American Journal of Botany

RESEARCH ARTICLE

Rapid alignment of functional trait variation with locality across the invaded range of Sahara mustard (*Brassica tournefortii*)

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Manuscript received 3 December 2017; revision accepted 27 April 2018.

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Citation: Winkler, D. E., J. R. Gremer, K. J. Chapin, M. Kao, and T. E. Huxman. 2018. Rapid alignment of functional trait variation with locality across the invaded range of Sahara mustard (*Brassica tournefortii*). *American Journal of Botany* 105(7): 1–10.

doi:10.1002/ajb2.1126

PREMISE OF STUDY: Mechanisms by which invasive species succeed across multiple novel environmental contexts are poorly understood. Functional traits show promise for identifying such mechanisms, yet we lack knowledge of which functional traits are critical for success and how they vary across invaded ranges and with environmental features. We evaluated the widespread recent invasion of Sahara mustard (*Brassica tournefortii*) in the southwestern United States to understand the extent of functional trait variation across the invaded range and how such variation is related to spatial and climatic gradients.

METHODS: We used a common garden approach, growing two generations of plants in controlled conditions sourced from 10 locations across the invaded range. We measured variation within and among populations in phenological, morphological, and physiological traits, as well as performance.

KEY RESULTS: We found nine key traits that varied among populations. These traits were related to phenology and early growth strategies, such as the timing of germination and flowering, as well as relative allocation of biomass to reproduction and individual seed mass. Trait variation was related most strongly to variation in winter precipitation patterns across localities, though variations in temperature and latitude also had significant contributions.

CONCLUSIONS: Our results identify key functional traits of this invasive species that showed significant variation among introduced populations across a broad geographic and climatic range. Further, trait variation among populations was strongly related to key climatic variables, which suggests that population divergence in these traits may explain the successful colonization of Sahara mustard across its invaded US range.

KEY WORDS Brassicaceae; *Brassica tournefortii*; common garden; desert; evolution; functional traits; greenhouse; invasion; multiple generations; Sahara mustard.

A major contemporary challenge in ecology is predicting when and where introduced species will be successful (Kolar and Lodge, 2001). Unfortunately, specific adaptive traits characterizing a successful invader often do not hold for all invasive species (Sakai et al., 2001). Trait-based ecology shows promise for identifying mechanisms that drive the success of invasives and predicting future patterns (Leishman et al., 2007; Tecco et al., 2010; van Kleunen et al., 2010; Murphy et al., 2016) because a functional approach can reveal the mechanisms underlying different phenological, morphological, and physiological characteristics that influence species' responses to the environment. A number of functional traits have been related to invasive performance and colonization success. These include rapid germination and flowering phenologies (Kimball et al., 2011; Colautti and Barrett, 2013), increased allocation to photosynthetic and reproductive structures (Leishman et al., 2007; Moroney et al., 2013; Erskine-Ogden et al., 2016), water-use efficiency matched to site-specific environments (Tecco et al., 2010; van Kleunen et al., 2010), and combinations of each (Kimball et al., 2014). That said, many iconic invasives occupy a wide breadth of environments (Colautti et al., 2009), so focusing on a subset of the invaded system may not adequately represent important traits and processes. We expect that three categories of functional traits that influence establishment, survival, growth, and reproduction will reveal mechanisms driving invasive success: phenological, morphological, and

physiological traits. Plasticity and rapid evolution of these traits in novel environments likely facilitates expansion in invaded ranges (Burton et al., 2010; Davidson et al., 2011).

Species invasions typically result from interacting features across ecological, evolutionary, and organismal processes. As such, the rapid alignment of phenological and morphological traits associated with favorable conditions for establishment (e.g., germination timing, seed size) as well as the timing of reproduction are likely necessary for most invasives to succeed (Muth and Pigliucci, 2006; Wolkovich and Cleland, 2011; Novy et al., 2013; Nguyen et al., 2016). Some invasive species have rapidly responded to invaded environments over short periods (e.g., <100 yr; Novy et al., 2012; Nguyen et al., 2016). This has been shown to be true in invasive species in desert systems worldwide (Chambers et al., 2007; Drenovsky et al., 2012; Marushia et al., 2012; Merrill et al., 2012; Erskine-Ogden et al., 2016). Thus, invaders in these systems may succeed only if traits affecting fitness are able to match local environments (e.g., rainfall variability and seasonal temperature covariance; Loik et al., 2004). Such patterns would be consistent with strategies associated with desert adaptation in ephemeral plants (e.g., Smith et al., 1997; Huxman et al., 2013) and would suggest that invasive species exploit trait relationships similar to those of native species that succeed in these environments, but also that they likely employ enhanced performance in several attributes that further success (e.g., Kimball et al., 2014).

The range of Sahara mustard (*Brassica tournefortii*) is rapidly expanding and negatively affecting natural ecosystems across the southwestern United States (Barrows et al., 2009; VanTassel et al., 2014). This invader has become increasingly common in arid and semiarid regions throughout the Southwest since its putative introduction in the 1920s (Sanders and Minnich, 2000). The species has invaded ecosystems ranging from coastal Mediterranean in California to hot desert localities from Arizona to Texas. Further, Sahara mustard has several features that hint at its capacity to rapidly evolve. The species is a generalist and, as such, germinates under a wide range of temperatures, light conditions, and soil depths (Thanos et al., 1991; Jurado and Westoby, 1992; Chahuan et al., 2006; Bangle et al., 2008). It is also highly fecund: the species is capable of self-fertilization (i.e., facultative autogamy) and produces seeds rapidly (~50 d from germination; Marushia et al., 2012) and in high quantities (Trader et al., 2006) that can remain viable ≥1 yr after production. The species also exhibits some level of dormancy (Adondakis and Venable, 2004; Chahuan et al., 2006), which may allow for buffered population dynamics during unfavorable or unpredictable conditions (Venable, 2007; Gremer et al., 2016). Individual plants can produce >16,000 seeds annually that disperse via small mammals, flowing water, wind, and human transport (Trader et al., 2006; Sánchez-Flores, 2007; Bangle et al., 2008; Berry et al., 2014).

Further, Sahara mustard's ability to self-fertilize and its large distribution likely promote local adaptation and rapid range expansion (Sakai et al., 2001) as well as establishment in new isolated localities by single individuals. In other words, Sahara mustard has many of the common traits associated with rapid population dynamics and invasive success (Grime, 2006; Ordonez, 2010), but the functional biology underlying its success, and how that varies across the invaded range, is poorly understood. Previous modeling work suggests that Sahara mustard might exist as a plastic, general-purpose genotype (*sensu* Baker, 1965) such that the invaded range environment matches that of the native range (Li et al., 2015). However, Sahara mustard occupies a large native range (Marushia et al., 2012; Li et al., 2015) and likely exists as several genetically distinct populations that have been separated by thousands of kilometers and generations (Parker et al., 2003; Lawson Handley et al., 2011). Further, it is most probable that Sahara mustard in the United States is representative of only a small regional population from its native range (i.e., Lombaert et al., 2010; Arnesen et al., 2017). Although a few ecological studies have examined the species' performance and impacts in a few invaded areas (Barrows et al., 2009; Marushia et al., 2010, 2012; VanTassel et al., 2014; Li et al., 2015), no research has been conducted to determine how functional trait variation may explain the success of this rapidly spreading invasive. Thus, Sahara mustard is an ideal system to explore the functional biology underlying species invasions.

Our study aimed to identify key functional traits that explain the success of Sahara mustard across a broad range of environments in the southwestern United States. We tested for population divergence in functional traits using multigenerational common garden experiments, whereby we grew plants in common garden environments and matched plant traits to features associated with their source environment locality. In doing so, we distinguished between environmental, maternal, and offspring-level variation effects on observed phenotypes. We predicted that phenological traits, particularly germination, would vary across populations with different environmental cues (Wolkovich and Cleland, 2014). Specifically, we expected higher germination rates in populations from more xeric sites because success of individuals at these sites would likely require that they take advantage of relatively rare, ephemeral rains. We expected that precipitation would best predict variation across all three functional categories of traits (phenological, morphological, and physiological) because Sahara mustard occupies water-limited environments that vary in precipitation regime in its native range, and variable precipitation is critical in the southwestern United States. We also expected to see variation among populations in allocation of biomass to leaves, with increased allocation in populations that experienced increasing aridity across the species range, suggesting increased competition for resources with native species. Last, we predicted that water-use efficiency (WUE) and leaf nitrogen investment would vary among populations, with more arid sites having higher WUE and leaf N, similar to other desert invaders (Huxman et al., 2013; Kimball et al., 2014). Further, we expected that winter precipitation would be a strong driver of reproductive allocation. Overall, we predicted that divergence in functional traits would explain Sahara mustard's current invaded range.

MATERIALS AND METHODS

Species natural history

Sahara mustard (Brassicaceae: *Brassica tournefortii* Gouan) is an annual native to the Mediterranean basin and much of the Middle East through to western India (Prain, 1898; Thanos et al., 1991; Aldhebiani and Howladar, 2013). It is considered a weedy species in agricultural fields in parts of its native range (Ahmed et al., 2015; El-Saied et al., 2015) but also has traditional dietary uses and economic value in regions where it is cultivated (Singh et al., 2015; Guarrera and Savo, 2016). Sahara mustard is an invasive throughout much of Australia (Chahuan et al., 2006), South Africa (McGeoch et al., 2009), Chile (Teillier et al., 2014), and western North America (Li et al., 2015). In North America, the first documented occurrence

of Sahara mustard comes from a herbarium sample collected in the Coachella Valley, California, in 1927. It is thought to have been introduced as a contaminant of date palm translocation into the hemisphere (Sanders and Minnich, 2000) and remained relatively unnoticed except in the Coachella and Imperial valleys of California's deserts, where it was observed to be locally established (Musil, 1948; Robbins et al., 1951). Herbarium records track its spread to coastal California in the late 1950s and to Tucson, Arizona, and Sonora, Mexico, in the early 1970s. The species apparently saw a population boom beginning in the 1980s when it spread rapidly throughout the Southwest (Sanders and Minnich, 2000).

Field sampling and common garden design

In spring 2015, we collected seeds from 20 individual plants from 10 locations spanning a ~10° latitudinal and ~15° longitudinal gradient across Sahara mustard's invaded U.S. range (Fig. 1 and Table 1). Sites ranged from coastal Mediterranean to hot desert ecosystems. Desert ephemerals such as Sahara mustard require exposure to summer temperatures to break dormancy and cue seeds for germination (Clauss and Venable, 2000; Huang et al., 2016). Thus, we stored field seeds in paper envelopes in the greenhouses at the University of California, Irvine (daily mean temperature range: 26–32°C) during summer 2015, after which we stored seeds at room temperature (~20°C) in the laboratory before growth experiments. Sahara mustard seeds can remain viable 4–5 yr after collection when stored in a dark cool place as we have done (Chauhan et al., 2006).

We grew field-collected seeds for two generations to account for the influence of maternal environment. From each maternal line, we randomly selected three seeds and sowed them into the top 1 cm of soil (*sensu* Chauhan et al., 2006) in 11.4 L containers. We used a custom mix of 85% unwashed sand, 10% perlite, and 5% cactus mix (Scotts Miracle-Gro). We placed containers randomly on greenhouse benches but grouped by sampling site to prevent fertilization across sites. Sampling sites were spaced out ~3 m. We randomly rotated sampling-site containers weekly to control for any small-scale environmental variation in the greenhouse. Greenhouse temperatures were kept above freezing and below 24°C, averaging 15–20°C for the duration of the experiment, via an automated climate control system (GEM Link; QCOM, Irvine, California, USA). Soils were watered regularly to keep seeds moist and encourage germination. We surveyed daily for germination and removed any additional germinants after the first individual emerged, to prevent competition for resources within each pot. It is possible that this introduced bias toward earlier-germinating plants in our study. These first germinants, however, likely represent a major portion of the trait variation in established seedlings in the field (e.g., Thompson et al., 2001; James et al., 2006). Plants were fertilized weekly after individuals produced two true leaves (Peter's 20-20-20 solution, Scotts Miracle-Gro). Outcrossing rates are incredibly low in Sahara mustard (<10%; Winkler, 2017) and plants were allowed to self-pollinate or cross-pollinate within sites. We harvested seeds from this first common garden generation once seedpods had visibly ripened but before pods burst. We weighed seed and sowed them as above. Only individuals of this second generation were used in analyses, to avoid

TABLE 1. Site codes, names, geographic locations, and elevation of Sahara mustard sampling sites.

Code	Location	Latitude, longitude	Elevation (m)
CA1	Nipomo	35.048, −120.512	128.22
CA4	In-Ko-Pah Park Road	32.647, −116.106	905.68
CA3	Coachella Valley Preserve	33.772, −116.304	24.64
CA2	Mojave National Preserve	34.803, −115.612	1193.11
NV	Las Vegas	36.090, −115.233	726.88
UT	Red Cliffs National Conservation Area	37.225, −113.406	985.23
AZ2	Saguaro National Park	32.177, −110.739	962.64
AZ1	Dateland	32.801, −113.541	130.86
NM	Mesquite	32.184, −106.678	1195.52
TX	Fort Hancock	31.299, −105.832	1114.53

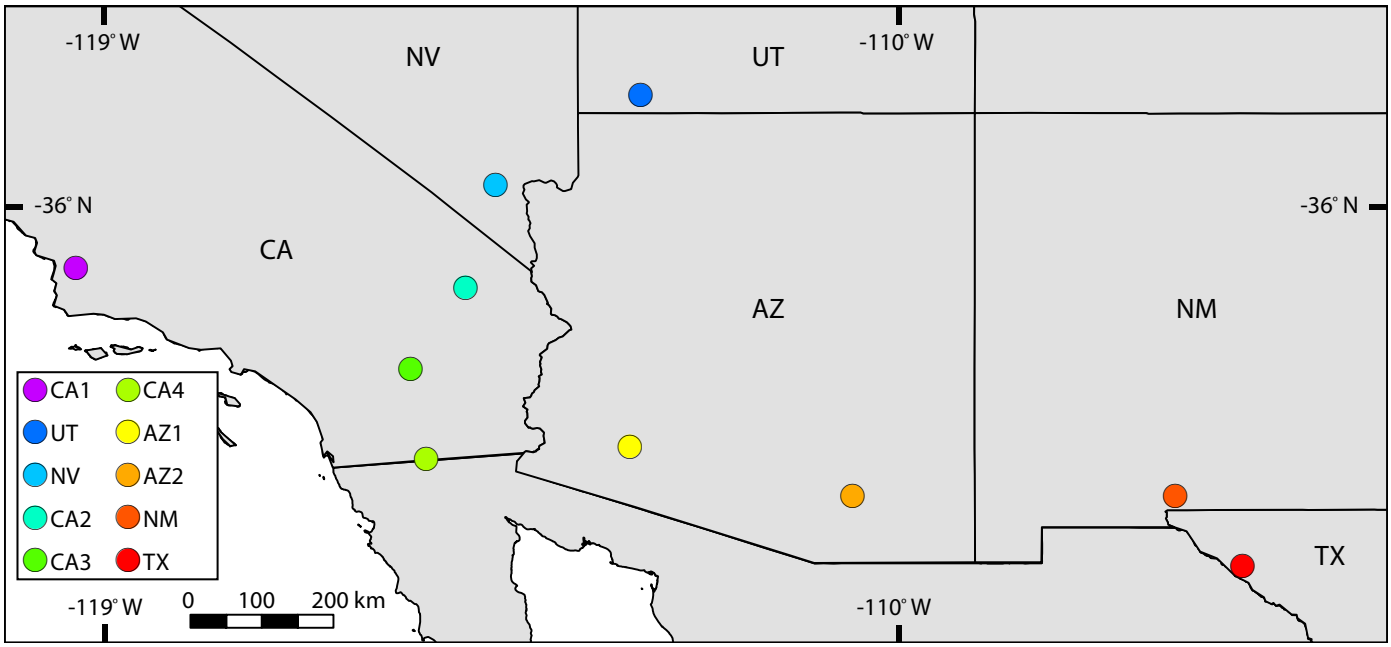

FIGURE 1. Sampling sites across the invaded range of Sahara mustard (*Brassica tournefortii*). See Table 1 for site characteristics.

the influence of maternal effects (Roach and Wulff, 1987). In total, we sowed 2000 field-collected seeds from 115 maternal lines and 10 sampling sites. Not all seeds were viable, resulting in 1600 seeds germinating from 87 maternal lines across the 10 sites.

Measurements

We measured phenological, morphological, and physiological functional traits of the second ex situ generation. We chose traits that have been shown to be important for invasives or that respond strongly to environmental conditions typical of the desert biomes invaded in North America (Leishman et al., 2007; Tecco et al., 2010; Huxman et al., 2013; Kimball et al., 2014; Murphy et al., 2016). Phenological traits included time to germination, leaf expansion, and flowering. We measured germination timing of each individual as the days from seed sowing to germination. We tracked leaf phenology daily during the first month and every other day thereafter. We recorded leaf expansion as the date of emergence for each of the first five true leaves each individual produced. We recorded time to flowering as the number of days from germination to anthesis.

We measured several morphological traits, including aboveground biomass components (including stem, leaf, and reproductive-structure dry weights), relative growth rate, allocation to leaf area, and allocation to reproduction. We randomly harvested three plants from each locality biweekly starting 1 mo after initial germination and ending when seeds ripened. Harvesting lasted for 3 mo, or 6 harvesting sessions. We cut aboveground components at the soil surface and sorted plant parts into leaves, stems, and reproductive structures. Leaves were counted, weighed, and digitally scanned using a Canon MF8200C printer (Canon, Tokyo, Japan) and a LI-3100C Area Meter (LI-COR, Lincoln, Nebraska, USA). We calculated leaf area for the 25 largest leaves (or all leaves if <25 were available) using ImageJ (Schneider et al., 2012). Any remaining leaves were grouped for area measurements. We calculated mean leaf area as the sum of the area of all leaves divided by the total number of leaves. We then dried all plant components for 48 h at 60°C to obtain dry weight. We estimated relative growth rates for each population as the slope of linear regressions between $\log_{10}$ transformed aboveground biomass and time (*sensu* Angert et al., 2007). Last, we calculated the percentage of biomass allocated to reproductive structures (% repro) as the dry weight of reproductive structures divided by the total aboveground biomass of each plant.

We also measured physiological traits, including water-use efficiency (WUE), leaf carbon (C_{mass}) and nitrogen (N_{mass}) content, and relative water content of leaves. We collected leaf tissues prior to flowering and concurrent with the third harvest for isotopic analysis. Leaf ^{13}C, C_{mass}, and N_{mass} were analyzed at the University of California, Davis Stable Isotope Facility via an elemental analyzer interfaced to a mass spectrometer (PDZ Europa, ANCA-GSL, and PDZ Europa 20-20; Secron, Cheshire, UK). We converted carbon isotope ratios to discrimination values (Δ, per mil δ—a time-integrated measure of water-use efficiency; Dawson et al., 2002) by the equation $\Delta = \delta_a - \delta_p / (1 + \delta_p) \times 0.0001$, where δ_a is the carbon isotope ratio of atmospheric CO_2 (assumed to be −8 δ) and δ_p is the measured carbon isotope ratio of the leaf tissue (Farquhar et al., 1989). Lower values of Δ indicate higher intrinsic WUE values (Dawson et al., 2002).

We measured relative water content (RWC) of leaves at peak productivity as a proxy for leaf turgor (Smart and Bingham, 1974). We sampled three individuals from each site and used leaf punches from the healthiest, fully emerged leaf from each plant. We obtained fresh weights of leaf punches and then floated leaves in distilled water in a Petri dish for 6 h in a dark room to allow for rehydration. We obtained the assumed turgid weights and dried leaves for 24 h at 60°C to obtain dry weights. We used these data to calculate RWC as $w_f - w_d / w_t - w_d$, where w_f, w_d, and w_t are fresh weight, dry weight, and turgid weight, respectively (Weatherley, 1950; González and González-Vilar, 2001).

Environmental data

We used BioClim climate variables from each sampling site to test for trait divergence and alignment with local environmental conditions (Hijmans et al., 2005). These climate variables represent annual and seasonal trends, as well as extremes in temperature and precipitation, which are often useful in describing species distributions. We evaluated 19 BioClim climate variables (BIO1–19; Hijmans et al., 2005) at a 30 arc-second resolution (~1 km^2) for inclusion in our models. We tested all variables for pairwise correlation across the study area using the Raster package in R to prevent overfitting (Hijmans and van Etten, 2012). We retained 7 of the 19 BioClim layers that had correlation coefficients under |0.70| (Appendix S1; see Supplemental Data with this article), four of which were related to temperature and three to precipitation. When variables were highly correlated, we retained those variables related most directly to our hypotheses. For example, we retained those related to winter precipitation, because our study system exists as a winter ephemeral plant, as well as variables that best captured the aridity gradient across the species' range. Temperature variables included isothermality ($temp_{iso}$; the mean monthly range divided by the annual range in temperatures; BIO3), temperature seasonality ($temp_{seasonality}$; standard deviation × 100; BIO4), and mean temperatures of the wettest ($temp_{wetqtr}$) and coldest ($temp_{coldqtr}$) quarters (BIO8–9). Precipitation variables included precipitation during the wettest ($precip_{wetmonth}$) and driest ($precip_{drymonth}$) months (BIO13–14), and precipitation of the coldest quarters ($precip_{coldqtr}$; BIO19).

Statistical analyses

We first calculated summary statistics by population for key functional traits associated with phenology, physiology, and morphology (Appendix S2). We then used Pearson correlation coefficients to identify which traits best represented these functional trait categories and removed autocorrelated traits ($r > |0.70|$). Nine key functional traits were retained for final analyses. (Appendix S3). These functional traits were combined with the reduced set of geographic and bioclimatic variables in subsequent analyses to understand variation across localities.

We used nested analysis of variance (ANOVA) to examine potential effects of site and maternal lineages as sources of variation in functional traits. We included age of the plant as a covariate for ANOVAs of non-phenology traits to account for potential time-dependent ontogenetic effects associated with different harvests. We $\log_{10}$ transformed measurements when needed to meet statistical assumptions. We then used hierarchical partitioning if the ANOVA showed significant population differences. Hierarchical partitioning allowed us to examine the relative contribution of geographic and bioclimatic temperature and precipitation variables in explaining variation in functional traits. Hierarchical partitioning enables better estimation of the relative importance of each variable

while also accounting for potential colinearity of explanatory variables (Chevan and Sutherland, 1991; Murray and Conner, 2009). For each hierarchical partitioning analysis, we first accounted for correlated error structures that arise from repeated measures (within populations) and used linear mixed-effects models with each functional trait as the response variable and maternal lineage nested within population as random effects and related the residuals to geographic and bioclimatic variables using hierarchical partitioning. We then performed randomization tests on each functional trait (1000 iterations each using an r^2 goodness-of-fit measure) to assess the significance of each geographic and bioclimatic variable. We computed *Z*-scores to determine the significance of each explanatory variable. Last, we used linear regression to test relationships between population means for each functional trait and the geographic and bioclimatic variables identified as significant by randomization tests (we report nonsignificant relationships in Appendix S4). All statistical analyses were carried out in R version 3.3.2 (R Core Team, 2014), and models were evaluated using the "effects" package (Fox, 2003).

RESULTS

We found strong differences among populations for all nine functional traits (Table 2), which suggests that trait divergence among populations may play a role in influencing plant performance across the invaded range of Sahara mustard. This was evidenced most strongly in phenological and morphological traits related to germination (days to germination: $F_{8, 501} = 7.88$, $P < 0.001$; seed weight: $F_{9, 119} = 3.70$, $P < 0.001$) and early growth (days to first leaf: $F_{8} = 4.97$, $P < 0.001$; days to first flower: $F_{8} = 5.41$, $P < 0.001$). These traits varied by 105%, 57%, 145%, and 99%, respectively, across the 10 localities evaluated from the invaded range in North America. However, populations also exhibited differences in additional morphological traits, including mean leaf area ($F_{7, 113} = 3.49$, $P = 0.002$) and proportion of biomass allocation to reproduction (% repro; $F_{8, 89} = 5.19$, $P < 0.001$), which varied by 1143% and 1300%, respectively. Populations also varied by 16%, 9%, and 121% for physiological traits related to water stress and nutrient allocation—RWC ($F_{8, 19} = 2.55$, $P = 0.045$), WUE ($F_{7, 9} = 51.68$, $P < 0.001$), and N_{mass} ($F_{7, 9} = 19.87$, $P < 0.001$). Variation within populations was observed for each category of trait variation (Table 2). Significant effects of maternal lineage were detected for days to germination ($F_{33, 501} = 5.92$, $P < 0.001$), first leaf ($F_{33, 489} = 4.97$, $P < 0.001$), first flower ($F_{31, 332} = 2.12$, $P < 0.001$), mean leaf area ($F_{27, 113} = 1.58$, $P = 0.05$), WUE ($F_{9, 9} = 84.16$, $P < 0.001$), and N_{mass} ($F_{9, 9} = 11.63$, $P < 0.001$).

Although several bioclimatic variables were important predictors of trait variation, no single variable was most important across all traits. $Precip_{wetmonth}$ explained four of the nine tested traits—primarily phenological features (i.e., germination time advanced, and number of days to first leaf increased with increasing precipitation) and morphological features (i.e., individual seed weight and

TABLE 2. Nested ANOVA results testing for effects of population, maternal lineage, and individual plant age on functional traits in Sahara mustard. Traits include phenological measurements of the number of days to germinate (days to germ), leaf phenology (first leaf), days to the first flower (first flower), individual seed weight (seed wt; mg), mean leaf area (mm^2), the percent of carbon allocated to reproductive structures (% repro), relative water content (RWC), water-use efficiency (WUE; Δ), and leaf nitrogen content (N_{mass}; μg). Significant *P* values are in bold.

	Population				Maternal line				Plant age				Error	
Trait	**df**	***SS***	***F***	***P***	**df**	***SS***	***F***	***P***	**df**	***SS***	***F***	***P***	**df**	***SS***
Days to germ	8.00	12.61	7.88	**<0.001**	33.00	34.26	5.19	**<0.001**	–	–	–	–	501.00	100.19
First leaf	8.00	10.15	4.97	**<0.001**	33.00	37.52	4.46	**<0.001**	–	–	–	–	489.00	124.79
First flower	8.00	907.00	5.41	**<0.001**	31.00	1378.70	2.12	**<0.001**	–	–	–	–	332.00	6958.30
Seed wt	9.00	0.72	3.70	**<0.001**	9.00	0.25	1.29	0.25	1.00	0.60	27.74	**<0.001**	119.00	2.59
Mean leaf area	7.00	7.60	3.48	**<0.001**	27.00	13.34	1.59	**0.05**	1.00	20.47	65.67	**<0.001**	113.00	35.31
% repro	8.00	0.13	5.20	**<0.001**	26.00	0.12	1.57	0.06	1.00	0.24	80.00	**<0.001**	89.00	0.27
RWC	8.00	3.30	2.55	**0.05**	15.00	2.87	1.18	0.36	1.00	0.10	0.60	0.45	19.00	3.07
WUE	7.00	0.01	51.68	**<0.001**	9.00	0.03	84.16	**<0.001**	1.00	0.00	59.11	**<0.001**	9.00	0.00
N_{mass}	7.00	1.14	19.87	**<0.001**	9.00	0.85	11.63	**<0.001**	1.00	0.33	40.05	**<0.001**	9.00	0.07

TABLE 3. Hierarchical partitioning results showing percentage of variance explained by individual geographic and bioclimatic variables. Asterisks indicate which variables explained a significant amount of variance based on randomization tests for hierarchical partitioning with an upper 95% confidence limit ($Z \geq 1.65$; statistical results reported in Appendix S5). Traits include phenological measurements of the number of days to germinate (days to germ), leaf phenology (first leaf), days to the first flower (first flower), individual seed weight (seed wt; mg), mean leaf area (mm^2), the percent of carbon allocated to reproductive structures (% repro), relative water content (RWC), water-use efficiency (WUE; Δ), and leaf nitrogen content (N_{mass}; μg).

Trait	**Latitude**	**Long**	**Elevation**	**$Temp_{seasonality}$**	**$Precip_{wetmonth}$**	**$Precip_{drymonth}$**	**$Precip_{coldqtr}$**
Days to germ	11.93	10.10	12.27	11.73	22.33*	15.24*	16.39*
First leaf	9.07	10.65	38.70*	11.34	16.55*	6.17	7.52
First flower	12.57	11.71*	7.77	36.93*	10.90	9.30	10.81
Seed wt	5.81	10.87	20.82*	4.82	26.07*	21.12*	10.48
Mean leaf area	23.82*	9.89	21.67*	13.63	17.06	8.44	5.49
% repro	17.55	9.29	7.17	7.07	27.02*	15.38	16.53
RWC	4.13	12.26	41.85	6.99	12.80	5.78	16.19
WUE	12.72	17.41	26.09	12.03	17.98	7.46	6.30
N_{mass}	17.63	24.80	2.96	27.81*	11.29	10.03	5.48

allocation to reproduction decreased with increasing precipitation; Table 3 and Appendix S5). Elevation was also clearly important, explaining ~40% of the variation in timing of first leaf and RWC (a phenological and a physiological trait, respectively). In both cases, elevation likely correlates with additional environmental variables that drive leaf phenology and potential cellular water deficit as indicated by RWC (a physiological trait that increased with elevation, tracking typical increases in precipitation with elevation). $Temp_{seasonality}$ also explained a substantial proportion of variation, but only for timing of the first flower (phenology; Table 3). For physiological traits, the only bioclimatic variable that explained variation was temperature seasonality, which had a positive relationship with leaf nitrogen content. All other geographic and bioclimatic variables explained <30% of the variation in functional traits.

$Precip_{wetmonth}$ explained a percentage of variance for the highest number of functional traits, including days to germination, timing of the first leaf, seed weight, and percentage of biomass allocated to reproductive structures (% repro). All of these are functional traits related to issues associated with aligning biological activity to conditions during germination and early stages of growth. Longitude explained a portion of variation in timing to first flower, reflecting typical phenology patterns from the coastal to interior sites associated with growing-season constraints arising from aridity. Similarly, variance in mean leaf area was explained by latitude. Finally, a percentage of variation in individual seed weights was explained by $precip_{drymonth}$, likely indicating a shift to investing in heavier seeds that could survive hot summers in relatively dry environments.

The number of days to germination decreased with increasing winter precipitation ($precip_{wetmonth}$; $r^2 = 0.49$, $P = 0.03$; Fig. 2). Time to first leaf increased with longitude ($r^2 = 0.50$, $P = 0.05$), again likely following typical phenology patterns moving inland. Time to first leaf also increased with increasing winter precipitation ($precip_{wetmonth}$; $r^2 = 0.56$, $P = 0.03$). Similar to hierarchical partitioning results, individual seed weights decreased with increasing winter precipitation and precipitation during the driest months ($precip_{wetmonth}$; $r^2 = 0.62$, $P = 0.01$; $precip_{drymonth}$; $r^2 = 0.52$, $P = 0.03$). This trend was also observed with percentage of biomass allocated to reproductive structures (% repro), which decreased with increasing winter precipitation ($precip_{wetmonth}$; $r^2 = 0.80$, $P < 0.01$; Fig. 2). Finally, the lowest RWC (i.e., highest cellular water deficit, although marginally significant; $r^2 = 0.43$, $P = 0.06$) was observed at the lowest elevations in desert sites. Concurrently, the highest water-use efficiency was observed at these low-elevation sites ($r^2 = 0.68$, $P = 0.01$) and followed $precip_{drymonth}$ (marginally significant $r^2 = 0.47$, $P = 0.06$; Fig. 2), indicative of adapting to water stress.

DISCUSSION

Invasive populations may encounter unique selective pressures and limitations across their ranges, including differences in abiotic conditions such as drought, temperature, and seasonality. Identifying which plant traits have contributed to and may predispose invasives to spread into novel environments allows us to better understand the mechanisms driving invasion, predict future patterns, and provide targets for management (Funk et al., 2008). The results of the present study demonstrate significant variation in key functional traits in Sahara mustard in a common garden environment, which suggests that this species has responded to variable selection pressures with different phenological, physiological, and morphological strategies across a broad range of environmental conditions in the southwestern United States. Further, we quantified the relative contributions of geographic and bioclimatic factors in explaining variation in observed phenotypes, showing that functional strategies of Sahara mustard corresponded with local variation in seasonally available precipitation. The shifts in phenological, morphological, and physiological traits observed among populations of Sahara mustard are likely to have facilitated its successful invasion across the region. This variation reflects altered water-use efficiency to tolerate drought stress, adjustment in the timing of key biological events within the context of aridity, and investment in reproduction to ensure future success. These patterns are consistent with the generalized strategies of desert adaptation used by ephemeral plants (e.g., Smith et al., 1997; Huxman et al., 2013). This suggests that Sahara mustard likely exploits trait relationships similar to those of native species that are successful in these environments, but also that it likely employs enhanced performance in several attributes that further contribute to success (e.g., Kimball et al., 2014).

While the ecological and evolutionary patterns in arid systems like those occupied by Sahara mustard are similar overall, regional environmental contexts vary considerably, particularly in rainfall variability and seasonal temperature covariance (Loik et al., 2004). Functional trait approaches that relate species performance to environmental variation have proven useful for determining effects of contemporary climate change (e.g., Kimball et al., 2010) and can be powerful in elucidating the mechanisms that promote the success of invasive species (Colautti and Barrett, 2013; Funk, 2013; Wolkovich et al., 2013; Winkler et al., 2016; Gilbert et al., 2017). However, a grand challenge in ecology and evolutionary biology is understanding how invasive species respond to and leverage environmental variation during establishment. This challenge is made more urgent by the need to forecast ecological and evolutionary dynamics in the face of climate change and future invasions.

Sahara mustard has colonized multiple ecoregions of North America in <100 yr and appears well poised to continue to dominate arid environments and expand its range. Part of this success has been attributed to the ability of some invasives to self-fertilize (Schemske, 1984; Barrett et al., 2008; Marushia et al., 2012; Pannell, 2015). Our results identify shifting phenologies, investment in leaves and reproductive structures, and water-use efficiencies to match environmental drivers as critical for establishment and survival in the invaded range. Sahara mustard responded to decreasing winter precipitation ($precip_{wetmonth}$) by increasing allocation to reproductive structures, thereby ensuring that seeds could tolerate drought stress in the driest sites. Together, these reproductive and functional traits likely allow Sahara mustard to overcome recruitment barriers that challenge species in novel environments (Weber and Schmid, 1998).

We found that Sahara mustard exhibits substantial population variation in germination and growth related to local, seasonal precipitation. In doing so, this species may be able to synchronize its growth to local conditions, which would not only increase its reproductive success, but also increase its competitiveness with native species (Powell et al., 2011; Wolkovich and Cleland, 2011). Thus, the level of trait divergence observed in our common gardens is consistent with local adaptation, given the unlikely alternatives that many distinct Sahara mustard genotypes invaded (Lawson Handley et al., 2011; Colautti and Barrett, 2013; Oduor et al., 2016; but see Genton et al., 2005; Oduor et al., 2015) or that genetic drift serendipitously resulted in environmental correlations. That

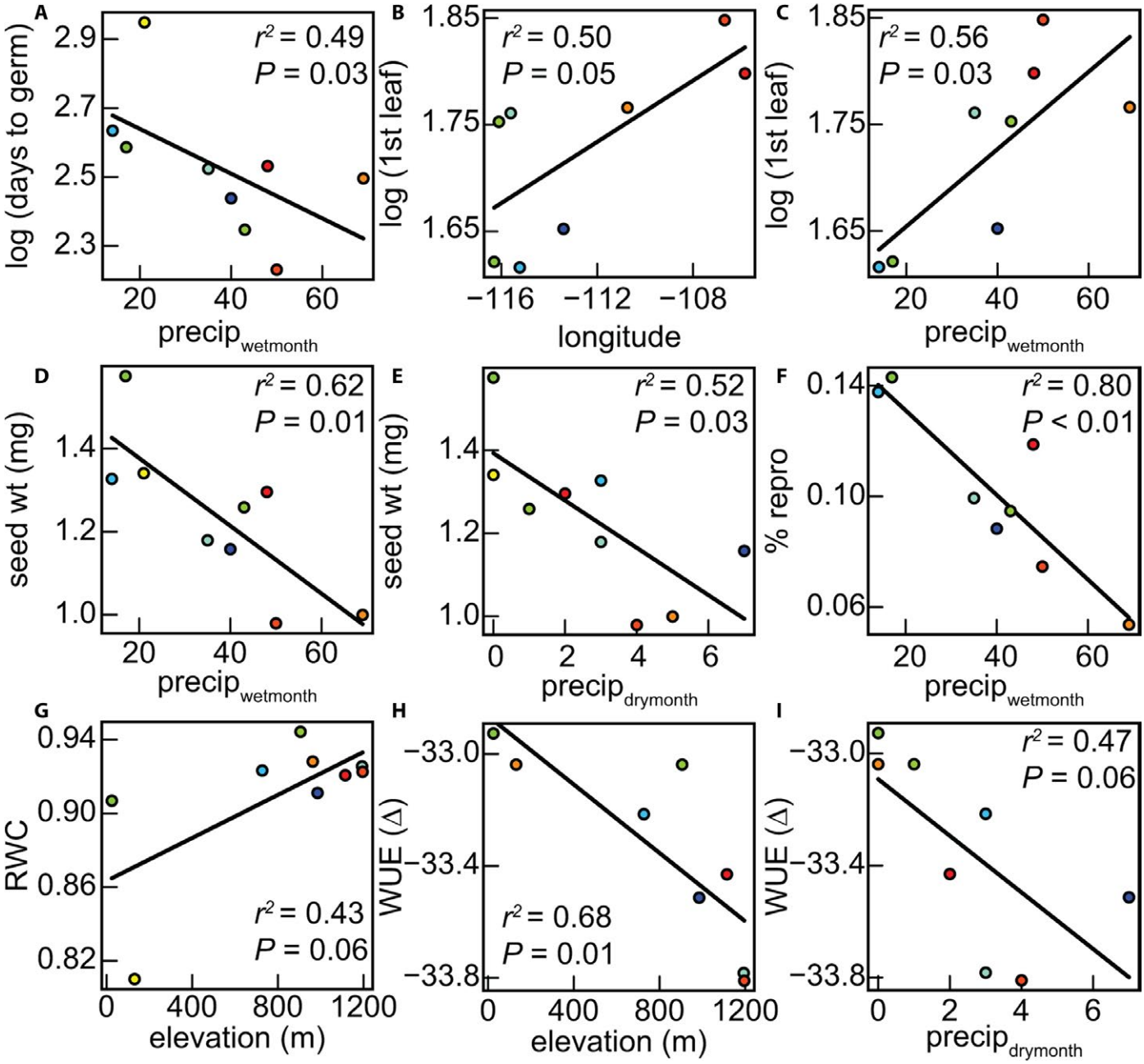

FIGURE 2. Linear regressions of functional traits and geographic and bioclimatic variables identified as significant in hierarchical partitioning analyses and with significant linear regressions (r^2 and P values are reported in each panel). Circle colors match those of each population in Figure 1. Graphs illustrate relationships between (A) days to germination and precipitation during the wettest month, (B) days to first leaf and longitude, (C) days to first leaf and precipitation during the wettest month, (D) individual seed weight and precipitation during the wettest month, (E) individual seed weight and precipitation during the driest month, (F) percentage of biomass allocated to reproductive structures and precipitation during the wettest month, (G) relative water content (RWC) and elevation, (H) water-use efficiency (WUE) and elevation, and (I) WUE and precipitation during the driest month.

said, plasticity may also explain part of the trait variation we observed. Nonetheless, our results suggest a genetic component to the variation in functional traits in Sahara mustard, which likely contributes to the continued success of the populations we sampled. Given these populations' variability across their range, the ability to rapidly adapt to new environments may enable the species to spread into additional semiarid or pulse-driven systems (Drenovsky et al., 2012).

Phenotypic plasticity is often important for successful establishment of invasives early in the invasion process (Sexton et al., 2002; Richards et al., 2006; Funk, 2008; Davidson et al., 2011; Castillo et al., 2014). Plasticity can promote local adaptation by enabling populations to persist in novel environments, in which they experience new selection pressures and potentially lose plasticity through time (Parker et al., 2003; Franks et al., 2007; Ghalambor et al., 2007; Crispo, 2008). While we cannot fully distinguish between fixed

and plastic variation in traits from our data, we did address possible maternal and ontogenetic effects on trait variation and have evidence for population differentiation in traits in a common garden environment. It is likely that Sahara mustard also exhibits plasticity, given its large range that contains many similar environments (Tecco et al., 2010; Drenovsky et al., 2012). Future work to quantify the relative contributions of fixed and plastic variation in traits in response to precipitation, temperature, and geographic position would be productive for understanding the mechanisms driving intraspecific variation in traits. This would also elucidate the microevolutionary dynamics associated with the successful invasion of this species and would be valuable to pursue using a reciprocal garden design in both native and invaded ranges (Moloney et al., 2009). An open question is how these processes interact to influence plant behavior, encompassing the complex system of multiple traits, and how plasticity, population divergence, and ontogenetic dynamics are combined across the range.

Overall, our results demonstrate that this species exhibits functional trait variations across populations that correspond to environmental variability across thousands of kilometers in its invaded range. We have thus shown that linking life-history strategies, functional traits, and responses to environmental variation can assist in producing a mechanistically based predictive framework for ecologists to understand the behavior of invasive species in space and time (Huxman et al., 2013). Although many invasions arise as a result of accidental introductions (Lehan et al., 2013), range expansions of already established invasives may occur under future climate scenarios (Novy et al., 2012; Nguyen et al., 2016), and Sahara mustard seems poised for such an expansion. Sahara mustard's range of functional strategies across multiple environments, coupled with self-compatibility and high production of propagules, make it a strong contender for continued invasion under future scenarios (DeFalco et al., 2003; Nguyen et al., 2016).

ACKNOWLEDGEMENTS

This research was supported by the Tubb Canyon Desert Conservancy, the Robert Lee Graduate Student Research Grant through the Joshua Tree National Park Association, the Howie Wier Memorial Conservation Grant through the Anza-Borrego Foundation, the Forrest Shreve Student Research Fund through the Ecological Society of America, the Mildred E. Mathias Graduate Student Research Grant through the UC Natural Reserve System, the Mayhew Graduate Research Award through the Boyd Deep Canyon Desert Research Center, a Graduate Assistance in Areas of National Need Research Grant (GAANN), UCI's Department of Ecology & Evolutionary Biology, the Ayala School of Biological Sciences, the UCI Data Science Initiative at the University of California, Irvine, and the Victor and Virginia Voth Family Trust. Additional funding (to M.K.) was provided by UCI's Summer Undergraduate Research Program (UCI SURP). Plant material was collected under National Park Service permit MOJA-2015-SCI-0021. Field, laboratory, and greenhouse work was made possible with the help of A. Choi, A. Collins, C. Bell, A. Dang, A, Desai, J. Dong, G. Ferguson, P. Holm, D. Hughson, A. Kaiser, H. Kooner, A. Kearns, M. Li, K. Lund, K. Phan, K. Rabbani, T. Scott, L. Smith, R. Staehle, C. Vagnier, S. Weller, and W. Yang. Thanks to the Huxman and Gremer lab members and Center for Environmental Biology staff for feedback on the manuscript, and to three anonymous reviewers for their helpful comments.

DATA ACCESSIBLITY

Data have been archived through figshare under https://doi.org/10.6084/m9.figshare.6175808.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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