$.

naturalized accessions. There was, however, no significant gradient in fitness-related traits (i.e. fruit count plasticity). To account for a possible longitudinal effect, we also re-ran the analysis after removing both Japanese accessions (considered to be non-native by various authors) from the naturalized group and found no difference in the pattern of the results [comparing naturalized (which includes Japan) with naturalized (East Coast USA, which excludes Japan)].

When mean trait values for both high- and low-water conditions were considered (instead of a plasticity measure), we observed a negative latitudinal trend for the low-water condition only where greater variation was observed (data not presented, consistent with the patterns observed in Fig. 1). Mean rosette diameter (coeff. = −2.15, $P = 0.004$) and mean blade length (coeff. = −0.59, $P = 0.0003$) were also negatively related to latitude in naturalized accessions alone (Table 5).

Correlations with global precipitation patterns

We found a significant positive relationship between total yearly precipitation and bolt height plasticity in naturalized accessions (Table 5). Average monthly precipitation was also significantly positively related to plasticities of rosette diameter, petiole length, and blade length in naturalized accessions. For the standard deviation of yearly precipitation, rosette diameter and blade length plasticities of native accessions were positively related with the rainfall data.

DISCUSSION

The responses of native, non-native, and laboratory lines of *Arabidopsis thaliana* to water availability were plastic for both morphological traits and fruit production. In addition, we found statistically detectable differences in trait responses among origins and populations within origins to water level. Our examination of the concepts of Jack-of-all-trades and Master-of-some scenarios suggest that neither scenario describes the patterns of

Table 5. Relationships between yearly precipitation data and morphological trait plasticity

	Precipitation total		Average monthly precipitation		Stdev yearly precipitation	
Trait plasticities	Native	Non	Native	Non	Native	Non
Rosette diameter	N.S.	0.07*	N.S.	**0.04***	**0.007**	N.S.*
Petiole length	N.S.	0.07*	N.S.	**0.002***	N.S.	**0.02***
Blade length	N.S.*	**0.02***	N.S.*	**0.04***	**0.002***	N.S.*
Bolt height	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Stem diameter	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

Note: 'Precipitation total' is the sum of all the monthly averages; 'Average monthly precipitation' is the average precipitation over 12 months; 'Stdev yearly precipitation' is the standard deviation of year-long precipitation to capture the among-month variation in precipitation. Analyses were run separately for native and naturalized (Non) populations. All significant relationships were positive. Trait plasticities that were significantly associated with increased fitness are indicated by asterisks.

performance for this naturalized alien species. Populations from the native range outperformed non-native accessions, and accessions from both origins were plastic for fruit production with greater production in the low-water conditions. These patterns suggest that for both native and non-native geographies, plasticity to water may be important for *A. thaliana*. We found clinal patterns in both trait means and plasticities with latitude in both the Eurasian and North American groups. Negative relationships were found between morphological traits and latitude, suggesting overall smaller plants at higher latitudes on both continents. We also found evidence that climatic patterns of precipitation may play an important role in this trend.

Origins differ in response to water availability

We report significant plasticity and genetic variation in plasticity in response to water conditions among 42 distinct accessions of *Arabidopsis thaliana* from native and non-native geographies, and standard laboratory lines. These results confirm other reports of genetic variation to water availability in this taxon (e.g. McKay *et al.*, 2003; Engelmann and Schlichting, 2005), yet here we differentiate patterns of plasticity based on origin. We found significant genotype × environment interactions in both native and naturalized accessions for rosette diameter, bolt height, petiole length, and total fruit count. Our results contrast with an earlier study by Pigliucci *et al.* (1995), who found no significant genetic variation for plasticity to water. This disparity may be explained by the large difference in the total number and diversity of accessions investigated (42 in our study, 4 in the earlier study). We also maintained constantly saturated soil in the high-water treatment groups. Flooding has been shown to affect many morphological traits in *Arabidopsis* (Kolodynska and Pigliucci, 2003), and localized flooding has been observed in the native range in Spain and non-native range in South Carolina (C.J. Murren and L. Ferguson, personal observation), and rainfall variance is an important component of global climate change.

Laboratory lines were plastic for a variety of traits to water conditions, and varied in their responses across treatments. These results are in keeping with other studies that detected significant divergence between laboratory lines and natural accessions (e.g. Pigliucci and Byrd, 1998;

Murren *et al.*, 2005). These laboratory lines may be a reasonable starting point as model comparison for further investigation of the molecular genetics of plasticity. Yet given the phenotypic differences of laboratory and field accessions, investigations into the molecular genetics of plasticity of natural accessions should accompany these studies of laboratory lines (Pigliucci and Byrd, 1998; Murren *et al.*, 2005).

Plasticity across populations with different evolutionary histories

Both theoretical and experimental studies have emphasized the role of phenotypic plasticity in the colonization and subsequent expansion of populations of introduced species (Baker, 1965; Thompson, 1991; Williams and Black, 1993; Williams *et al.*, 1995; Baret *et al.*, 2004; Yeh and Price, 2004). Geng *et al.* (2007) demonstrated the importance of plasticity empirically in the invasive alligator weed, *Alternanthera philoxeroides*, an exotic of concern in almost 30 countries (Julien, 1995; Garbari and Pedulla, 2001). Geng *et al.* (2007) found that developmental plasticity of root and shoot morphology in *A. philoxeroides* allows the plant to colonize both aquatic and terrestrial habitats. In similar fashion, invasive genotypes of reed canary grass have been documented to exhibit higher plasticity to soil moisture than their native European counterparts (Lavergne and Molofsky, 2004).

If genetic variation for plasticity exists in non-native populations, and if there is a fitness advantage to those genotypes with greater plasticity, then evolution of plasticity via natural selection could occur in the non-native range (Richards *et al.*, 2006; this study). Those genotypes that successfully colonize the non-native range may be descendants from populations that evolved plasticity elsewhere (Dudash *et al.*, 2005; Bossdorf *et al.*, 2008). Distinguishing whether plasticity evolved pre- or post-invasion is not possible in most cases. Emerging evidence across systems suggests that all three scenarios put forth by Richards *et al.* (2006) to examine relationships of plasticity and invasiveness (Jack-of-all-trades, Master-of-some, Jack and Master) are detected in invasive taxa (e.g. Muth and Pigliucci, 2007; McAlpine *et al.*, 2008). Yet our data suggest that naturalized species may not fit these models, although plasticity is expressed in both native and naturalized accessions to an important and variable environmental characteristic.

All but two of the naturalized accessions of *Arabidopsis* that we studied are from North America, yet *Arabidopsis* is a recent addition to American flora (herbarium records in South Carolina date back approximately 150 years). We found evidence of differential plasticities for petiole length and rosette diameter in naturalized versus native accessions. To offer a cautionary note, given that we observed reduced phenotypic variation in the high-water treatment, these relationships may be largely driven by correlations with fitness within the low-water treatment [for discussion of the issue of cross-environment means, see Pigliucci (2004)], and warrant further investigation with additional levels of water availability. Collectively, the degree of morphological plasticity, as well as the positive relationship between fitness and this plasticity of morphological traits, may in part account for the wide geographic distribution in a ruderal species in the native range as well as being a component of persistence of *Arabidopsis* across a wide latitudinal variation in the New World. Thus in naturalized species (those that are not considered invasive pests), plasticity may also play a role in population establishment and persistence.

Latitudinal cline

Recent work has demonstrated that investigating clinal patterns in non-native environments may be key to a full understanding of success outside the native range (e.g. Colautti *et al.*, 2009), including range change in response to climate change (Thomas, 2010). The importance of understanding the clinal variation and its potential role in invasion success is demonstrated in *Drosophila melanogaster* populations in its non-native range of eastern Australia (Hoffmann and Weeks, 2007), and in European non-native *Mimulus* (van Kleunen, 2007). As many environmental factors vary with latitude, we might expect that plasticity may also vary with latitude. We found a significant negative latitudinal trend for the plasticities of four morphological traits in the native accessions, and three morphological traits in naturalized accessions. Such latitudinal trends were barely observable when trait means alone were considered. This variation in plasticity with latitude may reflect different patterns of evolutionary ecology in the native and non-native regions. A previous study by Li *et al.* (1998) found a negative latitudinal gradient in relative growth rate in 40 accessions of *Arabidopsis*, but did not include naturalized North American accessions. Evidence of genetic variation in trait means exists for leaf traits along latitudinal clines (Hopkins *et al.*, 2008) and both latitudinal and longitudinal clines in flowering time (Stinchcombe *et al.*, 2004; Samis *et al.*, 2008) in this species. Montesinos-Navarro *et al.* (2011) detected clinal variation in life-history traits and morphological traits along a European altitudinal gradient. To the best of our knowledge, ours is the first study to document a latitudinal trend in *plasticity* values across both the native and non-native geographical range of a species, and consider latitudinal variation in plasticity an important component of establishment.

Plasticity trends and global rainfall patterns

To examine if the observed significant genetic diversity for plasticity among populations is evidence of regional adaptation, we examined the relationship between plasticity values with 30-year global precipitation data (New *et al.*, 2002). Specifically, we looked at the relationship between the plasticities of all morphological traits and both the annual precipitation and monthly variability in rainfall for each accession origin site. Our results show modest evidence of a relationship between plasticity and these measures of precipitation. When we considered measures of total precipitation (i.e. the annual total and the average monthly total), we found a significant relationship between plasticity values of several morphological traits and precipitation in the naturalized accessions. In contrast, when we looked at measures of rainfall variability (i.e. the standard deviation of the yearly precipitation), significant relationships between plasticity and local climate began to emerge for the native accessions. It is possible that regional adaptation is responsible for the positive relationship between rainfall variability and plasticities in native accessions. An earlier study by Pollard *et al.* (2001) found evidence of regional adaptation to photoperiod in native populations of *Arabidopsis*. In an analysis of 21 accessions of *Arabidopsis* grown in a common garden experiment, Rutter and Fenster (2007) found that latitude and climatic history (using data of New *et al.*, 2002) predicted accession performance in a non-native field location. We noted in our climate effect analysis that many of the trait plasticities that were significantly related to rainfall variability (native accessions) and total rainfall (naturalized accessions) were also those trait plasticities that we found to be positively related to cross-environment fitness. These results could be further evidence of regional adaptation

to rainfall patterns. In the naturalized accessions, we consider that the positive relationship with total rainfall might be due to line sorting, i.e. selection for those lines that could establish and persist under rainfall patterns differing from their native range. Given the relationships uncovered here, further investigation into this relationship is warranted, particularly expanding to three or more manipulated environments in the greenhouse and a multi-site field experiment (*sensu* Moloney *et al.*, 2009). The next step in investigating the influence of precipitation is to examine the evolutionary history and whether genetic complement, mixture of genetic/evolution or bottleneck is primarily responsible for these patterns.

CONCLUSIONS

We found a substantial amount of genetic variation for plasticity (i.e. genotype × environment interactions) to water among accessions, as well as evidence of a significant negative latitudinal gradient in the phenotypic plasticities of several morphological characters in both naturalized and native accessions. These trends were not apparent for the trait means alone. These results highlight the importance of considering developmental processes as well as phenotypic characters when investigating trends among cosmopolitan species. Lastly, while the results of our investigations into relationships between population plasticities and rainfall data were modest, we argue that future studies investigating adaptive processes involved in global distribution patterns should consider the use of similar climate data sets. It is important to quantify crucial mechanisms, such as plasticity, that may influence the successful colonization and range expansion of species across the globe and movement patterns in response to climate change.

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