Competition × drought interactions change phenotypic plasticity and the direction of selection on Arabidopsis traits

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Summary

- Populations often exhibit genetic diversity in traits involved in responses to abiotic stressors, but what maintains this diversity is unclear. *Arabidopsis thaliana* exhibits high within-population variation in drought response. One hypothesis is that competition, varying at small scales, promotes diversity in resource use strategies. However, little is known about natural variation in competition effects on Arabidopsis physiology.
- We imposed drought and competition treatments on diverse genotypes. We measured resource economics traits, physiology, and fitness to characterize plasticity and selection in response to treatments.
- Plastic responses to competition differed depending on moisture availability. We observed genotype–drought–competition interactions for relative fitness: competition had little effect on relative fitness under well-watered conditions, whereas competition caused rank changes in fitness under drought. Early flowering was always selected. Higher $\delta^{13}C$ was selected only in the harshest treatment (drought and competition). Competitive context significantly changed the direction of selection on aboveground biomass and inflorescence height in well-watered environments.
- Our results highlight how local biotic conditions modify abiotic selection, in some cases promoting diversity in abiotic stress response. The ability of populations to adapt to environmental change may thus depend on small-scale biotic heterogeneity.

Introduction

The persistence of genetic variation in phenotypes in spite of the forces eliminating diversity is a central puzzle in biology (Mitchell-Olds *et al.*, 2007). Though experiments often show strong selection under abiotic stress, populations still exhibit (perhaps surprising) diversity in response to such treatments (Hosgood & Parsons, 1968; Sultan & Bazzaz, 1993). Understanding diversity within populations is an important research goal partly because this diversity affects the adaptability of populations to environmental change (Pease *et al.*, 1989; Lynch & Lande, 1993; Jump *et al.*, 2009).

The effects of climate conditions (like precipitation) on organisms occur within the context of fine-scale environmental heterogeneity, which can exacerbate or mitigate climatic conditions (Urban *et al.*, 2013; Farrior *et al.*, 2013b; Clark *et al.*, 2014; Moran & Alexander, 2014). This heterogeneity might select for phenotypic plasticity in a single optimal genotype. Alternatively, heterogeneity can promote genetic variation within populations by favoring different genotypes in different environments; that is, a genotype × environment (G × E) interaction causing a fitness trade-off across environmental gradients (Levene, 1953; Hamrick & Holden, 1979; Schmitt *et al.*, 2003).

Limiting resources that are influenced by climate (e.g. moisture) may be especially likely to exhibit interactions with competition. In plants, for example, different levels of allocation to roots for water acquisition may be favored depending on the presence of neighboring individuals that compete for water (Farrior *et al.*, 2013a). Differing water use efficiencies (WUEs) can be favored under moisture limitation depending on whether competitors are present (Campitelli *et al.*, 2016). Specifically, competition can favor more resource-acquisitive strategies when resources are limited (Farrior *et al.*, 2013a).

Our current study system *Arabidopsis thaliana* (hereafter, Arabidopsis) is useful for studying these processes for several reasons. First, it exhibits substantial diversity in drought response within populations. Studies of genetic variation in $\delta^{13}C$, a proxy for WUE, and stomata have found statistically significant but weak relationships with climate of origin (Dittberner *et al.*, 2018), as have studies of survival (Exposito-Alonso *et al.*, 2018). These weak relationships may be surprising given the tendency for local adaptation in Arabidopsis populations (Fournier-Level *et al.*, 2011) and stand in contrast to cold tolerance, which is more closely tied to local winter temperatures (Ågren & Schemske, 2012; Monroe *et al.*, 2016; Gienapp *et al.*, 2017). Second, though Arabidopsis occurs in a wide range of precipitation regimes (Hoffmann, 2002) it also occupies a wide range of microhabitats (Baron *et al.*, 2015), suggesting the opportunity for precipitation × microhabitat interactions. Some published data suggest the potential for competition × climate interaction

effects on performance (Baron *et al.*, 2015; Campitelli *et al.*, 2016), though the physiological basis of these interactions is largely unknown. Third, previous research has yielded insight into genetic and physiological mechanisms of drought adaptation, providing a basis for specific hypotheses about how moisture and competitive gradients interact to select for different traits (McKay *et al.*, 2003; Juenger *et al.*, 2010; Des Marais *et al.*, 2012; Lovell *et al.*, 2013; Kenney *et al.*, 2014; Lasky *et al.*, 2014, 2018; El-Soda *et al.*, 2015; Bac-Molenaar *et al.*, 2016; Dittberner *et al.*, 2018; Exposito-Alonso *et al.*, 2018, 2019; DeLeo *et al.*, 2020).

Arabidopsis drought responses have been characterized into a stereotypical tradeoff between avoidance and escape (McKay *et al.*, 2003; Kenney *et al.*, 2014). Avoidance involves phenotypes that minimize water loss (e.g. stomatal closure) and maximize gain (e.g. root growth). Escape involves phenology and rapid development that matches with time periods when moisture is abundant (Ludlow, 1989). Escape may be adaptive when low soil moisture occurs at the end of growing seasons (Kenney *et al.*, 2014), whereas avoidance may be adaptive when moisture is limited throughout a growing season (Campitelli *et al.*, 2016). Escape has been characterized by rapid flowering, high specific leaf area (SLA), high leaf nitrogen (N), high carbon (C) assimilation rate A, low root : shoot mass ratio, and low WUE (Ludlow, 1989; Des Marais *et al.*, 2012; Kenney *et al.*, 2014; El-Soda *et al.*, 2015), whereas avoidance is characterized by the opposite values (but see Ferguson *et al.*, 2019). Arabidopsis is a rapidly maturing annual, which is an early successional strategy that may be adaptive when neighbors are better resource competitors. In disturbed habitats where Arabidopsis frequently occurs, competition likely increases over time as colonists grow. In this situation, moisture availability may decrease across a season due to greater uptake combined with increasing evaporative demand as temperatures warm, favoring drought escape (Cohen, 1970; McLeod *et al.*, 2012; Campitelli *et al.*, 2016).

Despite the importance of Arabidopsis as the model plant, there exists little information on how diverse ecotypes respond physiologically to the presence of neighboring plants. Plant responses to neighbors may use a variety of cues, including nutrient availability (Schenk, 2006), red : far-red light ratios (Aphalo *et al.*, 1999), or chemicals (Badri *et al.*, 2012). In Arabidopsis, Campitelli *et al.* (2016) found large biomass reductions and lower WUE in response to grass neighbors, even under ample water supply. One nonresource-based mechanism for sensing neighbors is perception of root exudates, which are used by diverse species for belowground sensing of neighbors (Badri *et al.*, 2012; Schmid *et al.*, 2013; van Dam & Bouwmeester, 2016). Strigolactones (SLs) are exuded belowground by most plants (Al-Babili & Bouwmeester, 2015) and have been implicated in neighbor avoidance in a moss (Proust *et al.*, 2011). Furthermore, Arabidopsis plants can suppress inflorescence branching (Scaffidi *et al.*, 2014) and close stomata (Lv *et al.*, 2018) in response to SLs in growth media. To the extent that apical dominance in the presence of competitors enhances fitness (Baron *et al.*, 2015), it may be adaptive for a plant to suppress branching in response to SLs of neighbors.

We studied how competition interacts with moisture to drive plasticity and selection on life history and physiology in Arabidopsis. Although additional resources vary with competition (e.g. nutrients), we controlled these in our experiments to focus on competition for water.

We focused on these specific questions:

(**1**) How does Arabidopsis respond to competition and drought via changes in life history and physiology? We hypothesized that drought would induce greater WUE due to stomatal closure, induce greater SLA and leaf N as part of a drought escape strategy, and induce lower performance (biomass and fitness). We hypothesized that competition would induce inflorescence elongation, induce greater investment in resource acquisition (greater SLA, leaf N, lower WUE) partly due to perception of SLs in soil, and induce lower performance.

(**2**) Does competition induce rank-changing G × E in fitness, suggesting that competitive gradients could promote diversity in response to abiotic stress within populations? We hypothesized that, under conditions with ample resources, the presence of neighboring plants would have little influence on the relative fitness of diverse genotypes. By contrast, under moisture limitation, we expected that competition would favor genotypes that differ in multiple traits (i.e. competition would change whether drought escape or avoidance strategies were favored) compared with when competitors are absent.

(**3**) What traits explain genetic variation in fitness response to competition (G × E)? We hypothesized that genetic trade-offs are associated with alternate drought response strategies, such that contrasting treatments change the sign of directional selection coefficients across treatments.

(**4**) Do traits exhibit genetic variation in plasticity that is under selection across competitive environments? We hypothesized that changes in some traits across competitive environments would be associated with higher average fitness across competitive environments.

Materials and Methods

Plant material

We studied 17 diverse genotypes from across the native range of Arabidopsis and the reference genotype (Columbia) for a total of 18 genotypes (Supporting Information Tables S1, S2). These genotypes mostly represent diverse lines used to create a multi-parent linkage mapping population (Kover *et al.*, 2009). We obtained seeds from the Arabidopsis Biological Resource Center. However, it was later discovered that two lines (Can-0 CS76740 and Wu-0 CS78858) were contaminants from the supplying laboratory; that is, they were not the original labeled genotype, though they were unique unidentified genotypes (Pisupati *et al.*, 2017) and we included them in the experiments. Seeds were grown for one generation in the laboratory at 16°C with a 16 h photoperiod and the resulting next generation of seed was used in the present experiments. For competitors, we used three genotypes (Adi-10, Bd21-3, and Bd30-1) of *Brachypodium distachyon*, a widespread Mediterranean annual grass. Both Arabidopsis and

B. distachyon occur broadly across mesic Mediterranean sites, making them potential natural competitors. However, these plant communities are diverse (Alados *et al.*, 2004) and it is likely selection on species interactions has been diffuse and not specific to this pair of species. The *B. distachyon* genotypes had similar growth form and rate and were simultaneously bulked in a glasshouse.

Experimental design and conditions

To characterize genetic variation in response to moisture differences and their interactions with competition, we grew these genotypes in a split-plot design with two crossed treatments (for a total of four conditions): (1) well-watered, no competition (i.e. a single Arabidopsis plant in a pot); (2) well watered, with competition, (3) intermittent drought, no competition; and (4) intermittent drought, with competition (Fig. S1). Each Arabidopsis genotype in each treatment had 10 total replicates per treatment, five for an initial harvest before flowering and five for a post-senescence harvest (total Arabidopsis plants was 720).

We grew plants in a walk-in Conviron C1210 growth chamber (Conviron Ltd, Winnipeg, MB, Canada). We designed a temperature and photoperiod program (Figs S2, S3; Table S3) to mimic a growing season starting with warm temperatures early in the local growing season, which we reasoned would be a potential site for moisture limitation, and centrally located in the species range (Methods S1).

Competition was imposed by sowing six seeds of *B. distachyon*, along the outside perimeter of each pot. To focus on competition for water, we limited light competition by restraining *B. distachyon* tillers to the pot perimeter with a mounted stainless steel ring (Fig. S4). Drought treatments were imposed by removing bottom water at 16 d after planting (DAP), when all plants had at least the first true leaves fully expanded (Methods S1). To limit nutrient competition, pots in all treatments were fertigated at the same time of day with the same nutrition strength and volume.

Plant harvest and phenotyping during the vegetative stage To measure phenotypes during vegetative growth that required destructive harvest, we randomly selected five replicates for each genotype and treatment combination for harvest at 55–56 DAP, just before the initiation of the first flowering genotypes. In this harvest, *B. distachyon* shoots were cut at soil level, dried at 90°C, and weighed. Roots of Arabidopsis plants under no-competition treatments were washed, dried at 90°C, and weighed (roots in competition were too difficult to separate from *B. distachyon* roots). Rosettes were removed from pots 1–2 cm below the soil level and were preserved in 75% ethanol at 4°C. These rosettes were later measured for total leaf area, dry rosette biomass (excluding root), root diameter at 1 cm below the soil surface, stomatal density using a representative mid-aged leaf, SLA using one representative mid-aged leaf, leaf $\delta^{13}C$, leaf $\delta^{15}N$, and total leaf C and N composition. Leaf tissue samples for $\delta^{13}C$, $\delta^{15}N$, and total C and N composition were prepared by drying the complete rosettes in coin envelopes for 12–24 h at 65.6°C, then grinding

and homogenizing all leaves from the rosette to a fine powder using a mortar and pestle. Based on our estimated N content, we packaged a 1.5–2.0 mg aliquot of finely ground leaf tissue from each rosette into an $8 \times 5\ mm^2$ tin capsule (EA Consumables, Pennsauken, NJ, USA). Samples were sent to the University of California Davis Stable Isotope Facility (SIF) for $\delta^{13}C$, $\delta^{15}N$, total C and N analyses using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer. We measured whole-plant Arabidopsis gas exchange on a separate set of plants in an experiment that replicated the temperature, soil, and photoperiod conditions in the main experiment (Methods S1).

Response to simulated root exudate strigolactones of neighbors We used a synthetic SL applied to the soil, GR24^{rac} (ChemPep Inc., Wellington, FL, USA), to explore how SLs from neighboring *B. distachyon*, which exude SLs from their roots (Changenet, 2018), might affect Arabidopsis performance and traits. Four of our genotypes were selected: two that were highly sensitive to competing grass neighbors (Sf-2 and Ct-1), and two that were less sensitive to neighbors (Wil-2 and Ws-0) under well-watered conditions. Plants were grown alone in pots (no competition). Growing conditions were as already described in the main experiment. Plants received bottom water until the first true leaves were expanded, at which point the water was removed and treatment applications were started. Plants were then top watered evenly throughout the top of the potting mix around the rosette using a pipette every day with 3 ml of either 7.8 μM GR24 solution, 0.78 μM GR24, or tap water, with five individuals per genotype per treatment. All plants were harvested 52 DAP, before flowering initiation. Rosette biomass and quantum yield of photosystem II (PSII) using a MultispeQ v.2.0 (Kuhlgert *et al.*, 2016) were measured. Leaf $\delta^{13}C$ and total leaf C and N were measured from tissue analyzed at the UC Davis SIF.

Plant harvest and phenotyping at maturity Fecundity of those Arabidopsis plants that survived to reproduction was estimated when all siliques reached maturity (dried and brown) and the rosette leaves had senesced, using total fruit length as an estimate of fecundity (Gnan *et al.*, 2014). We measured total silique number and length of six siliques corresponding to the 10th, 20th, 40th, 60th, 80th and 90th percentiles of silique positions along the inflorescence in order to represent silique length along the inflorescence (e.g. the 10th percentile silique was higher up the inflorescence than 10% of siliques). For each plant, we also measured inflorescence height and the number of inflorescence branches. After siliques were measured, we dried the mature inflorescence and rosette separately (in addition to rosettes that did not flower) at 90°C for 24 h to get aboveground dry biomass.

Data analysis

Broad-sense heritability within treatments was calculated as the proportion of variation in phenotypes explained by genotype identity within each treatment, using a general linear model. We used linear mixed models to study sources of phenotype variation, with drought and competition treatments as fixed effects

and genotypes, genotype × treatment interactions, and trays as random effects. With these mixed models we tested the hypothesis that fixed effects were zero and calculated variance components for random effects using the R package VCA (Schuetzenmeister & Dufey, 2018). We calculated 95% confidence intervals (CIs) on variance components (constrained to be nonnegative) and report as significant components where the interval excludes zero. We calculated genotypes' breeding values for each trait in each treatment using similarly constructed linear mixed models, using the R package LME4 (Bates et al., 2013). To assess whether there were genetic correlations in traits often thought to represent coordinated strategies, we calculated Pearson's correlations between breeding values for flowering time (FT), SLA, leaf C : N, $\delta^{13}C$, and assimilation rate A.

We tested for evidence of selection within each treatment by fitting linear regression models of relative fitness (absolute fitness/mean fitness among genotypes within a treatment) as a function of breeding values for individual unit-standardized phenotypes. Flowering time was a trait under strong selection in all treatments, and thus we also tested trait correlations with fitness in multiple regression while also including a FT covariate, which allowed us to get better estimates of direct selection acting on a trait while accounting for FT selection (Lande & Arnold, 1983).

We tested for changing selection across competition treatments within the same moisture regime using t-tests. We focus on a soft selection scenario where individual fitness is density dependent, which may be particularly appropriate for comparisons across competitive treatments. Under this scenario, the appropriate approach is to relativize fitness within each treatment (i.e. combination of moisture and competitive conditions) (De Lisle & Svensson, 2017). For comparison, we included tests of changing selection when fitness was relativized across competitive treatments in the same moisture regimes, corresponding to a hard selection scenario (De Lisle & Svensson, 2017).

We also tested for selection on plasticity in response to competition, while accounting for differences among genotypes in their average traits. We fit linear models with breeding values and tested how trait change in response to competition within a given moisture treatment was associated with absolute fitness in each individual competition treatment. We employed a multiple regression that included trait means averaged across competition treatments (Stinchcombe et al., 2004). Greater detail on the commands used in statistical software can be found in Methods S1.

Results

Treatment effects on performance and physiology

We studied how drought and competition influenced individual Arabidopsis performance and physiology (question (1) in the Introduction section). Drought and competition generally reduced plant performance, causing plants to have significantly smaller rosettes at mid-experiment harvest (rosette weight$_v$ and total leaf area$_v$; v, vegetative), lower inflorescence weight, shorter

inflorescences, fewer total mature fruits (siliques), shorter fruits, and less aboveground biomass (AGB$_m$; m, mature, i.e. end of experiment harvest; linear mixed-effects models (LMMs), all $P < 0.05$; Fig. 1; Table 1). A notable exception was that plants had larger rosette weight$_m$ (at final harvest) under drought treatments compared with the well-watered treatment (LMM, drought fixed-effect estimate = 55.3 mg, $P < 10^{-6}$). The number of inflorescence branches was strongly reduced under competition (LMM fixed effect, $P < 10^{-8}$), without any significant drought or interaction effects.

There was a significant interaction between competition and drought for AGB$_m$, inflorescence weight, inflorescence height, fruit number, and average fruit length, such that under the combination of drought and competition these traits were greater than expected from the additive contribution of the two treatments (LMM fixed effects all $P < 0.05$; Table 1). However, rosette weight$_m$ and average fruit length were lower than expected under combined drought and competition (Fig. 1; Table 1).

Survival to reproduction was high across treatments, with 95% of plants surviving until flowering (only one plant survived but did not flower by the end of the experiment). There was no pre-flowering mortality in either no-competition treatment (100% survival). By contrast, with competition, survival was 98% under well-watered conditions and 84% under drought, indicating that competition combined with drought was the harshest treatment. Mean genotype absolute fitness (mean estimated total mature fruit length per initial seedling following thinning) was highest under well-watered conditions without crowding (1900 mm, SD = 599 among all individuals), followed by drought without crowding (656 mm, SD = 264), well-watered and crowding (387 mm, SD = 181), and drought and crowding combined (131 mm, SD = 95). We did not measure fecundity on *B. distachyon*, though its total AGB was greater in well-watered treatments than in drought treatments at the mid-experiment harvest (mean pot total biomass: well watered, 0.36 g, SD = 0.05; drought, 0.22 g, SD = 0.04).

In contrast to the whole plant performance measures described hitherto, traits associated with life history or water balance physiology showed more diverse responses to water and competition (Fig. 1). For example, mean FT showed a significant competition by drought interaction, such that flowering was significantly delayed only under combined competition and drought (LMM, competition × drought fixed effect $P = 0.0007$; Table 1). Competition resulted in significantly decreased root diameter (LMM, fixed effect $P < 10^{-8}$) and reduced $\delta^{13}C$ (a proxy for WUE, $P < 10^{-5}$) across moisture treatments (Table 1). Under drought, competition resulted in even greater reductions in root diameter (LMM, competition × drought fixed effect $P < 10^{-6}$) and greater SLA ($P = 0.0002$), whereas SLA was not affected by competition in well-watered conditions. Under well-watered conditions, competition resulted in greater leaf C : N (LMM, competition × drought fixed effect $P < 10^{-6}$) and reduced $\delta^{15}N$ ($P < 10^{-8}$), whereas these were not affected by competition under drought (Fig. 1; Table 1).

Drought treatments (apart from competition effects) resulted in reduced root weight and root : shoot ratio, greater stomatal
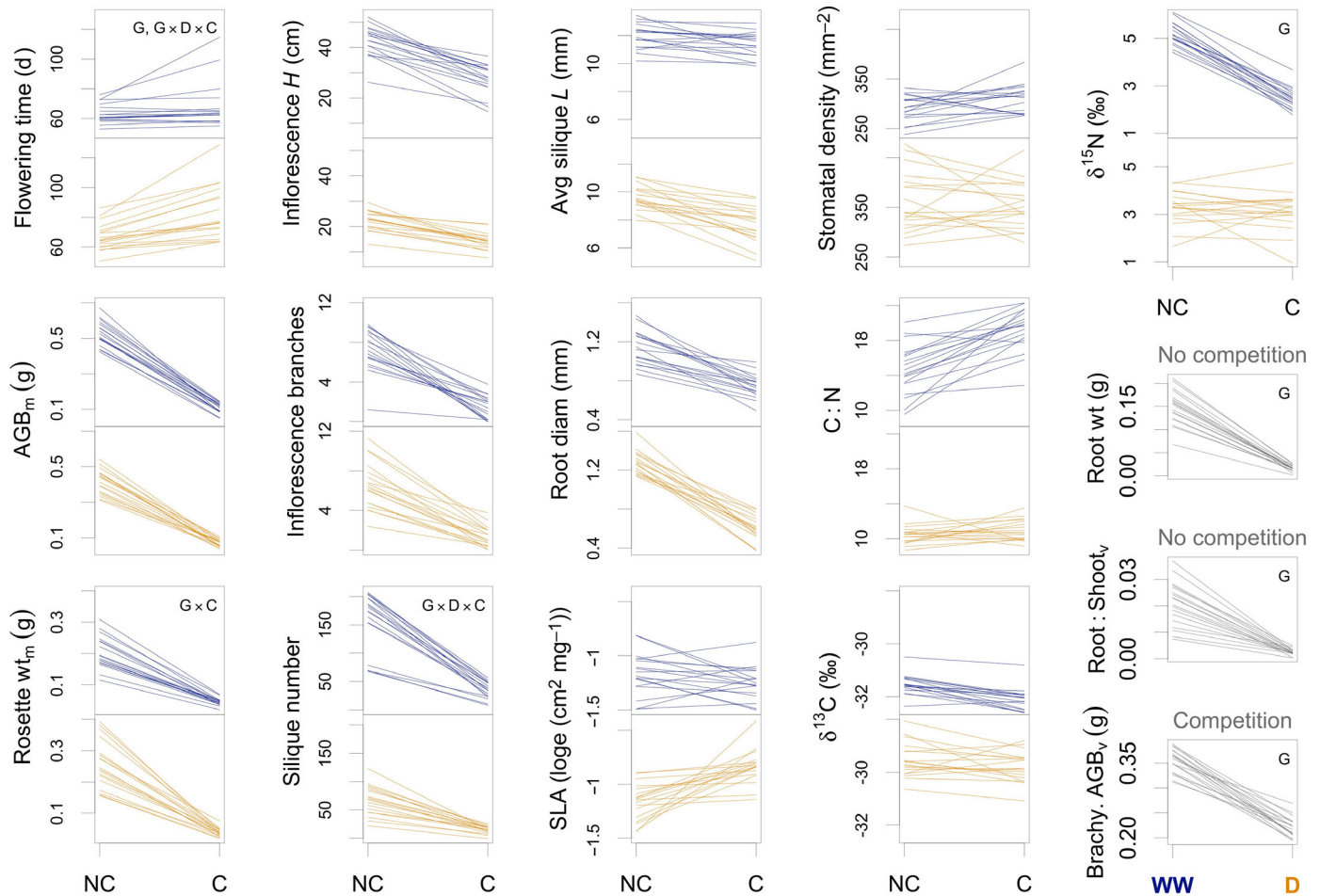
Well watered   Drought

Fig. 1 Reaction norms for traits across 18 Arabidopsis genotypes (each line represents one genotype). Lines show breeding values estimated from linear mixed models. NC, no competition; C, competition; WW, well watered; D, drought. At right in gray are three traits that were only measured in a single competition/no-competition treatment. Three traits showing significant variance components for genotype (G) or genotype × treatment (e.g. G × D) interactions are indicated. All traits showed significant (false discovery rate < 0.05) fixed effects for at least one treatment or treatment interactions (Table 1 for details). AGB, aboveground biomass; C : N, carbon : nitrogen; H, height; L, length; SLA, specific leaf area; v, vegetative harvest; m, mature harvest.

density, lower leaf C : N, greater $\delta^{13}C$, and lower $\delta^{15}N$ (all traits from mid-experiment vegetative harvest, LMM, all drought fixed effects $P < 0.004$; Fig. 1; Table 1).

We also addressed whether plastic responses to competitor plants were consistent with the effects of SLs in exudate. Consistent with responses to *B. distachyon* neighbors, Arabidopsis showed reductions in aboveground vegetative biomass with increased SL levels ($GR24^{rac}$) under well-watered conditions (Fig. S5, ANOVA on log proportional biomass with ranked GR24 treatment covariate, $P < 10^{-15}$, genotype × GR24 interaction $P = 0.7398$). However, the SL treatment affected other traits in ways inconsistent with responses to *Brachypodium*, causing increased $\delta^{13}C$ (ANOVA $\delta^{13}C$ response to ranked GR24 treatment covariate, $P = 0.0004$, genotype × GR24 interaction $P = 0.1588$) and decreased leaf C : N (ANOVA, $P < 10^{-6}$, genotype × GR24 interaction $P = 0.2508$; Fig. S5). GR24 had genotype-specific effects on the quantum yield

of PSII, with some genotypes having greater PSII yield with increasing GR24 and one having decreased PSII yield with increasing GR24 (ANOVA quantum yield of PSII response to ranked GR24 treatment covariate, $P = 0.4047$; genotype × GR24 interaction $P = 0.0088$).

Genetic and genotype × environment interaction effects on traits

Broad-sense heritability within treatments differed widely among traits, with FT having the highest heritability in every treatment (ranging from 0.88 in drought and competition to 0.96 in well watered and competition; Table S4). Heritability averaged among traits was highest in the well-watered no-competition treatment, followed by well-watered competition, drought no competition, and drought competition. Heritability was higher for leaf C : N than

Table 1 Results of treatment fixed effects on Arabidopsis phenotypes from a linear mixed-effects model where genetic and tray effects were modeled as random effects.

	P-value					
	Competition–no competition (fixed effect)	*P*-value	Well watered–drought (fixed effect)	*P*-value	Competition and well watered–competition and drought (fixed effect)	*P*-value
Total silique length	−1513.893	**< 0.0001**	1246.150	**< 0.0001**	−974.521	**< 0.0001**
AGB$_m$	−0.422	**< 0.0001**	0.111	**< 0.0001**	−0.075	**0.0006**
Rosette weight$_m$	−0.158	**< 0.0001**	−0.055	**< 0.0001**	0.061	**< 0.0001**
Inflorescence weight	−0.263	**< 0.0001**	0.167	**< 0.0001**	−0.136	**< 0.0001**
Inflorescence height	−15.149	**< 0.0001**	20.249	**< 0.0001**	−6.960	**< 0.0001**
Inflorescence branches	−5.844	**< 0.0001**	0.751	0.0927	−0.654	0.2148
Flowering time	5.061	0.0572	−3.601	0.0841	−10.510	**0.0007**
Silique number	−124.911	**< 0.0001**	92.501	**< 0.0001**	−73.055	**< 0.0001**
Average silique length	−0.643	**0.0141**	2.379	**< 0.0001**	1.172	**0.0005**
Root weight$_v$			0.132	**0.0019**		
Root diameter$_v$	−0.385	**< 0.0001**	−0.154	**0.0178**	0.295	**< 0.0001**
Root : shoot			0.018	**0.0023**		
Total leaf area$_v$	−37.098	**< 0.0001**	6.798	**0.0054**	−2.442	0.0920
Stomatal density	19.723	0.0873	−71.873	**0.0031**	27.946	**0.0315**
Rosette weight$_v$	−5.543	**< 0.0001**	0.470	0.2632	0.609	0.1278
log(SLA)	−0.091	0.0814	−0.004	0.9610	−0.397	**< 0.0001**
Leaf C : N	4.598	**< 0.0001**	4.082	**0.0006**	4.167	**< 0.0001**
δ^{13}C	−0.569	**< 0.0001**	−1.964	**< 0.0001**	−0.322	0.0533
δ^{15}N	−2.761	**< 0.0001**	1.916	**< 0.0001**	−2.528	**< 0.0001**
Brachypodium AGB			0.135	**< 0.0001**		

Fixed effects are in units of the trait. Bold *P* values are significant at false discovery rate < 0.05 for each contrast across traits.
AGB, aboveground biomass; C, carbon; m, mature harvest; N, nitrogen; SLA, specific leaf area; v, vegetative harvest.

leaf proportion N in most treatments, and thus in the following we focus results on C : N.

We generally found that FT and δ^{13}C were negatively correlated: later flowering genotypes had lower δ^{13}C (well watered, competition $r = −0.50$; drought, no competition $r = −0.49$; drought, competition $r = −0.50$) with the exception of well-watered, no-competition treatments where the two were unrelated ($r = −0.07$). As expected, SLA and leaf C : N were always negatively correlated (Figs S6, S7). These traits were not closely related to assimilation rate A in well-watered conditions, but under drought and no competition we observed that genotypes with greater A had greater SLA ($r = 0.43$), lower C : N ($r = −0.56$), and lower δ^{13}C ($r = −0.48$).

We also tested for genetic variation in environmental responses to further address question (1) in the Introduction section. Total fitness (Fig. 2) and total silique number showed significant genotype × competition × water treatment interactions but not significant genotype interactions with competition or water alone (95% CIs of variance components excluded zero; Table S5), suggesting the potential for genetic trade-offs in performance due to drought × competition interactions. Flowering time exhibited a strong genetic variance component and also a significant genotype × competition × treatment interaction but no genotype interaction with competition or water alone. Rosette weight$_m$ showed significant genotype × competition interactions but other traits did not (Fig. 1; Table S5). Root : shoot, root weight, and δ^{15}N (vegetative harvest) and *Brachypodium* AGB showed significant Arabidopsis genotype variance components but no

significant genotype × treatment interactions. Inflorescence height, inflorescence branch number, silique length, root diameter, SLA, stomatal density, C : N, δ^{13}C, and total rosette leaf area (vegetative harvest) did not show significant genotype × treatment variance components or significant genotype variance components (Table S5).

To assess the existence of fitness trade-offs across environments (question (2) in the Introduction section), we calculated the correlation in relative fitness between competitive treatments. Under well-watered conditions, competition did not have a strong effect on the relative fitness of genotypes (absolute fitness correlation across environments, $r = 0.82$, $P < 10^{−5}$; Fig. 2). However, under drought, competition had a strong impact on relative fitness, such that absolute fitness was weakly related across competitive contexts ($r = 0.38$, $P = 0.1170$; Fig. 2). Comparing moisture treatments under no competition, relative fitness was weakly correlated across environments, suggesting possible trade-offs ($r = 0.33$, $P = 0.1813$). Under competition, fitness was more correlated across moisture treatments, indicating genotypes selected under competition have traits making them robust to moisture inputs ($r = 0.52$, $P = 0.0263$).

Selection on phenotypes within and across environments

To identify traits affecting fitness variation (question (3) in the Introduction section), we tested for univariate and multivariate selection on traits within each environment. Earlier FT was favored in all four environments (linear models: well watered, no

competition $P < 10^{-6}$; well watered, competition $P = 0.0020$; drought, no competition $P = 0.0162$; drought, competition $P = 0.0231$; only well watered significant at false discovery rate (FDR) < 0.05; Table 2). Greater inflorescence height (linear model $P = 0.0001$, significant after FDR) and inflorescence branch number ($P = 0.0337$, not significant after FDR) was linked to higher fitness in well-watered competition treatments but not in other treatments (all $P > 0.05$). Inflorescence height in well-watered competition treatments was selected even after conducting multiple regression also including an FT effect (inflorescence height $P = 0.0214$, FT $P = 0.0469$). Smaller rosettes (mature harvest) were selected under no-competition treatments of both moisture regimes (well watered, no competition $P = 0.0095$; drought, no competition $P = 0.0030$; both significant FDR < 0.05), though these patterns were not statistically significant after including FT in multiple regression (Table 2). AGB_m was positively selected under well-watered competition treatments ($P = 0.0002$, significant after FDR), negatively selected under drought no competition ($P = 0.0223$, not significant after FDR), but unrelated with fitness in well-watered no-competition treatments ($P = 0.5625$) and drought competition ($P = 0.4926$). Even after including FT in multiple regression, AGB_m was positively selected in well-watered treatments with competition (AGB_m $P = 0.0020$, FT $P = 0.0159$) but not so in drought treatments without competition (AGB_m $P = 0.4383$, FT $P = 0.2785$). In the harshest environment, drought and competition, we found that $\delta^{13}C$ was positively selected ($P = 0.0291$, not significant after FDR) though this was not significant after including FT ($\delta^{13}C$ $P = 0.1830$, FT $P = 0.1433$). Stomatal density, SLA, root : shoot, root biomass, photosynthetic rate, C : N,

$\delta^{15}N$, and root diameter did not show significant selection in any environment (Table 2).

To determine the traits responsible for genotype-level tradeoffs across treatments (question (3) in Introduction section), we tested for changes in the coefficients of selection across competition treatments within a given moisture environment. When relativizing fitness within each treatment (De Lisle & Svensson, 2017), we found significant changes in selection depending on the competitive environment for inflorescence height and AGB_m under well-watered conditions, with plants with taller inflorescences (two-tailed t-test $P = 0.007$, significant with FDR < 0.05), greater inflorescence mass ($P < 0.0001$, significant after FDR) and greater AGB_m ($P = 0.0003$, significant after FDR) being more fit under competitive environments but with no detectable effect on fitness under no competition (Fig. 2; Table 3). These changes in selection on these traits are surprising given the strong correlation (i.e. weak trade-offs) between relative fitness of genotypes in well-watered conditions when comparing plants growing alone or with competitors (Fig. 2). By contrast, we had observed changing ranks of relative fitness across competition treatments under drought (Fig. 2). We did not find significant changes in selection on any phenotypes under drought across competition treatments (aside from the trivial case of silique number), though stomatal density showed the most substantial change (t-test $P = 0.0630$; Table 3). To further investigate the fitness trade-offs across competition treatments under drought, we tested change in relative fitness between treatments and found it to be most closely associated with AGB_m under drought and competition (relative fitness of drought under no competition – relative fitness under competition vs AGB_m under drought and competition, general linear
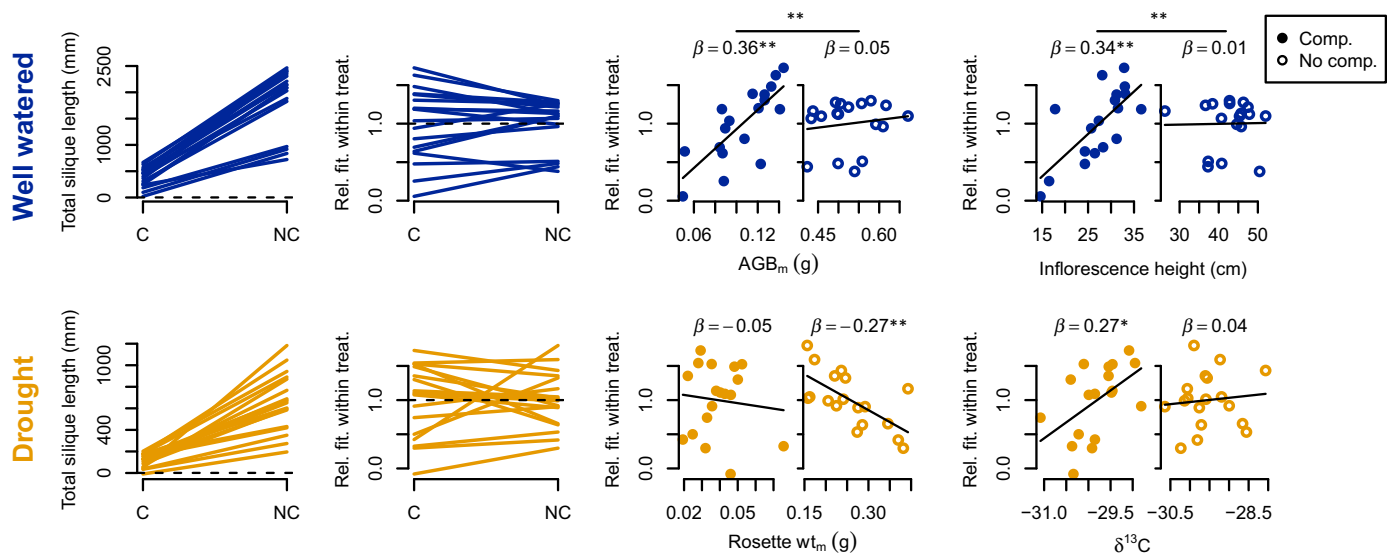

Fig. 2 Reaction norms of absolute fitness (i.e. total silique length, first column) and relative fitness (standardized by dividing by mean fitness within each treatment, second columns) across competition treatments for the 18 genotypes studied (each line represents a genotype). Note that competition treatments are on the left and no-competition treatments on the right, so as to keep consistent x-axes for traits under selection (right columns). Lines show breeding values estimated from linear mixed models. The well-watered (top row) and drought (bottom row) treatments are shown (note their changing scales). Changing selection on traits among treatments (third and fourth columns). Standardized selection coefficients are shown: *, $P < 0.05$; **, false discovery rate (FDR) < 0.05. Horizontal bars with ** indicate slopes that differ significantly (t-test) between competition treatments in the same moisture regime with FDR < 0.05. AGB, aboveground biomass; m, mature harvest.

Table 2 Standardized selection coefficients on breeding values for Arabidopsis traits under different treatments.

	Well watered				Drought			
	No competition		Competition		No competition		Competition	
	Coeff. est.	P-value	Coeff. est.	P-value	Coeff. est.	P-value	Coeff. est.	P-value
AGB_m	0.0461	0.5625	0.3600	**0.0002**	−0.2149	0.0230	0.0905	0.4926
Rosette weight$_m$	−0.1871	**0.0095**	−0.1074	0.3638	−0.2658	**0.0030**	−0.0537	0.6852
Inflorescence weight	0.2078	**0.0029**	0.4280	**0.0000**	0.1930	0.0448	0.2343	0.0622
Flowering time	−0.2728	**0.0001**	−0.3198	**0.0020**	−0.2252	0.0162	−0.2782	0.0231
Inflorescence height	0.0060	0.9401	0.3360	**0.0009**	−0.0363	0.7229	−0.0186	0.8883
Inflorescence branches	−0.0272	0.7335	0.2370	0.0337	−0.1639	0.0947	0.0182	0.8909
Silique number	0.3075	**0.0000**	0.4598	**0.0000**	0.3933	**0.0000**	0.4601	**0.0000**
Average silique length	0.0218	0.7850	0.2272	0.0431	0.1864	0.0538	0.3808	**0.0006**
Root weight$_v$	0.0633	0.4249	0.0693	0.5607	0.1494	0.1308	0.1602	0.2165
Root diameter$_v$	−0.0410	0.6074	0.0887	0.4551	−0.0478	0.6397	0.0743	0.5739
Root : shoot	−0.0038	0.9620	−0.0610	0.6094	0.1307	0.1902	0.1719	0.1830
Stomatal density	−0.1140	0.1406	−0.1461	0.2111	0.0417	0.6831	−0.2333	0.0636
Rosette weight$_v$	0.1139	0.1410	0.1904	0.0968	−0.0749	0.4614	0.1073	0.4142
log(SLA)	−0.0991	0.2041	−0.0243	0.8390	0.1008	0.3177	−0.0174	0.8958
Leaf C : N	0.1244	0.1054	0.1269	0.2807	−0.0454	0.6568	0.0352	0.7907
A (whole plant assimilation)	0.0742	0.3478	0.1217	0.3014	−0.0693	0.4959	−0.0107	0.9361
$\delta^{13}C$	0.0406	0.6112	0.1863	0.1049	0.0406	0.6911	0.2689	0.0291
$\delta^{15}N$	0.0646	0.4148	0.0197	0.8692	0.0629	0.5372	0.1258	0.3363

Bold P-values are shown to indicate significance with false discovery rate < 0.05. Note that root weight, root : shoot, and A were measured only on plants grown in the absence of competition. All other traits had breeding values and estimated fitness compared within each of the four treatments. All selection coefficients are in units of relative fitness (individual measures divided by the mean in each treatment) per standard deviation of the trait breeding values within treatment. AGB, aboveground biomass; C, carbon; m, mature harvest; N, nitrogen; SLA, specific leaf area; v, vegetative harvest.

Table 3 Tests for changing selection on Arabidopsis traits between competition treatments within the same moisture treatment.

	Well watered			Drought		
	Slope			Slope		
Trait	Competition	No competition.	t-test P-value	Competition	No competition	t-test P-value
AGB_m	2.77	0.15	**0.0003**	0.82	−0.57	0.1886
Rosette weight$_m$	−0.84	−0.32	0.4907	−0.50	−0.43	0.9487
Inflorescence weight	2.40	0.47	**<0.0001**	1.58	0.47	0.1448
Inflorescence height	0.54	0.01	**0.0070**	−0.03	−0.05	0.9340
Inflorescence branches	0.69	−0.04	0.0213	0.06	−0.22	0.4723
Flowering time	−0.25	−0.52	0.0568	−0.25	−0.40	0.4410
Silique number	2.32	0.44	**<0.0001**	2.25	0.49	**<0.0001**
Average silique length	0.24	0.02	0.1244	0.43	0.31	0.5045
Root diameter$_v$	0.19	−0.06	0.3369	0.20	−0.15	0.4690
Stomatal density	−0.14	−0.13	0.8890	−0.27	0.04	0.0630
Rosette weight$_v$	1.15	0.16	0.0917	1.26	−0.25	0.2883
log(SLA)	−0.03	−0.09	0.6743	−0.03	0.14	0.4839
A (whole plant assimilation)	0.12	0.07	0.7313	−0.01	−0.07	0.7234
Leaf C : N	0.18	0.15	0.8567	0.03	−0.05	0.6264
$\delta^{13}C$	0.22	0.05	0.3260	0.29	0.04	0.1094
$\delta^{15}N$	0.07	0.20	0.7646	0.11	0.07	0.7892

Slopes give the relationship between traits and relative fitness, where relative fitness is standardized within the treatment combination of competition and moisture conditions (corresponding to a model of soft selection), and traits are standardized across competition treatments being compared. Bold values indicate where slopes differ significantly between competition treatments with false discovery rate < 0.05. For results when fitness is relativized across environments, see Supporting Information Table S6.
AGB, aboveground biomass; C, carbon; m, mature harvest; N, nitrogen; SLA, specific leaf area; v, vegetative harvest.

model, $P = 0.0118$), whereas AGB_m under drought no competition did not explain the fitness changes ($P = 0.8333$). When relativizing fitness across competition treatments in the same moisture environment (corresponding to a scenario of hard selection) (De Lisle & Svensson, 2017), FT in well-watered conditions was the only trait under significant changing selection across

competition treatments, with relaxed selection under competition due to lower absolute fitness in this treatment (Table S6).

When testing for evidence of selection on traits averaged across competitive environments and independently on plasticity (question (4) in Introduction section), we found significant selection under well-watered conditions for a plastic increase in inflorescence height under competition compared with no competition (multiple linear regression, $P = 0.0034$), whereas average inflorescence height across treatments was not under significant selection, although this result was not significant after FDR control. For other traits where the average value was under selection across competitive environments, we found no independent selection on plasticity (Table S7).

Discussion

Organismal responses to abiotic conditions can be influenced by biotic interactions, such as interactions that affect general organismal health (e.g. parasitism; Price, 1991), change the balance of optimal allocation to abiotic stress tolerance (e.g. facilitation in arid systems; Bertness & Callaway, 1994), or directly change the availability of abiotic resources (e.g. competition for water; Cohen, 1970). Given rapid global climate change, we are particularly interested in limiting resources that are influenced by climate, like moisture. Such resources are likely to exhibit interactions between climate and competition in their effects on organisms. Though a broad literature exists studying plant performance responses to drought combined with competition (e.g. Callaway & Walker, 1997; Young *et al.*, 2017), less is known about the underlying physiology and genetic variation. Here, we studied the model plant Arabidopsis to characterize plastic responses to drought and competition as well as to determine how competition can change selection for traits related to water balance. We found strong plastic responses to neighboring plants that differed between drought and well-watered conditions. Furthermore, we found that under drought there are major rank changes in relative fitness depending on the presence of competitors.

Plastic responses to competition and moisture

We found plastic changes in most phenotypes, with strong interactions between competition and moisture. Competition and drought reduced performance in both well-watered and drought treatments, although plants in drought and competition had higher performance (biomass and total silique length) than expected from the additive contribution of each stressor. This interaction may indicate multiplicative growth responses to increased resources available in the absence of competition or with sufficient water. Additionally, plants under drought without competition generally had larger rosettes at maturity than in other conditions (Fig. 1), perhaps signifying an adaptive conservative response that reduces reliance on inflorescence (cauline) leaves for photosynthesis.

By contrast, life history and physiology showed diverse plastic responses to our treatments. Generally, drought responses showed a strategy partly indicative of adaptive escape; that is, a resource acquisitive strategy: lower leaf C : N and greater stomatal density, perhaps allowing plants to rapidly increase photosynthesis and take advantage of pulses of water. At the same time, higher $\delta^{13}C$ under drought indicated higher WUE and stomatal closure. Des Marais *et al.* (2012) found that Arabidopsis tends to increase SLA and decrease C : N under drought, which the authors interpreted as drought escape. However, several nonvernalization-requiring genotypes in Des Marais *et al.* (2012) showed opposite patterns: greater C : N and lower SLA under drought. Our study genotypes were nonvernalization requiring, and we found that drought increased SLA only under competition. There was no drought effect on SLA when plants were alone. These drought × competition interactions suggest the escape strategy might be specific to certain life history strategies or combined competitive and drought conditions.

Responses to competition differed between drought and well-watered conditions, demonstrating the interdependence of abiotic and biotic effects. Under well-watered conditions, response to competition was characterized by higher leaf C : N, suggesting a decrease in a photosynthetic rate per leaf mass, although this was coupled with a consistent but slight decrease in $\delta^{13}C$, the latter of which suggests an acquisitive growth strategy via greater stomatal or mesophyll conductance to escape competition and is consistent with findings by Campitelli *et al.* (2016). By contrast, competition under drought increased SLA, with some genotypes also reducing $\delta^{13}C$, perhaps indicating an acquisitive escape strategy (allowing greater whole-plant C assimilation; Des Marais *et al.*, 2012). We found that, under drought, genetic variation in SLA was positively associated with whole-plant C assimilation (Figs S6, S7). In one of the few relevant studies, Ehleringer (1993) found that the desert shrub *Encelia farinose* (Asteraceae) showed no $\delta^{13}C$ response to competitor removal.

$\delta^{15}N$ was elevated in well-watered no-competition treatments, which we interpreted as a shift in Arabidopsis use of N pools among treatments. Synthetic fertilizers (e.g. Miracle Grow used here) cause lower leaf $\delta^{15}N$ relative to organic sources like peat humus (used in our media), as fertilizer has more ammonium, which requires a single assimilation event (in roots) vs multiple assimilation events (in roots and shoots) for soil nitrate sources (Evans *et al.*, 1996; Bateman *et al.*, 2005; Trandel *et al.*, 2018). We infer that well-watered Arabidopsis plants without competition used more N from the peat humus vs fertilizer. Under well-watered conditions with competitors, the fertilizer N source may have been favored by the Arabidopsis plants due to smaller root systems for exploitation of soil N, causing low leaf $\delta^{15}N$. Under drought, N uptake may have been restricted to brief periods following fertigation, favoring the fertilizer source and causing low leaf $\delta^{15}N$.

Even under well-watered conditions with fertilizer and direct light, Arabidopsis responded to competition with reduced performance. Such a strong response suggests Arabidopsis plants were using a chemical cue, such as root exudates (Pierik *et al.*, 2013), to sense the neighboring *Brachypodium* (Badri *et al.*, 2012; Schmid *et al.*, 2013). Previous studies have shown that SLs in growth media can suppress inflorescence branching by Arabidopsis

(Scaffidi *et al.*, 2014) and cause stomatal closure (Lv *et al.*, 2018). Our treatments with a synthetic SL reduced vegetative rosette biomass, suggesting SL signaling could partly explain Arabidopsis response to neighbors. The yield of PSII was greater for two genotypes under SL treatment, consistent with findings in tomato that the synthetic SL GR24 upregulated light-harvesting genes (Mayzlish-Gati *et al.*, 2010). However, two other genotypes showed *lower* PSII yield in response to SL; these genotypes had lower biomass response to SL, for reasons that are unclear. We found that experimental SL addition caused an increase in $\delta^{13}C$ (likely signaling stomatal closure; Lv *et al.*, 2018) and a decrease in C : N, patterns that were opposite to the Arabidopsis response to *Brachypodium* in our well-watered treatment. This result indicates that other non-SL cues are required to explain the responses to *Brachypodium* that we observed under putative nonresource-limited conditions (our well-watered treatment).

Genetic correlations among traits

We found that genetic variation in FT was negatively associated with leaf $\delta^{13}C$, suggesting that early-flowering plants had higher intrinsic leaf-level WUE due to lower stomatal conductance or higher assimilation rate *A* (Ferguson *et al.*, 2019). This positive correlation between FT and $\delta^{13}C$ might be a result of mal-adapted late-flowering genotypes having lower *A* for a given stomatal conductance. Our findings contrast with some previous studies that found the early-flowering plants had low leaf $\delta^{13}C$ (McKay *et al.*, 2003; Lovell *et al.*, 2013; Kenney *et al.*, 2014). Our panel of natural genotypes lacked genotypes requiring vernalization; thus, these genotypes might partly be responsible for the discrepancies with these publications. Additionally, Ferguson *et al.* (2019) did not find an FT relationship with leaf $\delta^{13}C$ in comparisons of near isogenic lines at major FT quantitative trait loci.

Selection under competition and changes in selection depending on competition

Researchers have more commonly investigated how competition × drought interactions affect different species in a community (Marks & Strain, 1989; Miranda-Apodaca *et al.*, 2015; Napier *et al.*, 2016), or have studied changing selection driven by the interaction between drought and herbivory (Sthultz *et al.*, 2009; Huttunen *et al.*, 2010; Grinnan *et al.*, 2013) or between competition and herbivory (Tiffin, 2002). However, there are few studies of changing selection due to drought × competition interactions. In one of the few such studies, Ehleringer (1993) found that, in the desert shrub *Encelia farinose*, $\delta^{13}C$ was not under selection in the presence of competitors. However, upon competitor removal, lower $\delta^{13}C$ was associated with higher growth (but not survival), possibly due to increased soil moisture.

Here, we observed significant genotype × competition × moisture treatment interactions for performance-related traits (fitness components and AGB) and FT. The genotype × competition × moisture effects on fitness indicate that the effects of competition on relative fitness are conditional on moisture environment. This competition × moisture effect on selection could be seen in the substantial changes in relative fitness depending on competition under drought, but the fairly consistent relative fitness despite the presence of neighbors in well-watered conditions (Fig. 2). Rank changes in relative fitness across treatments differing in competition were observed among natural Arabidopsis genotypes at a moist field site (Baron *et al.*, 2015) and among genotypes segregating for a single WUE locus under glasshouse drought (Campitelli *et al.*, 2016). Here, we show selection among natural genotypes under drought. In nature, the heterogeneity of competition may select for alternate Arabidopsis traits in water-limited environments, suggesting a potential mechanism promoting their high genetic diversity in drought responses (Dittberner *et al.*, 2018; Exposito-Alonso *et al.*, 2018).

We identified several traits associated with fitness in specific competitive contexts. Inflorescence height and weight as well as AGB_m showed the strongest evidence for changing selection depending on competition, both when well watered. Under well-watered competition, plants with greater AGB_m and larger inflorescences had greater fitness, but not in the absence of competition. Selection for AGB_m may indicate that the investment in leaves for resource capture (comprising much of nonreproductive of AGB, and including both rosette and cauline leaves) is adaptive when surrounded by competitors, while allocation to reproduction may be selected when competitors are absent. The lack of selection for greater AGB_m and taller inflorescences in drought may indicate that aboveground investments are less useful when competitors are smaller. We also found positive selection for the plastic increase in inflorescence height under well-watered competition treatments. Thus, inflorescence height may only be a good measure of fecundity under the treatment with the most competitor biomass (well watered), where competitors lead to suppressed inflorescence branching (Schmitt *et al.*, 2003; von Wettberg *et al.*, 2008).

Under drought and competition, plants with greater $\delta^{13}C$ had higher fitness (though this was not significant after FDR control), indicating greater leaf-level WUE was adaptive, but not in other treatments. We expected lower WUE would be favored under drought with competitors to rapidly complete development before competitors depleted resources too low (Campitelli *et al.*, 2016). Instead, higher WUE may have been favored because conditions were too dry to permit success of a rapidly developing drought escape strategy; thus, higher WUE may be necessary in these environments. Alternatively, despite the dramatically lower performance of plants in response to competition under drought, the intermittent watering may have been enough to favor conservative drought-avoidance strategies (high $\delta^{13}C$). Our findings contrast with those of Kenney *et al.* (2014), who found terminal drought and well-watered treatments selected for lower $\delta^{13}C$ and plants with greater AGB_m, suggesting escape strategies were favored. Here, early flowering was favored in competitive treatments as it was in all treatments, similar to the consistently observed selection for earlier flowering in many experiments (Austen *et al.*, 2017), including those on Arabidopsis under terminal drought (Kenney *et al.*, 2014).

Conclusions

The effects of abiotic stress on phenotypic plasticity and natural selection depend on biotic context. Arabidopsis represents an important model system for plants, including for its responses to environment. Our results highlight how natural variation in environmental responses should be interpreted in light of biotic interactions.

Author contributions

CML carried out experiments, analyzed data, and wrote the manuscript. JRL planned the experiments, analyzed data, and wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Images of experimental treatments, including drought treatment under competition and no competition, and well-watered treatment under competition and no competition.

Fig. S2 Time series of temperature (°C) conditions using a Hobo data logger (Hobo®; Onset Computer Corp.).

Fig. S3 Percent volumetric water content (%VWC) of potting mix within pots for each treatment was monitored using EM-50 dataloggers and EC-5 probes (Meter Group Inc., Pullman, WA, USA).

Fig. S4 Image of experimental plant with stainless steel wire installed to prevent *B. distachyon* shading.

Fig. S5 Response of four genotypes to increasing concentrations of GR24 applied to soil.

Fig. S6 Bivariate relationships between traits often thought to be exhibit coordinated variation.

Fig. S7 Principal components of trait variation within each treatment.

Methods S1 Supplemental methods about experiments.

Table S1 The 18 parent genotypes from the Multiparent Advanced Generation Inter-Cross (MAGIC) used in this study.

Table S2 Climate mean conditions for non-contaminant ecotypes using WorldClim (Hijmans *et al.*, 2005) and CGIAR CSI Aridity (Zomer *et al.*, 2008) data.

Table S3 Temperature and photoperiod program for Conviron growth chamber, to simulate early spring germination for a spring annual.

Table S4 Broad sense heritability of traits within each treatment.

Table S5 Variance components estimates for linear mixed-effects model where genotype, genotype-treatment interactions, and tray effects were modeled as random effects and treatments were fixed effects.

Table S6 Tests for changing selection between competition treatments within the same moisture treatment.

Table S7 Selection on mean and plasticity of trait values across competition treatments.

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