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**Main Manuscript for**

Multivariate mapping of phenological genotype-by-environment interactions identifies two environmental cues for flowering in switchgrass (*Panicum virgatum*)

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**Author Contributions:** T.E.J. designed research. D.B.L. contributed plant material and resources. J.B., D.B.L., and T.E.J. designed and executed field experiments. A.H.M. and L.Z. conducted statistical and computational analyses. The manuscript was written by A.H.M., L.Z., and T.E.J. with contributions from all authors.

**Competing Interest Statement:** Disclose any competing interests here.

**Classification:** Biological Sciences; Population Biology.

**Keywords:** genotype-environment covariance, antagonistic pleiotropy, photoperiod, cumulative growing degree days, genetic variation

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Main Text

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Tables 1 to 2

**Abstract**

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Plant phenological timings are major fitness components affected by multiple environmental cues; thus, phenological traits can have important genotype-by-environment (GxE) interactions. Here, we map the genetic basis of, and assign environmental cues to, GxE in phenology in two highly divergent switchgrass (*Panicum virgatum*) populations. We evaluate the genetic basis of green-up and flowering as functions of weather-based cues (e.g. daylength, temperature) using a diversity panel grown at eight common gardens spanning the central United States. We use multivariate adaptive shrinkage (mash) to determine the prevalence of and map the genomic effects covarying with environmental cues and/or major data-derived effect patterns. >26% of Gulf population SNPs affecting flowering covaried with photoperiod cues, while >34% of Midwest upland population SNPs affecting flowering covaried with cumulative growing degree day cues. An independent pseudo-F2 cross of Gulf and Midwest individuals mapped 23 additive QTLs for flowering at the same common gardens, all with significant mash associations and ten with enrichment of highly significant mash associations. We demonstrate that we can identify QTL with GxE and assign them to specific environmental drivers and/or data-derived patterns. Breeding for particular alleles at these loci could change flowering responsiveness to photoperiod cues in switchgrass. More broadly, this approach could be used to identify genetic marker-environment interactions in any species with related populations phenotyped in multiple environments.

**Significance Statement**

The timing of plant seasonal development (phenology) has major impacts on fitness because of the negative consequences of plant-environment mismatches. Here we map the genetic basis of two phenological events, plant greenup and flowering date, in two genetically and phenologically distinct populations of switchgrass. We do this at eight field locations spanning the latitudinal range of both switchgrass populations. Our approach allows us to identify regions of the genome that covary with specific weather-related environmental features at every location. The Midwest population had genetic variation that covaried with cumulative growing degree days, a temperature-related measure, while the Gulf population had genetic variation that covaried with photoperiod, a day-length-related measure. This mapping could help many researchers explore gene-environment interactions.

**Main Text**

**Introduction**

The timing of plant vegetative and reproductive development are major components of plant fitness affected by multiple external environmental cues (e.g. degree of winter chilling, day length, temperature, and water availability) that signal existing or upcoming growing conditions (1–3). Genetic responses to environmental cues determine the speed, timing, and energy apportioned to vegetative and reproductive growth and shape both the individual’s lifespan and its lifetime production of viable seed. Day length (or photoperiod) is one of the most predictable environmental cues, and genetic sensitivity to photoperiod protects plants from potentially fatal consequences of phenological responses to temperature cues at the “wrong” time of year. However, species with wide natural distributions can segregate for multiple distinct environmentally-cued phenological responses: distinct populations of sunflower (*Helianthus annuus*) exhibit day-neutral, facultative short day, and facultative long-day flowering responses, which vary with their environments (4, 5). Distinct genetic responses in different environments are known as genotype by environment interactions, or GxE.

Flowering time, in particular, is a common subject of GxE research (4–10), a key output of selection driving adaptation to local environments (3, 11, 12), and a major target for crop improvement to adapt crops to local or future environments (13). Changing flowering responsiveness to photoperiod cues has allowed geographic range expansion and increased yields in a number of cereal species (14–18) and other crops (19, 20). Recent statistical advances in studying phenological GxE have involved determining critical environmental indices before the phenological event occurs, such as photothermal time within a critical growth window (9). However, most studies of flowering GxE focus on finding a single, best fitting form of genotype-environment covariance, even though we expect different genetic subpopulations, and even different genomic regions, to have evolved distinct patterns of GxE. Additionally, despite theoretical models that local adaptation should involve antagonistic pleiotropy, or sign-changing GxE, at the level of individual loci (21–24), previous work has found limited evidence of antagonistic pleiotropy (11, 25), and in fact has suffered from a known statistical bias that reduced detection of antagonistic pleiotropy (25–27). Thus, despite substantial interest in the frequencies of various forms of GxE, the prevalence of antagonistic pleiotropy relative to other forms of GxE remains unknown.

Switchgrass (*Panicum virgatum*) is considered a short-day plant with reproductive development strongly linked to day of the year (28). However, as part of its wide environmental adaptation across the eastern half of North America, its photoperiodicity has been predicted to differ by plant latitude of origin (29, 30). We previously found divergent Midwest and Gulf genetic subpopulations of switchgrass which segregate for distinct sets of climate adaptations (31). The Midwest genetic subpopulation is primarily composed of individuals from the well-studied upland switchgrass ecotype (32, 33), while the Gulf subpopulation has individuals from the lowland ecotype and the phenotypically intermediate coastal ecotype. Here, we test if these divergent populations differ in their phenological adaptations and hence their phenological GxE. We phenotype a diversity panel of hundreds of switchgrass genotypes from the Midwest and Gulf subpopulations for the start of vegetative development (“green-up”) and reproductive development (flowering) at eight common garden locations spanning 17 degrees of latitude. These gardens cover the majority of the latitudinal and climatic range of switchgrass and therefore capture the most comprehensive picture to date of the environmental variation this species encounters. We determine the genetic component of variation for green-up and flowering dates, then genetically map these traits using multivariate adaptive shrinkage (mash), which allows us to specify multiple ways genetic markers may covary with the environment, and does not have a statistical bias in detecting frequencies of different forms of GxE. To confirm the genetic mapping of GxE using mash, we compare to results from an outbred pseudo-F2 cross grown at the same sites. Taken together, our results allowed us to describe the environmental cues, genes, and alleles affecting flowering across two divergent natural populations of switchgrass.

**Results**

In our diversity panel of tetraploid switchgrass (31), genotypes from the Gulf and Midwest genetic subpopulations had distinct phenological responses and distinct patterns of phenological correlations across our common garden sites (Fig. **1a-b**). At the three Texas common gardens (hereafter ‘Texas’ gardens), located within the natural range of the Gulf subpopulation, Gulf green-up occurred before Midwestern green-up, and Gulf flowering occurred after Midwestern flowering (Fig **1a**). At the four northernmost common gardens (hereafter ‘North’ gardens), located within the natural range of the Midwest genetic subpopulation, both Gulf green-up and flowering occurred after Midwest green-up and flowering. At the Oklahoma common garden, located near the natural range limits of both the Gulf and the Midwest subpopulations, Gulf and Midwest green-up occurred over the same time period. These patterns led to strong negative phenotypic correlations for green-up between the North and Texas common gardens and contributed to positive phenotypic correlations for flowering time of larger magnitude at more northern gardens (Fig. **1b**).

Narrow-sense heritabilities (h2) indicated that rank-changing genotype by environment (GxE) interactions for these phenotypes were present across the eight common gardens (Fig **1c**). h2 were typically quite high at individual gardens: 59% on average for green-up date, and 87% for flowering date. However, h2 were variable across common gardens, and green-up dates were uncorrelated (r2 < 0.2) or negatively correlated across gardens (Fig. **1b**). These negative and small correlations undoubtedly contributed to the low h2 values for green-up and flowering date when estimated jointly at all eight gardens: h2 was 0.8% for green-up and 23.2% for flowering date in models including all gardens.

Genetic (G) and GxE effects explained little variation in green-up date across all gardens (<10%), but did explain substantially more variation when green-up was defined as functions of weather-based cues (Fig. **S1**). G and GxE explained more variation in green-up date (up to 60%) when the sites were restricted to either the Texas or North set of gardens, but in this case, defining green-up as functions of weather-based cues did not explain additional variation in green-up date (Fig. **S1**). Interestingly, G and GxE effects were larger for populations grown at gardens outside of that population’s native range.

In contrast to green-up date, G and GxE effects explained moderate variation in flowering date, and explained significantly more variation when flowering was defined, not as a Julian date, but as a function of a weather-based cue (Fig. **1d**). In the Gulf subpopulation, defining flowering as a function of daylength explained more G and GxE than as a function of Julian date (Fig. **1d**). In the Midwest subpopulation, a cumulative GDD (green-up to flowering) cue explained more G than flowering date, while three additional cues (daylength, rainfall between green-up and flowering, and rainfall in the five days before flowering) explained more G and GxE than flowering date (Fig. **1d**). The variation explained by G and GxE was also higher when the common gardens were restricted to either the Texas or the North gardens. For subpopulations growing outside their native ranges, G and GxE explained a substantial amount of variation in flowering as a function of rainfall cues, particularly for rainfall on the day of flowering. Taken together, these data indicate moderate additive genetic variation for a cumulative GDD-based flowering cue in the Midwest subpopulation, and similar genetic variation for a daylength-based flowering cue in the Gulf subpopulation. They also suggest the presence of GxE for rainfall, cumulative GDD, and photoperiod cues for flowering.

*Genotype-by-environment effects on green-up and flowering as functions of environmental cues* We further explored how genetic variation in phenology covaried with environmental cues using mash to jointly estimate SNP-associated trait effects across all common gardens for the Midwest, Gulf, and ‘Both’ subpopulations. We included “hypothesis-based” covariance matrices in each mash model that captured the covariance of weather-based phenological cues for cloned genotypes across our common gardens (Table 1; Supplement). These matrices differed substantially by weather-based cue and by population of origin of the genotypes included (Fig **2a, d**). For mash models estimating SNP effects for Both subpopulations, the hypothesis-based covariance matrices significantly improved the model fit (green-up likelihood ratio (LR) = 774; flowering LR = 2942). For single subpopulation mash models, the hypothesis-based covariance matrices improved model fits for Midwest green-up and for Gulf flowering, but did not improve it for the other phenotype (Midwest green-up LR = 866; flowering LR = -3063; Gulf green-up LR = -318; flowering LR = 1279).

SNP-associated effects covaried with different weather-based phenological cues in the different subpopulations (Fig **2b,e**). In total, 28.6% of the posterior weight of SNP effects in the mash model of Midwest green-up fell on a covariance matrix of the average temperature in the 10 days prior to Midwest green-up. Mash models of Gulf and Both subpopulation green-up did not have high weights on this matrix; instead, they had small but non-zero weights on two other hypothesis-based matrices, average temperature and cumulative GDD in the 18 days prior to green-up.

For flowering, too, distinct weather-based phenological cues captured SNP-associated effects in the two subpopulations. 12.1% of SNP effects on flowering in the Gulf subpopulation covaried with daylength in the time period when Gulf and Midwest genotypes were flowering, while 14% of SNP effects covaried with daylength change shortly before Gulf genotypes were flowering (when Midwest genotypes were flowering, Fig. **2e**). In contrast, many SNP effects on flowering in the Midwest subpopulation covaried with cumulative GDD from green-up to the time period during (14.6%) and after (14.0%) when Midwest genotypes were flowering (i.e. when Midwest or Midwest & Gulf genotypes were flowering, Fig. **2e**). SNP effects in the Midwest subpopulation did not covary with patterns of daylength or daylength change at flowering. Few (2.3%) SNP effects in the Gulf subpopulation covaried with flowering cumulative GDD. In Both subpopulations, all three of these matrices had large posterior weights, indicating that mash detected covariance with both sets of environmental cues in effects estimated using the combined population. Overall, flowering posterior weights on hypothesis-based matrices were higher than green-up weights for all three genetic subgroups (Fig **2c,f**). This indicated that our hypothesized environmental drivers captured more variation in SNP effects for flowering than for green-up.

*Major additional patterns of genotype-by-environment effects on green-up and flowering* In all six mash models, the hypothesis-based covariance matrices captured a minority of the significant SNP effects present in the data (Figure **2c,f**). Most SNPs had high posterior weights on the data-derived (“DD”) covariance matrices specific to each mash model; we thus explored patterns of SNP effects described by these matrices. We also characterized the overall patterns of differential sensitivity and antagonistic pleiotropy for SNP effects at all pairs of gardens.

For green-up mash models, one of the two major data-derived effect patterns was a pattern of antagonistic pleiotropy between pairs of Texas and North gardens. The largest fraction of SNP effects had high posterior weights on the DD\_tPCA matrices; 61-91% of the variation in the DD\_tPCA matrices was explained by two garden-based patterns of effects (Fig. **3a-c**), corresponding to the patterns of the first eigenvectors of DD\_PCA\_1 and DD\_PCA\_2, two additional data-driven matrices which also had non-zero mash posterior weights (Fig **2b**). For all three subgroups, one of these two effect patterns was characterized by large magnitude (>|0.5|) effects delaying green-up in the Texas gardens and in Oklahoma, with small (<|0.2|) to moderate (|0.2| to |0.5|) magnitude effects advancing green-up in MO and MI. Fewer SNPs exhibited antagonistic pleiotropy in the Midwest subpopulation than in the Gulf and Both subpopulations (Fig **3d-f**), where thousands of SNP effects exhibited antagonistic pleiotropy between pairs of southern and northern gardens.

For flowering mash models, very little antagonistic pleiotropy was seen between pairs of gardens; instead, there was substantial differential sensitivity between southern and northern pairs of gardens (Fig. **3j-l**). For each model, similar fractions of SNP effects had high posterior weights on the DD\_tPCA and DD\_PCA\_1 data-driven matrices, which captured fairly consistent patterns across subpopulations (Fig **3g-i**). This pattern was characterized by large magnitude effects of consistent sign that differed in their magnitude by garden (Fig **3g-i**). In other words, the major data-derived effect patterns for flowering showed differential sensitivity, but no antagonistic pleiotropy, between gardens.

*Confirmation of genotype-by-environment effects using an outbred F2 cross*

We sought additional experimental support for our mash intervals using an independent pseudo-F2 mapping population created from Gulf & Midwest individuals grown at the same common gardens (Fig. **4a,b**). We conducted QTL mapping of flowering as functions of four environmental cues with high posterior weights in mash, and identified eight QTL for flowering date, six QTL for flowering GDD, ten QTL for flowering daylength, and eight QTL flowering daylength change, all of which showed QTL by environment interactions. All QTL for flowering overlapped one or more homologs from rice or *A. thaliana* with functionally validated roles in flowering (Table **S2**). All flowering QTL intervals contained at least one SNP significant in at least one mash run at a log10-transformed Bayes Factor > 2, or in the 1% tail of significance, whichever was stricter. We also looked for enrichments of mash SNPs in the 1% tail of significance (the ‘mash 1% tail’) within each QTL interval. At the 5% level, ten QTL had enrichments of SNPs in the mash 1% tail. Overall, there were 16 significant enrichments (p < 0.05, hypergeometric test) of SNPs in the mash 1% tail in the QTL intervals. We chose 1000 sets of 23 genomic regions of the same size randomly distributed throughout the genome, then calculated enrichments of the mash 1% tail in these random intervals. Our QTL intervals had more enrichments than were found for all but three of these sets of random genomic intervals (Fig. **4c**, p = 0.003). Thus, we were able to experimentally support our mash intervals from the diversity panel with a QTL mapping experiment using a separate mapping population.

**Discussion**

As the climate and the natural environment change, it is increasingly critical to understand how patterns of gene-environment and plant-environment interactions will change in response. To do this, we must understand the current patterns of trait covariation across environments, the genetic underpinnings of these patterns, and the cases where this covariation can be altered. Here, we demonstrate that we can associate multiple patterns of GxE with specific genomic regions using a switchgrass diversity panel grown at eight common gardens, and also that we can assign specific SNP-associated patterns of GxE to both weather-based cues and to other, data-derived patterns. We use this approach to study GxE in both green-up and flowering phenological data in the deeply genetically diverged Gulf and Midwest subpopulations of switchgrass.

Our analysis of green-up in the Gulf and in Both subpopulations revealed substantial antagonistic pleiotropy in effects between the Texas and North common gardens (Figure **3a**). This result supports theoretical models that local adaptation should involve antagonistic pleiotropy at the level of individual loci (21–24) (Levene 1953; Felsenstein 1976; Kawecki and Ebert 2004; Hedrick 1986), and is the first experimental work using QTL mapping and GWAS across common gardens to find antagonistic pleiotropy to be common in small genomic regions (11, 34, 35).

Our analysis of flowering showed that the Gulf and Midwest subpopulations are segregating for multiple distinct photoperiod-related flowering responses: the Midwest subpopulation is day neutral, and flowering is cued primarily by a cumulative GDD threshold; in contrast, the Gulf subpopulation is photoperiod sensitive, and flowering is cued by the transition to shortening days. This result was supported by observations that expressing flowering date as a function of the daylength at flowering increased its heritability in the Gulf subpopulation, while expressing flowering date as a function of cumulative GDD between green-up and flowering increased the heritability of flowering in the Midwest subpopulation (Fig. **1d**). The genomic intervals affecting flowering found in mash were also supported by a QTL mapping experiment using a separate mapping population (Fig. **4c**).

**Materials and Methods**

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