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Phenological and fitness responses to climate warming depend upon genotype and competitive neighbourhood in *Arabidopsis thaliana*

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Abstract

1. Increasing temperatures during climate change are known to alter the phenology across diverse plant taxa, but the evolutionary outcomes of these shifts are poorly understood. Moreover, plant temperature-sensing pathways are known to interact with competition-sensing pathways, yet there remains little experimental evidence for how genotypes varying in temperature responsiveness react to warming in realistic competitive settings.
2. We compared flowering time and fitness responses to warming and competition for two near-isogenic lines (NILs) of *Arabidopsis thaliana* transgressively segregating temperature-sensitive and temperature-insensitive alleles for major-effect flowering time genes. We grew focal plants of each genotype in intraspecific and interspecific competition in four treatments contrasting daily temperature profiles in summer and fall under contemporary and warmed conditions. We measured phenology and fitness of focal plants to quantify plastic responses to season, temperature and competition and the dependence of these responses on flowering time genotype.
3. The temperature-insensitive NIL was constitutively early flowering and less fit, except in a future-summer climate in which its fitness was higher than the later flowering, temperature-sensitive NIL in low competition. The late-flowering NIL showed accelerated flowering in response to intragenotypic competition and to increased temperature in the summer but delayed flowering in the fall. However, its fitness fell with rising temperatures in both seasons, and in the fall its marginal fitness gain from decreasing competition was diminished in the future.
4. Functional alleles at temperature-responsive genes were necessary for plastic responses to season, warming and competition. However, the plastic genotype was not the most fit in every experimental condition, becoming less fit than the temperature-canalized genotype in the warm summer treatment.
5. Climate change is often predicted to have deleterious effects on plant populations, and our results show how increased temperatures can act through genotype-dependent phenology to decrease fitness. Furthermore, plasticity is not necessarily adaptive in rapidly changing environments since a nonplastic genotype proved fitter than a plastic genotype in a warming climate treatment.

KEYWORDS
ambient temperature, climate change, competition, *FLOWERING LOCUS M*, *FRIGIDA*, *MADS AFFECTING FLOWERING 2/3*, plasticity, vernalization

1 | INTRODUCTION

Climate change has the potential to alter phenology in many species, affecting their interactions and fitness. For example, spring phenologies across diverse plant taxa and habitat types are advancing due to rising global temperatures, representing plastic and/or evolutionary shifts of flowering time as the period of winter cold shortens (Anderson, Inouye, McKinney, Colautti, & Mitchell-Olds, 2012; Badeck et al., 2004; Bradley, Leopold, Ross, & Huffaker, 1999; CaraDonna, Iler, & Inouye, 2014; Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Davis, Willis, Connolly, Kelly, & Ellison, 2015; Fitter & Fitter, 2002; Gordo & Sanz, 2010; Inouye, 2008; Menzel et al., 2006; Ovaskainen et al., 2013; Parmesan, 2006; Parmesan & Yohe, 2003). Extended winter cold (vernalization) and warm ambient temperature are important environmental cues for phenological tracking, but their effect on natural populations may depend upon the competitive environment in which a plant grows since temperature-responsive pathways interact with competition-sensing pathways (Casal, 2013; Franklin, 2008; Halliday, Salter, Thingnaes, & Whitelam, 2003).

Climate change will alter the relative strength of these signals since rising temperatures will decrease vernalization exposure but will amplify the high ambient temperature cue, all the while diminishing the historic correlation between temperature and daylength (Bradley et al., 1999; Parmesan & Yohe, 2003; Visser & Both, 2005; Wadgymar, Ogilvie, Inouye, Weis, & Anderson, 2018). Little is known about how increased temperature will affect plant populations with mixed levels of responsiveness to these temperature signals. Furthermore, though many plant species express genetic variation for temperature-dependent phenology (Doi, Takahashi, & Katano, 2010; Panchen et al., 2015; Parmesan & Hanley, 2015), few studies have manipulated the genotypic basis of specific temperature responses (Altpeter et al., 2016; Jung & Muller, 2009; McClung, 2013). However, the genetic model *Arabidopsis thaliana* (Brassicaceae) can provide mechanistic insight into ecological outcomes that depend on phenology since its temperature- and competition-responsive genetic networks have been well elucidated (Blumel, Dally, & Jung, 2015; Bouche, Lobet, Tocquin, & Perilleux, 2016; Glover, 2014). This study leverages the genetic pliability of *A. thaliana* to test the effects of climate change on fitness outcomes of genotypes that vary in temperature-dependent phenology across competitive gradients.

In *A. thaliana*, vernalization, warm ambient temperatures and long days promote flowering via distinct pathways that nevertheless interact (Bouche et al., 2016; Fornara, Montaigu, & Coupland, 2010; Glover, 2014; Pajoro et al., 2014; Pose, Yant, & Schmid, 2012; Song, Ito, & Imaizumi, 2013). Responses to chilling or high temperature are governed by a set of repressor genes that prevent activation of genes promoting flowering (florigens) (Johanson et al., 2000; Li et al., 2014; Mendez-Vigo, Gomaa, Alonso-Blanco, & Pico, 2013; Rosloski, Jali, Balasubramanian, Weigel, & Grbic, 2010; Salome et al., 2011; Stinchcombe et al., 2004; Werner et al., 2005). In particular, *FRIGIDA (FRI)* activates the floral repressor *FLOWERING LOCUS C (FLC)*, conferring late flowering which can be accelerated by vernalization (Hepworth et al., 2018; Kim & Sung, 2013; Lee & Amasino, 1995; Sung & Amasino, 2004; Wood et al., 2006). Across its range, *A. thaliana* segregates functional and nonfunctional versions of this gene, resulting in ecotypes that are responsive and nonresponsive to extended cold (Johanson et al., 2000; Shindo et al., 2005). Major allelic variants have also been identified for the floral repressors *MADS AFFECTING FLOWERING 2/3* (*MAF2/3*), which enhance the vernalization response, and in *FLOWERING LOCUS M (FLM)*, which ceases florigen repression during exposure to ambient high temperature (Capovilla, Schmid, & Pose, 2015; Lee et al., 2013; Lutzet al., 2017, 2015; Pose et al., 2013; Sureshkumar, Dent, Seleznev, Tasset, & Balasubramanian, 2016). Ecotypes harbouring functional versions of these alleles occur more frequently in climates with greater seasonal variation in temperature and precipitation patterns (Table S1, Supporting Information Figures S1–S5), suggesting their importance in enabling adaptive plasticity to temperature changes, though maps of contemporary climate variability may not always predict a population's potential to adapt to future climate change (Nadeau, Urban, & Bridle, 2017).

Furthermore, competition affects the timing of the reproductive transition in plants as an aspect of the shade avoidance syndrome. This syndrome is favoured under conditions of intense competition when it is more beneficial for short-lived annuals to reproduce rapidly rather than suffer resource depletion by neighbours (Donohue, Messiqua, Pyle, Heschel, & Schmitt, 2000; Dudley & Schmitt, 1996; Huber et al., 2004; McIntyre & Strauss, 2014; Roig-Villanova & Martinez-Garcia, 2016; Schmitt, Stinchcombe, Heschel, & Huber, 2003; Takeno, 2016). Thus, high ratios of red:far-red wavelengths characteristic of foliage shade cause *A. thaliana* to flower early (Devlin, Halliday, Harberd, & Whitelam, 1996; Donohue et al., 2000; Dorn, Pyle, & Schmitt, 2000; Franklin, 2008; Franklin & Whitelam, 2005; Halliday, Koornneef, & Whitelam, 1994; Mullen, Weinig, & Hangarter, 2006). Shade avoidant flowering can occur in the absence of extended vernalizing chilling, but this acceleration occurs more strongly in short days (Fraser, Hayes, & Franklin, 2016; Legris et al., 2016; Lorrain, Allen, Duek, Whitelam, & Fankhauser, 2008; Salter, Franklin, & Whitelam, 2003; Sellaro, Pacin, & Casal, 2017; Vandenbussche, Pierik, Millenaar, Voesenek, & Straeten, 2005; Wollenberg, Strasser, Cerdan, & Amasino, 2008), thus integrating temperature, daylength and shade avoidance signalling. The integration between abiotic and biotic signals is important because as

a ruderal species, *A. thaliana* frequently colonizes recently disturbed habitats as a primary successor (Le Corre, 2005; Thompson, 1994; Wilczek et al., 2009), so it naturally competes in dense stands against maternally related individuals as well as against genotypically disparate individuals even along microgeographic transects as small as 0.5 m (Bomblies et al., 2010; Brachi et al., 2013; Le Corre, 2005; Frachon et al., 2018).

Here we ask how warming climate interacts with competition to determine seasonal flowering time and fitness in phenologically uniform and mixed populations of *A. thaliana*. To answer this question, we generated near-isogenic lines (NILs) transgressively segregating weak and strong alleles of the temperature-responsive flowering time genes *FRI*, *MAF2/3* and *FLM*. These alternate allelic complements created an environmentally responsive NIL that could respond to vernalization and high ambient temperature, and a constitutively early-flowering unresponsive NIL that could not. However, both NILs harboured intact shade-sensing pathways so that they were able to respond to competition. By testing them along a low to high competition gradient, we could isolate the effects of temperature responsiveness, competition and their interaction. Since *A. thaliana* expresses season-specific phenology (Burghardt, Metcalf, Wilczek, Schmitt, & Donohue, 2015; Wilczek et al., 2009), these gradients were planted in two simulated seasons, fall and summer, and two climate simulations (contemporary and warming) to produce four combinations: fall-contemporary, fall-warming, summer-contemporary and summer-warming. We then asked (a) How does loss of function in temperature-responsive genes affect phenological responses to warming and competition? (b) How does the relative fitness of responsive and unresponsive genotypes depend upon season, climate and competitive environment?

2 | MATERIALS AND METHODS

2.1 | Plant materials

We used two *Arabidopsis thaliana* (L.) Heynh. NILs in this experiment: one that was transgressively rapid-cycling due to weak alleles at temperature-sensitive floral repressor genes and one that was transgressively slow-developing due to strong alleles at these loci. They were generated from recombinant inbred lines (RILs) of the parental ecotypes Col-*gl1* (hereafter, Col) and Kashmir-1 (hereafter, Kas) obtained from the Arabidopsis Biological Resource Center (Columbus, OH) (Wilson, Schiff, Hughes, & Somerville, 2001). RILs were genotyped by PCR at *FLM*, *MAF2/3* and *FRI*. To create the tri-locus NILs, we first selected four lines of bi-locus RILs that were homozygous for the Kas alleles at *FLM* and *MAF2/3*, crossed these lines against a RIL line homozygous for Kas at *MAF2/3*, identified segregating progeny from this cross homozygous for the Kas allele at the desired loci, and then backcrossed these lines to Col for six generations. The fast-developing NIL (hereafter abbreviated as "F") harboured a Col allele at *FRI* and Kas alleles at *MAF2/3* and *FLM*, whereas the slow-developing NIL (hereafter abbreviated as "S") harboured the opposite allelic configuration (Supporting Information Table S2). The Col *FRI* allele is nonfunctional (Johanson et al., 2000), as is the Kas allele of *MAF2/3* (Caicedo, Richards, Ehrenreich, & Purugganan, 2009; Rosloski et al., 2010); Kas alleles of *MAF2/3* and *FLM* are not expressed under inductive conditions and therefore likely nonfunctional (Kawakatsu et al., 2016). To control for maternal effects, we bulked S and F seeds in common growth conditions at 20°C, 12 light:12 dark hours, and then stratified experimental seeds in 0.25% agar in the dark at 4°C for 12 days. We then planted F and S seeds into competition treatments as shown in Figure 1, using Sunshine Soil Mix #2 in 4 cm × 4 cm pots that had been watered and monitored for two previous weeks. Each pot contained a focal plant (F or S) surrounded by either S or F neighbouring plants at different densities. Two seeds were sown in each position, and subsequent germinants were randomly thinned to a single plant after 7 days while still in the cotyledon stage. Plants were watered twice weekly and growth trays were rotated at each watering.

In total, 256 "focal" plants, or those in the centre of pots subjected to competition treatments, were assayed for phenology and fitness. Experimental pots were randomly positioned within a compartment of a Conviron E7/2 controlled environment chamber among eight blank pots that were monitored throughout the experiment to ensure that contaminant seeds did not disperse and grow in the chambers. Two chamber compartments replicated each of the four climate simulations. In total, there were four replicates for each multifactorial combination of focal genotype (F,S) × competition intensity (1/0.16, 2/0.16, 4/0.16, 6/0.16 plants/litres of soil) × competitor genotype (F,S) × climate (fall-contemporary, fall-warming, summer-contemporary, summer-warming), and each treatment cell was replicated twice within each chamber compartment.

2.2 | Climate treatments

Since *A. thaliana* is known to germinate throughout the summer, spring and fall in Norwich, England (Burghardt et al., 2015; Wilczek et al., 2009), we simulated contemporary and warmed climates for this site. By examining historical climate records of three independent weather stations curated by the National Oceanic and Aeronautic Agency that had ≥90% nonmissing temperature measurements for every hour between 1970 and 2000, we established average temperature profiles for fall (10-hr late October day) and summer (14-hr early August day). Temperature profiles for these days had similar amplitudes, so that differences in fluctuation range would not confound differences in baseline temperature. Furthermore, they encompass very different temporal niches occupied by *A. thaliana*, and they are relatively understudied seasons in climate change biology (Gallinat, Primack, & Wagner, 2015). To simulate increased temperatures in this site for the year 2,100, we uniformly increased each curve by 4°C (Figure 1), intermediate between long-term warming predictions from the RCP6.0 and RCP8.5 scenarios of the Intergovernmental Panel on Climate Change 5th Assessment Report (van Oldenborgh et al., 2013). Light was provided by fluorescent and LED bulbs producing a fluence rate of 230 μmol m^{-2} s^{-1} and a red:far-red ratio of 1.1:1.

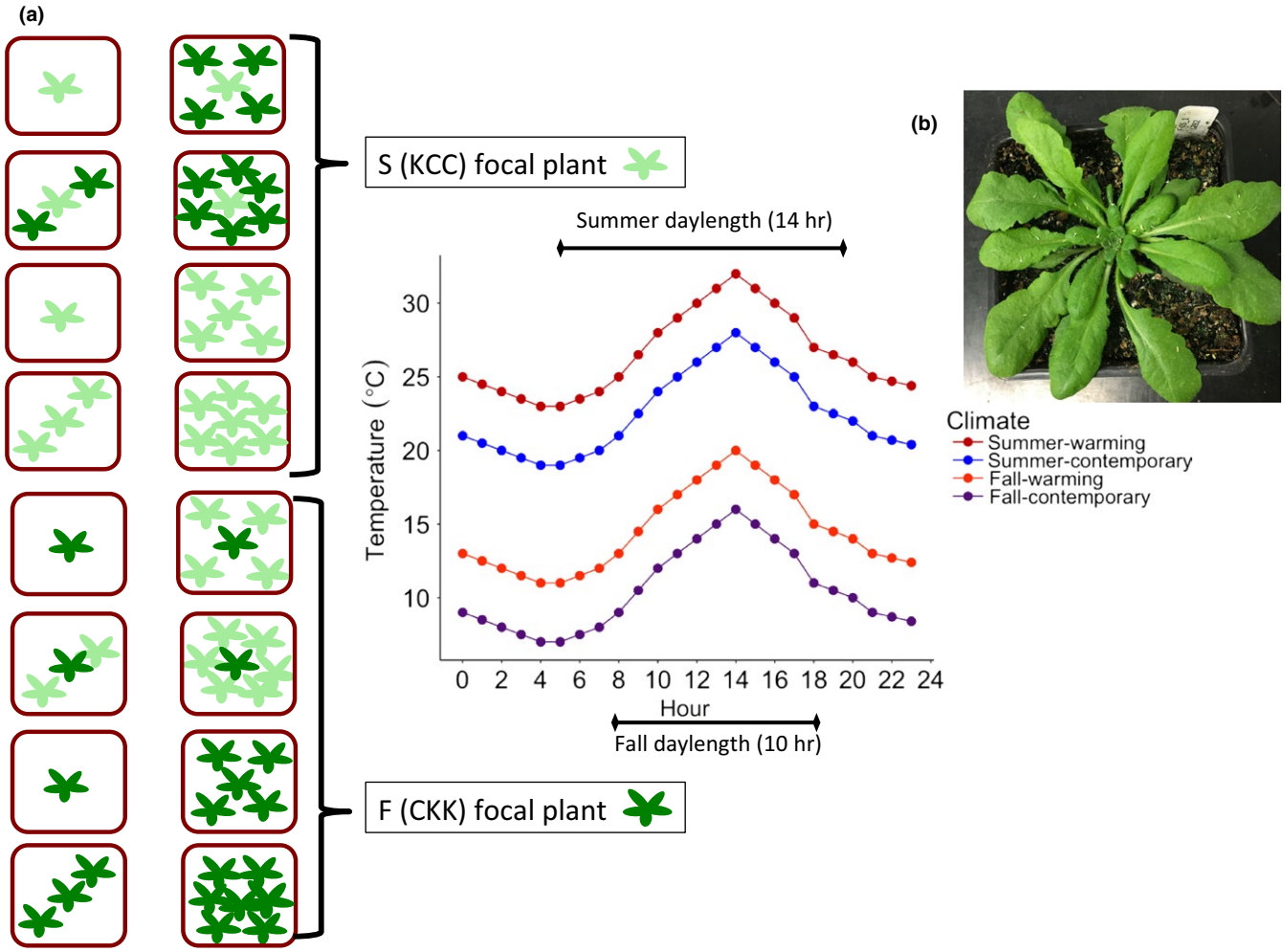

FIGURE 1 (a) Depiction of experimental set-up and daily fluctuating temperature schedules. Each pot was planted in each temperature schedule replicated four times. Daylength for fall was 10 hr, and for summer was 14 hr. (b) Picture of the primary study organism, *Arabidopsis thaliana*, in its rosette stage prior to bolting

2.3 | Phenological and fitness measurements

Following the cotyledon stage, we assessed growth rate of a random set of two plants (out of four) for each factorial treatment combination by counting rosette leaves 13 times during the first 38 days for the F NILs and 16 times during the first 50 days for the S NILs. We discontinued after the F NIL stopped adding rosette leaves and the S NIL displayed senesced leaves at the base of the rosette canopy. To assess days to bolting (DTB), we surveyed all focal plants every 3 days from germination until an inflorescence shoot at least 2 cm in length appeared at the centre of the rosette. Flowering time (DTF) was measured as the number of days after germination when the primary floral shoot produced the first flower with fully expanded petals.

In order to control for seasonal variation affecting growth rate, *A. thaliana* development has been modelled as a function of daylight and temperature, which scales developmental rate into photothermal time (Chew et al., 2012; Fournier-Level et al., 2013; Wilczek et al., 2009). This scaling is useful because it weights developmental progression by times when a plant is most photosynthetically active and accumulating biomass in preparation for reproduction. Our goal was not to estimate genotype-specific photothermal accumulation rates, but rather to scale developmental time across heterogeneous climate treatments to make phenological measurements across environments comparable (Brachi et al., 2010; Fournier-Level et al., 2013). To convert from calendar time in days to photothermal time in accumulated photothermal units (PTUs), we used the following equations (Wilczek et al., 2009):

$$\text{Photothermal unit PTU}(t) = \begin{cases} [T(t) - T_b] \times P, & T(t) > T_b \\ 0, & \text{otherwise} \end{cases}$$

$$P = \begin{cases} 1, & \text{Sunrise} < t < \text{Sunset} \\ 0, & \text{otherwise} \end{cases} \quad (1)$$

$$\text{Accumulated photothermal units (PTUs)} = \sum_{t=1}^{t=\text{trait end}} \text{PTU}(t) \quad (2)$$

where t is hour, $T(t)$ is the temperature at hour t, T_b is the base temperature which was held constant at 3°C as in Chew et al. (2012); P was the daylight filter with a nonzero value only when light shone on the plants;

t = 1 is the 12th hour of the day of germination; and t = trait end is the 12th hour of the day when a plant either bolted or flowered. Using these equations, we calculated photothermal units to bolting (BPTUs) and photothermal units to flowering (FPTUs). When the focal plant had fully senesced, it was harvested at the base, oven-dried and weighed. This reproductive biomass was taken as a proxy measurement of fitness, as previous data indicated that dry biomass correlates strongly to silique number (R^2 > 0.83), a direct fitness metric, across a variety of seasonal and competitive conditions (Taylor et al., 2017). We then calculated relative interaction intensity (RII) of fitness (w) for each focal plant with neighbours ($+N$) relative to focal plants without neighbours ($-N$) as

$$\mathrm{RII} = \frac{w_{+N} - w_{-n}}{w_{+N} + w_{-n}}$$

(Goldberg, Rajaniemi, Gurevitch, & Stewart-Oaten, 1999). W_{-n} was taken as the mean fitness of plants without neighbours within a growth chamber. RII is symmetric about zero enabling unbiased detection of competition and facilitation, and it is standardized so that the different competitive scenarios in this experiment can be directly compared (Diaz-Sierra, Verwijmeren, Rietkerk, Dios, & Baudena, 2017; Weigelt & Jolliffe, 2003).

2.4 | Statistical methods

To test whether focal NILs differed in rosette leaf number growth rates, we fit a repeated measures mixed model testing for a significant interaction between focal NIL and time, with subject plant modelled as a random effect. Similarly, in order to test the effect of genotype, competition and climate on phenology and fitness, we used generalized linear mixed effects models (GLMMs) implemented by the GLMER function of the LME4 package (Bates, Machler, Bolker, & Walker, 2015) in R version 3.0.2 (R Core Development Team, 2015). Replicate chamber was modelled as a random factor to account for the clustering of treatment replicates into two chambers; all other predictors were modelled as fixed factors. For DTF, DTB, BPTU, FPTU and fitness, we fit GLMMs under a gamma distribution (Supporting information Figure S6) with a log link function to each measured plant with focal genotype, competitor genotype, competitor number and climate. We initially fit a fully specified model with all possible factorial combinations of interaction terms and then trimmed models to terms that were significant at a Bonferroni-corrected p-value <0.05. Tests that revealed significant interactions with focal genotype were then split between focal genotypes, and separate GLMMs were fit for each focal genotype subset to assess genotype-specific responses, and p-values were adjusted by Bonferroni corrections.

3 | RESULTS

3.1 | Growth rates

Across all climate and competition treatments, rosette leaf addition was faster and lasted longer in the S NIL than the F NIL (Figure 2, Supporting Information Table S3). Within NILs, the S NIL showed faster leaf addition rates in high competition versus low competition, ultimately bolting with fewer rosette leaves at higher competition. Remarkably, S NILs in high competition in the fall-modern climate bolted with fewer than half the leaf number of low competition rosettes which grew to ~170 leaves (Figure 2b), though there was insufficient power to test this statistically. Furthermore, future temperature simulations slowed growth rate for the S NIL in the fall but not in the summer. Despite slower autumnal growth in the future, leaf addition plateaus occurred simultaneously at approximately day 42 in both the fall-contemporary and fall-warming treatments. This led to fall-warming plants having many fewer rosette leaves at bolting/flowering than fall-contemporary. In the summer, leaf addition was slower and terminated quickly due to the accelerated transition to reproduction. Similarly, the F NIL's rapid reproduction curtailed

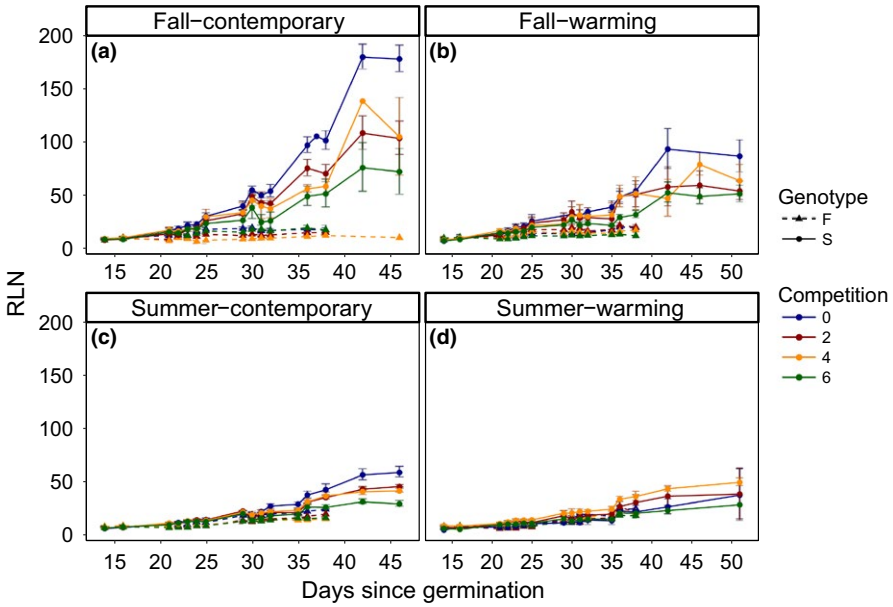

FIGURE 2 *Arabidopsis thaliana* growth curves for fully unfurled, nonsenescing rosette leaves (RLN: rosette leaf number). Genotype indicates the focal NIL genotype, and competition indicates the number of plants competing against the focal plant. Error bars are for standard errors

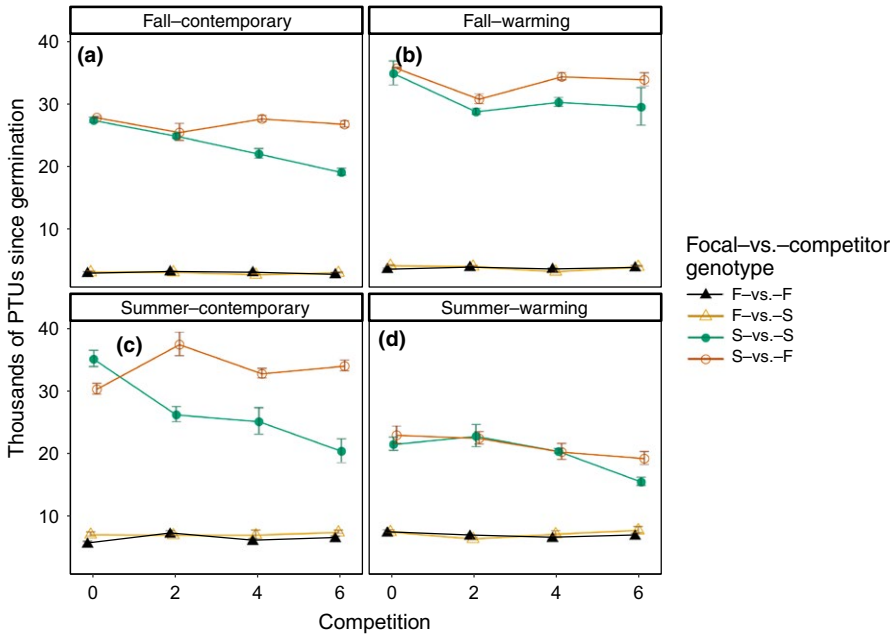

FIGURE 3 *Arabidopsis thaliana* bolting phenology in photothermal units (BPTUs). Competition on the *x*-axis indicates the number of plants competing against the focal plant. Error bars are for standard errors

leaf addition so that F NIL plants ceased to grow leaves beyond the 9th rosette leaf.

3.2 | Phenology

The NILs differed dramatically in response to climate, competition intensity and competitor identity, as well as interactions among these variables (Supporting Information Tables S4–S7). Focal genotype was the strongest driver of phenology with at least twice the effect magnitude of other treatment factors, followed by climate. The S NIL exhibited slow development and phenotypic plasticity to environmental treatments, in contrast with the F NIL's canalized rapid-cycling (Supporting Information Tables S8–S11).

3.2.1 | S NIL

Across most climate and competition treatments, S NIL phenology was delayed relative to the F NIL (negative focal genotype terms in GLMMs, Supporting Information Tables S4–S7). We also observed strong plasticity to temperature, competition and their interaction, shown by the significance of these terms in the GLMM for phenology (Supporting Information Tables S8–S11). However, the direction of this plasticity depended on season and time of temperature since a warmer climate delayed flowering in the fall but accelerated it in the summer (t = [15,21], $p < 0.001$; Figure 3; Table S9b). Across all temperature treatments, competition accelerated bolting and flowering but only when the focal S NIL was competed against other S NILs (significant interaction between competitor genotype and intensity in Supporting Information Tables S8–11b; Figure 3). In competition with F NIL plants, this phenological acceleration was largely absent (Figure 3), suggesting that small F neighbours did not elicit a strong shade avoidance response from focal S NIL plants.

3.2.2 | F NIL

In calendar time, the F NIL was constitutively rapid-cycling, transitioning to reproduction after approximately 20 days in all treatments (Supporting Information Figure S2). This transgressively abbreviated development was insensitive to competitor identity and competitor number. Though a GLMM for focal F NILs identified climate treatments as significant predictors of phenology, this result is driven by the extremely small range in development time across climate treatments so that just a few days of average difference between climates could be identified as significant but are unlikely to be ecologically relevant (Supporting Information Tables S8–11b). However, in summer temperatures, there was a large and significant photothermal time delay in flowering, but not in bolting. Together, this indicates that the F NIL transitioned to reproduction at the same time in calendar days but accumulated more growing degree hours in the long days and warm temperature of the summer-modern and especially the summer-warming climates.

3.3 | Fitness

Focal NILs differed significantly in their responses to climate, competition and competitor identity (Table 1). Though separate analyses for the F and S NILs revealed that the same treatment cells were significant for fitness as for phenology, the climate effect sizes on fitness were much greater, representing fold differences in both NILs.

3.3.1 | S NIL

The S NIL was generally more fit than the F NIL and its fitness responded to climate and competition (Tables 2). Specifically, fitness decreased with increasing competition with S neighbours but not with F neighbours (Figure 4). Effects of competitor genotype,

TABLE 1 Results of a fully specified generalized linear mixed model testing for genotype, competition and climate effects on *Arabidopsis thaliana* fitness

Term	Coef	*SE*	*t*	*p*
Competitor NIL	0.42	0.14	3.07	$<\mathbf{10^{-4}}$
Focal NIL	−1.67	0.14	−11.57	$<\mathbf{10^{-4}}$
Climate (fall-future)	−0.10	0.10	−1.05	0.29
Climate (summer-modern)	−0.12	0.10	−1.2	0.23
Climate (summer-future)	−0.48	0.10	−4.86	$<\mathbf{10^{-4}}$
Competition intensity	−0.14	0.02	−5.93	$<\mathbf{10^{-4}}$
Competitor NIL × Focal NIL	0.17	0.17	1	0.32
Focal NIL × Climate (fall-future)	0.79	0.14	5.69	$<\mathbf{10^{-4}}$
Focal NIL × Climate (summer-modern)	0.86	0.14	6.18	$<\mathbf{10^{-4}}$
Focal NIL × Climate (summer-future)	1.64	0.14	11.78	$<\mathbf{10^{-4}}$
Competitor NIL × Competition intensity	0.11	0.03	3.6	$<\mathbf{10^{-4}}$
Focal NIL × Competitor NIL × Competition intensity	−0.18	0.03	−5.82	$<\mathbf{10^{-4}}$

Note. Genotype terms (focal genotype and competitor genotype) are for the F near-isogenic line (NIL). Bold values indicate significant effects at $p < 0.05$.
Coef: coefficient estimate; *p*: *p*-value; *SE*: standard error; *t*: *t*-value.

competitor number and their interaction were significant for the S NIL, indicating that competition against other S NILs reduced fitness but not against F NIL competitors (Table 2). Furthermore, climate warming strongly reduced fitness in summer conditions, but less so in fall.

3.3.2 | F NIL

The F NIL showed decreased fitness in response to competition (F NIL in Table 2; Figure 4). The strength of this negative relationship increased with temperature, driven by increasingly high fitness at low competition as temperatures increased. This was most dramatically demonstrated in the summer-warming treatment in which competition-free F NILs' fitness exceeded that of the S NILs (Figure 4d).

Relative interaction intensity revealed that competition (negative RII) occurred more frequently than neutral (0 RII) interactions or facilitation (positive RII, Figure 5). The F NIL showed surprisingly strong fitness responses on the RII scale, whereas the S NIL's RII was dampened relative to its responses on the absolute fitness scale (Figure 4). This apparently large RII response by the F NIL is driven by its narrow absolute fitness range compared to the S NIL, so that even small shifts in fitness became amplified on the RII scale. Together, these RIIs revealed that deleterious S NIL competition was more intense against other S NILs, and that small fitness changes in the F NIL were relatively large on the RII scale independent of competitor genotype.

3.4 | Phenological plasticity to climate change and its fitness consequences

We visualized the joint response in bolting time and fitness to increasing temperatures in the fall and summer in order to understand how phenology and fitness could covary with increasing temperature. Figure 6 shows bivariate phenotypic responses of each genotype to within-season warming treatment in which edges connect contemporary and future warming treatments within a season. In the fall, warming temperatures delayed reproduction, concomitantly decreasing fitness in the low density treatments. In the summer, the S NIL also showed a decrease in fitness with warming, but this correlated to a reproductive acceleration. In contrast, the constitutively fast-developing F NIL showed minimal phenological response to warming, but substantial fitness increase, particularly in summer (Table 2a). Thus, phenological plasticity of the S NIL to temperature appears to be nonadaptive, and the increased fitness of the F NIL in response to warming is unrelated to phenology.

4 | DISCUSSION

An outstanding goal in climate change biology is to identify mechanisms mediating ecological outcomes as temperatures rise, a goal that depends upon the investigation of temperature-responsive traits and their genetic basis (Anderson & Gezon, 2015; Franks, Weber, & Aitken, 2014; Merila & Hendry, 2014; Pacifici et al., 2015). In annual plants, phenology is especially relevant since it determines the climate to which a plant will be exposed in seasonal environments (Donohue, 2005; Donohue et al., 2005; Hereford, Schmitt, & Ackerly, 2017). In *A. thaliana*, temperature-dependent phenology has been mapped to several major-effect quantitative trait loci (QTLs). These QTLs include functional and nonfunctional variants segregating in *FRI*, *FLM* and *MAF2/3*, which harbour an order of magnitude more nucleotide-level variation than genome-wide averages (Supporting Information Table S12). However, plant phenology is affected not only by genotype and the thermal environment but also by interaction with neighbours (Donohue et al., 2000; Franklin, 2008; Schmitt et al., 2003). Neighbour effects could mitigate or enhance the genetic and environmental drivers of phenology, yet how these interactions unfold in seasonal climates and their effects on fitness have rarely been assessed (Taylor et al., 2017).

Here, we investigated these interactions by contrasting temperature-sensitive and temperature-insensitive genotypes in seasonal, warmed climates across competitive gradients. Temperature insensitivity was conferred by nonfunctional mutations in genes that underpin the vernalization response, *FRI* and *MAF2/3*, and the ambient temperature response, *FLM*. This multilocus loss of

TABLE 2 Results of separate generalized linear mixed models for the F and S NILs testing for competitor genotype, competitor intensity and climate effects on *Arabidopsis thaliana* fitness

	Est	*SE*	*t*	*p*
(a) F NIL				
Competitor NIL	−0.23	0.18	−1.30	0.19
Competition intensity	−0.31	0.10	−2.92	**0.003**
Climate (fall-future)	0.56	0.17	3.19	**0.001**
Climate (summer-modern)	0.57	0.17	3.25	**0.001**
Climate (summer-future)	1.10	0.18	6.21	**$<10^{-4}$**
Competitor NIL × Climate (fall-future)	0.24	0.25	0.97	0.33
Competitor NIL × Climate (summer-modern)	0.33	0.25	1.33	0.18
Competitor NIL × Climate (summer-future)	0.12	0.25	0.48	0.63
Competitor NIL × Competition intensity	−0.21	0.16	−1.34	0.18
Climate (fall-future) × Competition intensity	0.04	0.17	0.26	0.79
Climate (summer-modern) × Competition intensity	−0.06	0.18	−0.37	0.71
Climate (summer-future) × Competition intensity	−0.008	0.16	−0.05	0.96
Competitor NIL × Climate (fall-future) × Competition intensity	0.18	0.24	0.74	0.46
Competitor NIL × Climate (summer-modern) × Competition intensity	0.19	0.25	0.77	0.44
Competitor NIL × Climate (summer-future) × Competition intensity	−0.10	0.24	−0.40	0.69
(b) S NIL				
Competitor NIL	0.41	0.07	6.00	**$<10^{-4}$**
Competition intensity	−0.38	0.05	−7.75	**$<10^{-4}$**
Climate (fall-future)	−0.03	0.07	−0.39	0.69
Climate (summer-modern)	−0.04	0.07	−0.60	0.54
Climate (summer-future)	−0.43	0.07	−6.25	**$<10^{-4}$**
Competitor NIL × Climate (fall-future)	−0.15	0.10	−1.53	0.13
Competitor NIL × Climate (summer-modern)	−0.15	0.10	−1.54	0.12
Competitor NIL × Climate (summer-future)	−0.09	0.10	−0.87	0.39
Competitor NIL × Competition intensity	0.40	0.07	5.66	**$<10^{-4}$**
Climate (fall-future) × Competition intensity	0.17	0.07	2.41	**0.02**
Climate (summer-modern) × Competition intensity	0.008	0.07	0.11	0.91
Climate (summer-future) × Competition intensity	0.13	0.07	1.9	0.06
Competitor NIL × Climate (fall-future) × Competition intensity	−0.20	0.10	−2.02	**0.04**
Competitor NIL × Climate (summer-modern) × Competition intensity	−0.14	0.10	−1.35	0.18
Competitor NIL × Climate (summer-future) × Competition intensity	−0.23	0.10	−2.29	**0.02**

Note. Genotype terms (focal genotype and competitor genotype) are for the F near-isogenic line (NIL). Bold values indicate significant effects at $p < 0.05$.
Coef: coefficient estimate; *p*: *p*-value; *SE*: standard error; *t*: *t*-value.

function produced an extreme, transgressively rapid-cycling life history in the F NIL that was largely canalized across climates and competition. The transgressively late-flowering annual S NIL, however, expressed considerable plasticity to increasing temperatures and competition. The covariation of this phenological plasticity with fitness indicated that increased temperature had a negative effect on fitness for the winter annual S NIL but a positive fitness effect for the rapid-cycling F NIL. In sum, this experiment has demonstrated how increased temperature leads to winners and losers, and that losers in contemporary temperature regimes may become winners in warmer conditions.

The transgressively rapid-cycling F NIL was constitutively early flowering and remarkably canalized to season, temperature and competition. Its transition to reproduction was so compressed that it may have reached the limit of rapid-cycling behaviour, so that there was no phenotypic variation in the direction of accelerated phenology available to be induced by experimental treatment. However, the F NIL's fitness generally increased with increasing temperatures across season and competition treatments. One possible explanation for this observation is that if phenology is canalized, then increased temperature might raise metabolic rate to permit increased reproductive effort (Dillon, Wang, & Huey,

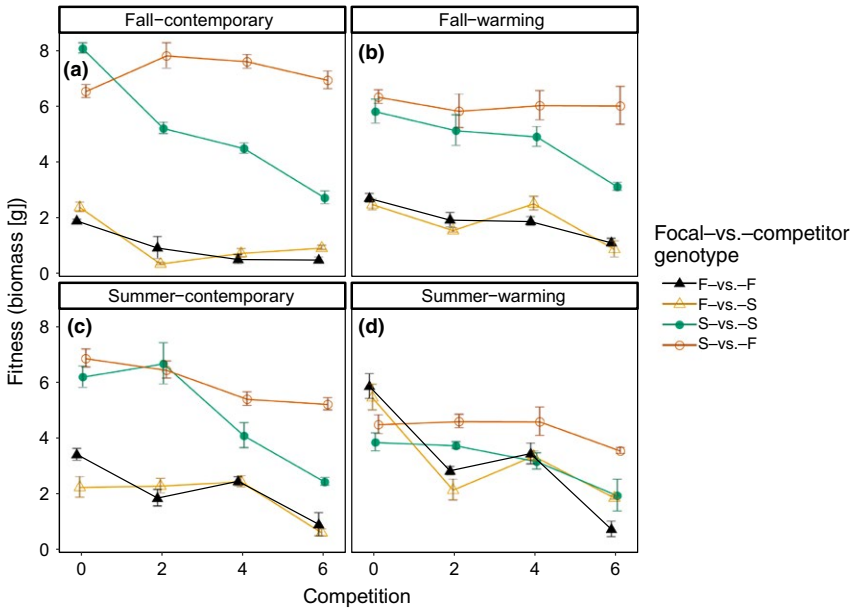

FIGURE 4 *Arabidopsis thaliana* fitness results. Competition on the *x*-axis indicates the number of plants competing against the focal plant. Error bars are for standard errors

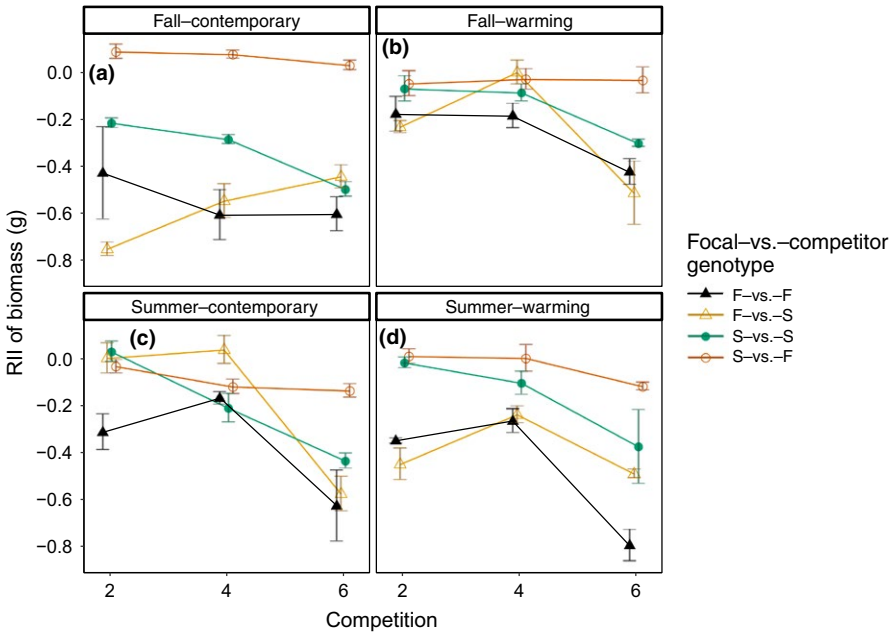

FIGURE 5 Relative interaction intensity of *Arabidopsis thaliana* in intragenotypic or intergenotypic competition. Error bars are for standard errors

2010; Gillooly, Brown, West, Savage, & Charnov, 2001; Mittler, Finka, & Goloubinoff, 2012). However, selection for early flowering at smaller sizes under climate warming may reduce population viability (Colautti, Ågren, & Anderson, 2017), so that slow development might still be important in population persistence under climate change.

Flowering of the S NIL was plastic to temperature and especially to competition. In particular, the vernalization requirement for accelerated flowering in the S NIL in short days (due to its strong alleles in *FRI* and *MAF2/3*) was apparently overridden by competition since shade avoidant flowering acceleration was clear (Figure 3a,b). This is consistent with previous findings that far-red light overrides *FLC*-mediated floral repression in strong *FRI* genetic backgrounds (Lee & Amasino, 1995; Wollenberg et al., 2008). Although this ecological outcome is consistent with phytochrome-mediated shade avoidance, it is possible that other competitive interactions, such as root competition, may have induced it. However, *Arabidopsis* accessions are known to use the spectral quality of ambient light to differentiate the proximity of kin versus nonkin (Crepy & Casal, 2015), resulting in phenotype matching among kin (Till-Bottraud & de Villemereuil, 2015). This lends support to our hypothesis that S NIL acceleration is due to phytochrome-mediated shade avoidance since the S NIL responds only to the spectral environment produced by other S NILs. Strikingly, in the hot summer-future climate in which the S NIL demonstrated accelerated phenology,

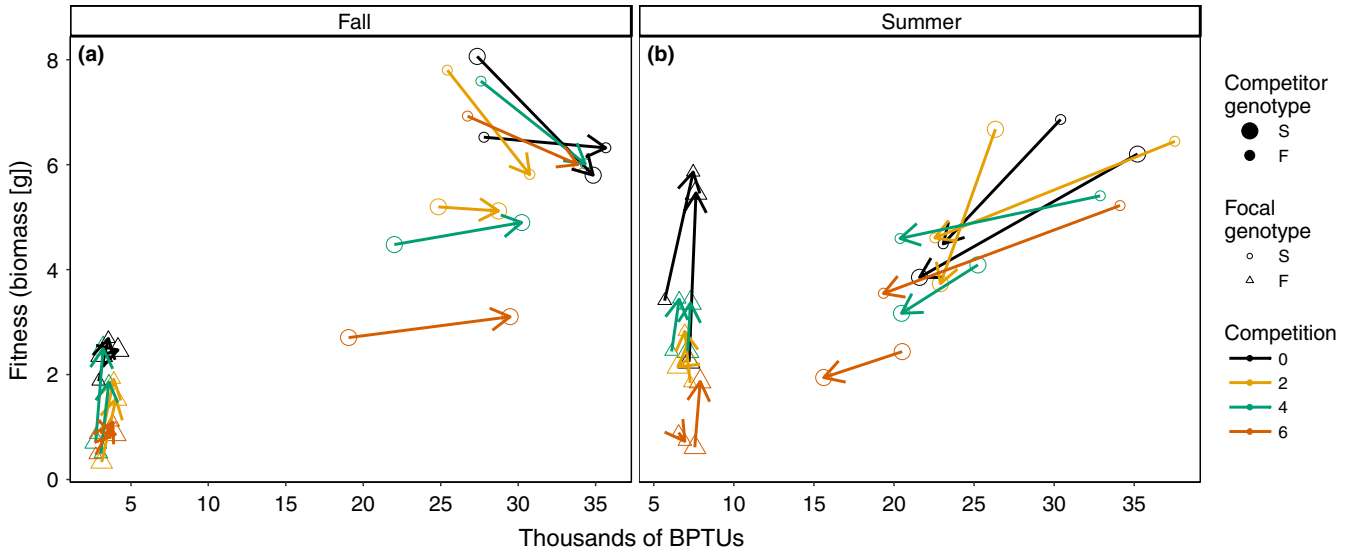

FIGURE 6 Reaction norms of *Arabidopsis thaliana* plasticity in phenology and its covariation with fitness to warming treatment. All panels show photothermal units to bolting (BPTUs) versus fitness. Points represent treatment means. In panels a and b, reaction norm lines connect modern and future temperature treatments with arrows facing towards the warmed climate treatments.

it had lower fitness than the F NIL (Figure 6d,h). This is a remarkable reversal in fitness and represents the only experimental condition in which a canalized rapid-cycling life history was favoured over a plastic one. This points to one way that climate change can shift ecological outcomes since a formerly high-fitness genotype (the S NIL) became less fit due in part to changes in developmental rate.

The winter annual S NIL switched between two plastic responses to climate warming based on season: delay in the fall and acceleration in the summer. Its future-fall delay may have been caused by the attenuation of the vernalization signal present in the fall-modern simulation (Angel et al., 2015; Burghardt et al., 2016; Duncan et al., 2015; Hepworth et al., 2018; Shindo, Lister, Crevillen, Nordborg, & Dean, 2006). On the other hand, increased temperature in the summer accelerated reproduction, likely mediated by *FLM* response to high ambient temperature (Lutzet al., 2017, 2015; Sureshkumar et al., 2016). Furthermore, plasticity in the rate at which delayed reproduction accumulated biomass also proved to be season-specific, diminished strongly in a warmed fall but not in a warmed summer (Figure 6cd, Supporting Information Figure S2cd). Thus, plastic responses to increased temperature can be gated by season and competition, but only if the baseline phenology set by flowering time genotype permits it.

The role of phenotypic plasticity in promoting or inhibiting persistence during climate change has received a great deal of attention but its importance relative to genetic adaptation remains unclear (Bay et al., 2017; Chevin, Lande, & Mace, 2010; Merila & Hendry, 2014). In some systems, genetic adaptation has been shown to dominate the climate change response (Balanya, Oller, Huey, Gilchrist, & Serra, 2006; Bradshaw & Holzapfel, 2006); in others, plasticity (Charmantier et al., 2008; Gibbin, N'Siala, Chakravarti, Jarrold, & Calosi, 2017; Przybylo, Sheldon, & Merila, 2000); and sometimes a combination of both (Anderson & Gezon, 2015). One possible reason for these conflicting findings is that plasticity itself can be under selection (Merila & Hendry, 2014). Relative to other important traits like recruitment, flowering time in *A. thaliana* has been found to be highly plastic, and this plasticity is associated with higher fitness (Exposito-Alonso, Brennan, Alonso-Blanco, & Pico, 2018). This study sheds light on the extreme ends of the flowering time plasticity spectrum by contrasting the highly plastic S NIL with the highly canalized F NIL. In keeping with previous studies, we have shown that the plastic genotype is more fit under most environmental conditions, but that the canalized genotype is more fit in one extreme warmed condition. Furthermore, this study showed that achieving this canalized early-flowering behaviour relies on nonfunctionalization in only three genes, and these genes have been hypothesized to be hotspots of recombination to facilitate rapid adaptation to short-term selection fluctuations like rapid warming (Theißen, Rümpler, & Gramzow, 2018). Thus, we have shown that adaptation to climate change that is mediated by a change in plasticity can be achieved relatively quickly and produce striking phenotypic results.

Arabidopsis thaliana competitor quality has been found to select on traits at group and individual levels in opposite directions, so that individuals were selected for larger traits and groups for smaller (Weinig, Johnston, Willis, & Maloof, 2007), a form of altruistic phenotype matching among kin (Crepy & Casal, 2015). Indeed, we found individual fitness decreased only in pure stands, not in mixed stands. This response was likely driven by more efficient partitioning of the temporal niche by mixed stands, in which focal and competitor genotypes were cycling through different life stages at different times. This finding supports the view that diverse populations utilize resources, in this case time, more efficiently than homogeneous ones (Finke & Snyder, 2008; Mason, Mouillot, Lee, & Wilson, 2005; Petchey & Gaston, 2002; Yachi & Loreau, 2007).

Furthermore, the decrease in phenological differences between the two NILs at higher temperatures suggests that climate change may diminish variation in traits that allow for diverse niche occupancy (Lancaster, Morrison, & Fitt, 2017; Wagg et al., 2017).

Indeed, increased temperature poses a near-term threat to plants not only because of the magnitude but also because of the rate of temperature increase (Smith, Edmonds, Harlin, Mundra, & Calvin, 2015; Urban, 2015; Visser, 2008; Wilczek, Cooper, Korves, & Schmitt, 2014). Adaptability to new temperature regimes depends upon many factors such as population size, outcrossing frequency, generation time and an often overlooked aspect of adaptation to severe environmental shifts: genetic variation for extreme phenotypes (Charmantier & Garant, 2005; Ellstrand, 2014; Frankham, 2015; Jump & Penuelas, 2005; Leimu & Fischer, 2008; Matesanz & Valladares, 2014; Wright, Kalisz, & Slotte, 2013). Because of *Arabidopsis'* pliancy as a genetic model, we were able to create NILs that expressed extreme phenotypes due to transgressive segregation of functional and nonfunctional variants of temperature-sensitive genes. The resulting variation in bolting and flowering time affected fitness in a way that depended on both competitive context and season. Indeed, this experiment showed that phenology can underpin fitness outcomes in populations that partition their niche temporally. However, phenology did not fully explain fitness outcomes since the F NIL was largely nonplastic in phenology but plastic in fitness. In sum, our results suggest that by using a model organism, we were able to dissect genetic controls of specific traits that mediate interactions among competitors to show how they are likely to change in complex, context-dependent ways as temperatures rise.

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AUTHORS' CONTRIBUTIONS

M.A.T. conceived and designed the experiment. M.D.C. generated the NILs, and M.D.C. and M.A.T. genotyped the NILs. M.A.T. set up the experiment and collected data. M.A.T. and J.S. analysed the data and wrote the manuscript, and all authors revised it.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.b0t9g0m (Taylor, Cooper, & Schmitt, 2018).

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