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PARTITIONING GENETIC AND ENVIRONMENTAL COMPONENTS OF
PHENOLOGICAL VARIATION IN *QUERCUS DOUGLASII* (FAGACEAE)

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ABSTRACT

Oaks (genus *Quercus*) often display a large range of phenotypic variation across many of their traits. The contribution of genetic and environmental sources, and their interaction, to this variation can be partitioned experimentally using common garden plantings in which several genotypes are grown in a single location and the phenotype of interest is measured. Due to their slow growth and complex genetic structure, oaks have rarely been grown to maturity in experimental conditions that would allow partitioning phenotypic variation in this traditional way. Here we present results from trees growing in two established experimental gardens of *Quercus douglasii* Hook. & Arn. planted in 1991. Data from these common gardens are combined with additional data collected at the original provenance populations that served as acorn source locations. We surveyed phenological progression through the spring at both garden and field sites and found significant associations between fall and spring minimum temperatures and spring phenology, represented here as the date of bud break. A genetic component of phenological variation associated with the provenance sites was identified at both common gardens and accounts for 16.4% of the total variation observed among trees, while 68.2% of the variation can be attributed to environmental plasticity, plus a genetic \times environmental interaction that accounts for about 1% of bud break variation. We discuss the implications of these components of phenological variation in Blue Oak, especially with respect to climate change, local adaptation, restoration, and assisted gene flow.

Key Words: Blue Oak, common garden, environment, genetics, phenology, phenotypic variation.

California oaks show large variation in the timing of bud break and flowering across their range in any given year. This variation is commonly associated with both geographic differences among sites and local topographic variation within sites. Attempts to explain phenological variation in temperate trees tend to focus on analyses of weather variables such as temperature or precipitation, cumulative metrics such as growing-degrees, or geographic proxies such as latitude or elevation (Polgar and Primack 2011; Roberts et al. 2015). Among California oaks, previous research has shown that winter and spring temperature and precipitation are important drivers of spring phenology (Koenig et al. 2015; Gerst et al. 2017). These results are further confirmed by additional research reported in this special issue by Armstrong-Herniman and Greenwood (2021) and Koenig et al. (2021). Conflicting results among these studies concerning the effects of particular predictors suggest that phenological responses in these oaks may result from complex interactions, potentially integrated over more than one growing year. Additionally, the combination of multiple highly correlated weather variables, or especially weather and geographic variables, in a single phenological model makes identifying their independent effects even more difficult.

Temperature and the availability of water or sunlight prior to or early in the growing season are direct environmental drivers of phenology. Genetic phenological adaptation of populations to longer-term local conditions has often been found in previous research as well (Savolainen et al. 2007; Wilkinson et al. 2017; Dixit et al. 2020), including for the California oak *Quercus lobata* Née (Valley Oak) as reported by Wright et al. (2021) in this special issue. Genetic differentiation among populations is expected in a variable environment when environmental, population, or community interactions that depend on phenology have fitness effects. The timing of spring phenology (bud break and flowering) has several potential fitness effects for trees, via pollen limitation (Knapp et al. 2001), freezing damage (Augsburger 2013), and herbivory (Pearse et al. 2015). Direct influences of resource availability in the environment on phenological timing are a plastic response that allows individuals to respond to variation from year to year, including responses to progressive directional changes associated with climate change. Genetic adaptation to historical climate, on the other hand, limits the potential range of responses to the immediate environment. These limits can be adaptive if they dampen responses to short-term anomalies, but they also constrain the potential

to respond to directional change and can result in non-adaptive climate change responses and evolutionary lags (Browne et al. 2019).

Climate change simultaneously challenges California oaks with increased mortality from extreme events at the trailing edge of their distribution (Brown et al. 2018) and a potential dispersal lag at the leading edge that would prevent them from expanding into newly suitable locations (Serra-Diaz et al. 2014). The ability for oaks to respond to both of these challenges crucially depends on acorn production, which has been shown to be influenced by spring phenological timing, both as a result of flowering synchrony (Koenig et al. 2015) and herbivore pressure early in the season (Pearse et al. 2015). High fecundity in local populations at the trailing edge could preserve the adaptive potential of those populations against dieback due to extreme weather events by increasing genotypic diversity. Simultaneously, at the leading edge, greater acorn production can increase the rate of longer distance dispersal.

In the contexts of conservation and ecological restoration, climate change has given new impulse to debates over how to preserve the evolutionary potential of local populations while also encouraging migration into suitable habitats. Climate-informed assisted gene flow recommends sourcing seeds for restoration from sites that have historical climates more similar to the restoration site's predicted future climate, on the assumption that local adaptation to the historical location will make them better adapted in the new location compared to locally sourced seed (Aitken and Whitlock 2013). More recently, genome-informed assisted gene flow has also been suggested, which involves selecting seed sources based on empirically confirmed relationships between source genotypes and fitness measures, such as growth rate or reproductive success, at a target site (Browne et al. 2019). The restoration community has responded with skepticism to the suggestions for assisted gene flow due to a long-established preference for local seed sources in order to avoid disrupting existing patterns of local adaptation (McKay et al. 2005; Vander Mijnsbrugge et al. 2010). A lack of information concerning how much local adaptation there is among oaks, what the natural rates of gene flow are, and whether assisted gene flow is likely to disrupt locally adapted genotypes has left restoration specialists uncertain how to best proceed with restoration of degraded oak ecosystems in light of climate change (Spotswood et al. 2017; Baumgarten et al. 2020).

Reciprocal transplant and common garden experiments, in which individuals from several different local populations are grown and observed in one or more common environment, provide the clearest ways to address questions about the relative importance of local environment and genetic adaptation on phenotype (Clausen et al. 1941; Howe et al. 2003). Here we present results from established common

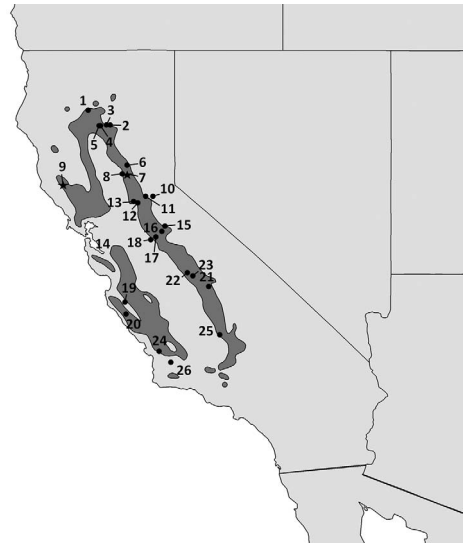


FIG. 1. The distribution of *Quercus douglasii* in California. The 26 acorn provenance locations and field survey sites used in this study are shown with black markers. Two common gardens are planted close to provenance 9 (Hopland) and provenance 7 (Sierra Foothills), indicated with stars on the map.

garden plantings of the California endemic blue oak (*Quercus douglasii* Hook. & Arn.), along with observations of adult trees at the original acorn provenance field sites sampled for the common gardens. Using spring bud break phenology as a readily observed measure of phenotypic differentiation, we examine the relative roles of local environment and genetics on the timing of bud break. We also investigate the roles of local weather at the garden sites and climate history at the provenance locations to identify how patterns of temperature and precipitation variation affect bud break phenology in blue oaks over both long and short timescales.

METHODS

Acorns for the common garden plantings were originally collected in 1990 at 26 provenance sites spanning the range of *Quercus douglasii* (Blue Oak), including the species' entire latitudinal range, as well as five transects across its elevational range in the Sierra Nevada (Fig. 1, Appendix S1). Acorns were collected from 10 maternal trees at each provenance site and grown together for the first year at a greenhouse location in Magalia, CA. In 1992, the one-year-old seedlings were then planted out at two common gardens, one in Mendocino County at the Hopland UC Research & Extension Center (N39.0137, W123.0959) and the other in Yuba County at the Sierra Foothills UC Research & Extension Center (N39.2467, W121.3173). The plantings followed a randomized complete block design consisting of ten blocks, each with nine sub-replicate seedlings

from each of the 26 provenance sites. Plots were weeded, but not irrigated during the first 2 yr of seedling growth and were protected by deer fences. In 2001–2002, six of the ten original blocks at each garden were thinned from nine to three sub-replicates per provenance. For additional details on the establishment of the garden plantings, refer to McBride et al. (1997). Trees were more than 25 yr old at the time of this study and only trees growing in the thinned blocks were surveyed, as growth in the blocks that had not been thinned was clearly reduced due to crowding. Mean tree height across all populations in the thinned blocks at Hopland was 3.79 m (SD = 1.15 m) and at Sierra Foothills was 3.67 m (SD = 0.93 m). Of the 468 trees originally planted in the six survey blocks at each garden, 13 had died by 2017 at Hopland and 105 had died Sierra Foothills. Despite their age and size, flower production was only sporadically seen on some trees over several years of observation.

In addition to the common gardens, 21 of the original 26 acorn provenance sites were re-identified and surveyed for this study in 2017. In 2018, three additional provenance sites were identified for a total of 24. The exact original maternal trees could not be located using the collection records, but the sites selected to represent the provenance populations are within 4 km of the original collection trees and ± 50 m elevation. At each provenance field site, 7 to 12 trees at least the same size as the trees currently growing in the common gardens were selected for phenological observation.

Spring phenology was surveyed on each tree at the common garden and provenance sites in 2017 and 2018 using a bud break index that ranged from 0 to 8 (see Appendix S2 for descriptions of each index stage). Common garden sites were surveyed every 7 to 14 d between mid-February and late-April. Provenance field sites were surveyed a minimum of two times during the same period.

The phenological index was designed to show a linear progression during leaf out across index values 1–7. This was confirmed using common garden trees surveyed at high frequency. As a result, a linear model could be fitted to the periodic survey data and used to interpolate a common phenological stage for all trees even though they were not all surveyed at the same stage. Phenological index value 3 (bud break) is used as the common stage for all analyses reported here.

Using the phenological variation observed in the common garden plantings, we ran two-way ANOVA (R 3.5.2, R Core Team, Vienna, Austria) to partition the phenotypic variation in the date of bud break into separate environmental and genetic components. Common garden location \times observation year (four levels in total) represents the environmental component while acorn provenance location (26 levels) represents the genetic component. The interaction between them is a genotype-by-environment (G \times E) effect and was included in the model.

Next, combining phenological data from both common gardens and the 24 provenance field sites, we sought to explain the environmental and genetic components of variation in terms of weather and climate variations using linear regression models. For the environmental component, weather variables at the individual growing location (common gardens or field sites) were used from the current water year, which runs from October of the previous year to September of the growth year in order to capture precipitation patterns in California's Mediterranean-type climate. To identify the genetic component explained by adaptation to local climate, we used 30-yr climate means from 1951–1980 (the 20th century climate baseline) at the provenance collection sites.

Gridded weather and climate data were extracted from the Basin Characterization Model (BCM) for California, which models weather and hydrology using the PRISM weather models topographically downscaled to 270 m resolution (Flint et al. 2013). Monthly estimates of minimum and maximum temperature and precipitation (36 total raster layers) were used for both the study period 2017–2018 as well as the climate baseline 1951–1980 (Appendix S3). To maximize explanatory power (adjusted R^2) while reducing multicollinearity among the 72 weather and climate variables, we used automated AIC-based stepwise model selection (function *stepAIC* in the R package *MASS*). This was followed up by manually removing individual remaining variables to reduce multicollinearity (as measured by the variance inflation factor, VIF) and highlight important variables.

RESULTS

More phenological variation was found across the provenance field sites than was found within either of the gardens. Mean date of bud break for populations at the provenance field sites in 2017 spanned 32 d from March 6 to April 7 in 2017 and 78 d in 2018 from February 18 to May 7. At the Sierra Foothills common garden, the mean date of bud break among the provenance populations spanned 19 d from February 26 to March 17 in 2017 and 35 d from February 10 to March 17 in 2018. At the Hopland common garden, mean date of bud break spanned 23 d from March 12 to April 4 in 2017 and 25 d from March 15 to April 9 in 2018. The longer period covered by bud break in 2018 compared to 2017, especially in the Sierra Foothills common garden and provenance sites located in the Sierra Nevada foothills, may be associated with a cold snap with freezing temperatures in early March of 2018. When data from the two common gardens are combined, the variation in bud break timing in the gardens covered approximately the same range of dates as the field provenance sites (Fig. 2).

In addition to the difference in bud break timing between the Hopland and Sierra Foothills common gardens and some differences between the 2017 and

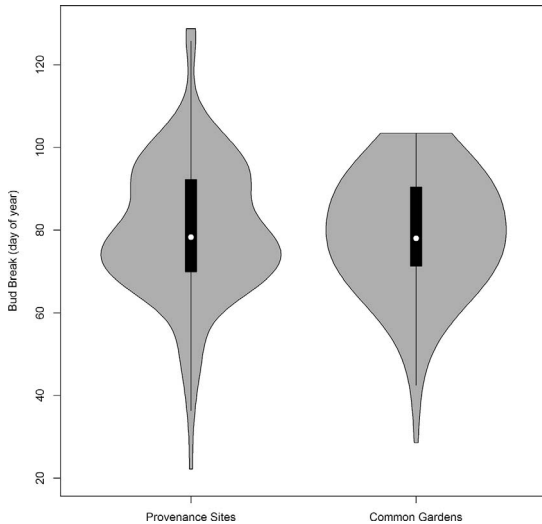


FIG. 2. Variation in the date of bud break in *Quercus douglasii* observed in 2017 and 2018. Wild trees growing at 24 provenance field sites throughout the species' range (left) compared to study trees growing at two common gardens (right). Central box plots show the the median date of bud break (white dot) and 1st and 3rd quartile values (black box bounds) while the surrounding curves show the distribution of individual bud break observations over the course of the season. Provenance sites served in 1990 as the original acorn sources for the common garden plantings.

2018 seasons, consistent phenological variation associated with individual provenance populations is readily identifiable in the common garden trees. Reaction norms plotted as mean bud break of trees from each provenance between the two garden locations show little difference in slope (lines are parallel) for the 26 provenance populations, indicating a consistent genetic effect of provenance site and similar degrees of plastic response across all of them (Fig. 3). This is confirmed by ANOVA models, which identify major components of phenological variation associated with both environment (two garden locations across 2 yr for four categories) ($F = 981.116$, $df = 3$, $P << 0.0001$) and genetics (acorn provenance site) ($F = 29.314$, $df = 25$, $P << 0.0001$) for the trees growing in the common gardens, as well as a significant, but very small interaction effect between environment and genetics ($F = 1.624$, $df = 75$, $P = 0.001$). Omega-squared (ω^2) calculated from the sums of squares in the ANOVA model shows 68.2% of the observed phenological variation at the common gardens can be associated with environment (garden location \times observation year) and 16.4% is associated with genetics (provenance location) while only about 1% of the observed variation is a $G \times E$ interaction (Table 1).

Using stepwise model selection on linear regressions with 36 weather variables for the 2017–2018 water years (monthly minimum temperature, monthly maximum temperature, and monthly pre-

TABLE 1. ANOVA PARTITION OF PHENOLOGICAL VARIATION AMONG OAK TREES GROWING AT TWO COMMON GARDEN LOCATIONS INTO COMPONENTS EXPLAINED BY PROVENANCE SITE (GENOTYPE, G), GARDEN LOCATION \times OBSERVATION YEAR (ENVIRONMENT, E), AND THE INTERACTION TERM ($G \times E$).

	Df	SS	F-statistic	P-value	ω^2
G	25	17203	29.314	2.136×10^{-82}	0.1642
E	3	69091	981.116	1.483×10^{-211}	0.6822
$G \times E$	75	2859	1.624	0.00143	0.0109
Residual	511	11995			0.1427

cipitation), we found that only a handful of these were needed to explain a large portion of the observed phenological variation. First, for bud break phenology observed at the provenance field sites, the full set of water year 2017–2018 weather variables explains 59.5% of the variation ($F = 27.49$ on 36 and 333 df, $P << 0.0001$). Fall and spring monthly minimum temperatures have the most important effect in the models. November minimum temperature and March minimum temperature in the current water year alone explain 33.3% of the observed phenological variation at the provenance sites in 2017 and 2018 ($F = 93.23$ on 2 and 367 df, $P << 0.0001$).

The single variable November minimum temperature of the current water year (i.e., prior calendar year) was particularly powerful in explaining observed bud break variation, across both provenance field sites and the two common gardens, with an R^2 of 42.0% across all sites in 2017 and 2018 and an effect size of -10.5 d for every degree-Celsius ($F = 713.7$ on 1 and 983 df, $P << 0.0001$) (Figs. 4A and 5A). Multicollinearity between weather variables is common, though, and despite variance inflation factor (VIF) between November and March minimum temperature of <2.0 , indicating very low collinearity, parameter estimates of the effect size may still be unreliable. What is clear, though, is that higher minimum temperatures, especially in fall and spring months, advanced the timing of bud break at these sites.

The remaining phenological variation observed among trees at the common gardens, which cannot be explained by the current year weather they experienced, is partly explained by the climate of the acorn provenance sites sampled to plant them. The same 36 monthly temperature and precipitation variables, but as 30-yr climate mean from 1951–1980 rather than the current water year, in a combined model explain (adjusted R^2) 12.9% of the variation observed among the common garden trees ($F = 4.828$ on 25 and 589 df, $P << 0.0001$). Multicollinearity was again a problem for these climate-based analyses, but maximum temperatures appear stronger in the climate effect. March maximum temperature for 1951–1980 was the single best predictor from the provenance populations of bud break in the common garden locations, although it explains only 2.4% of

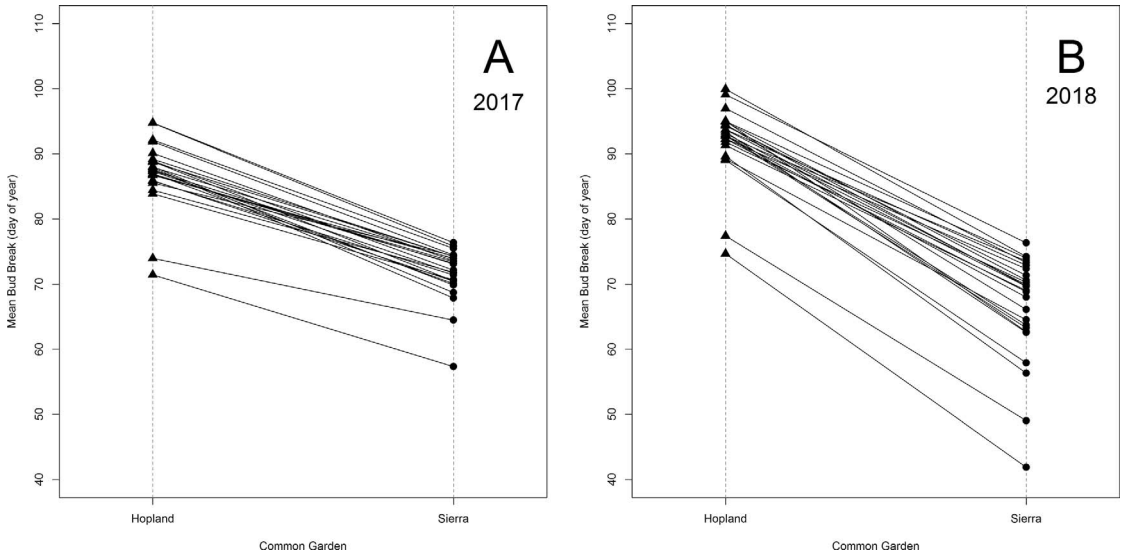


FIG. 3. Mean date of bud break in 2017 (A) and 2018 (B) for 26 provenance populations of *Quercus douglasii* growing at two common garden locations.

the observed variation, with a fairly consistent effect size of one day of bud break advancement for every degree-Celsius ($F = 12.57$ on 1 and 613 df, $P = 0.0004$) (Figs. 4B and 5B). In addition, 1951–1980 average March and September precipitation at the provenance sites were also identified as significant predictors, associated with later bud break in the common gardens. In combined models with March maximum temperature, all three climate variables

were able to explain a total of 4.8% of phenological variation in the common gardens.

Finally, these findings of genetic effects associated with provenance climate in the common gardens were applied back to both the garden and provenance field sites by including both the current water year weather variables (November and March minimum temperature) and the 1951–1980 30-yr mean of March maximum temperature and March

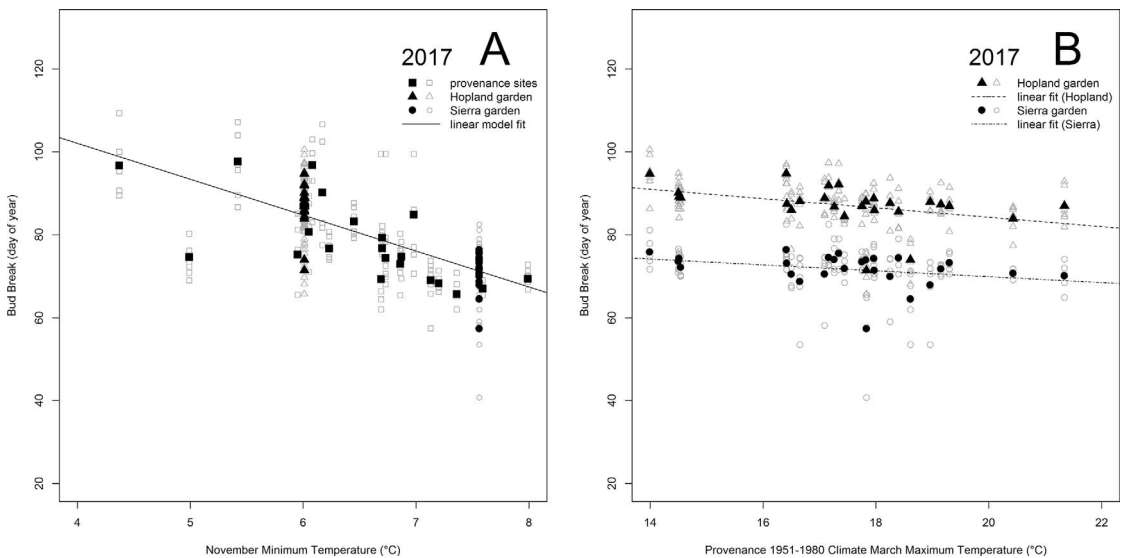


FIG. 4. 2017 bud break phenology for *Quercus douglasii*. (A) Bud break for all surveyed trees across two common gardens and 21 provenance field sites as a response to minimum temperature the previous November. (B) Bud break in the two common gardens (Hopland and Sierra Foothills) as a response to 1951–1980 climate March maximum temperature at the original acorn collection provenance sites. Open shapes in grey represent individual trees, while closed shapes are population means.

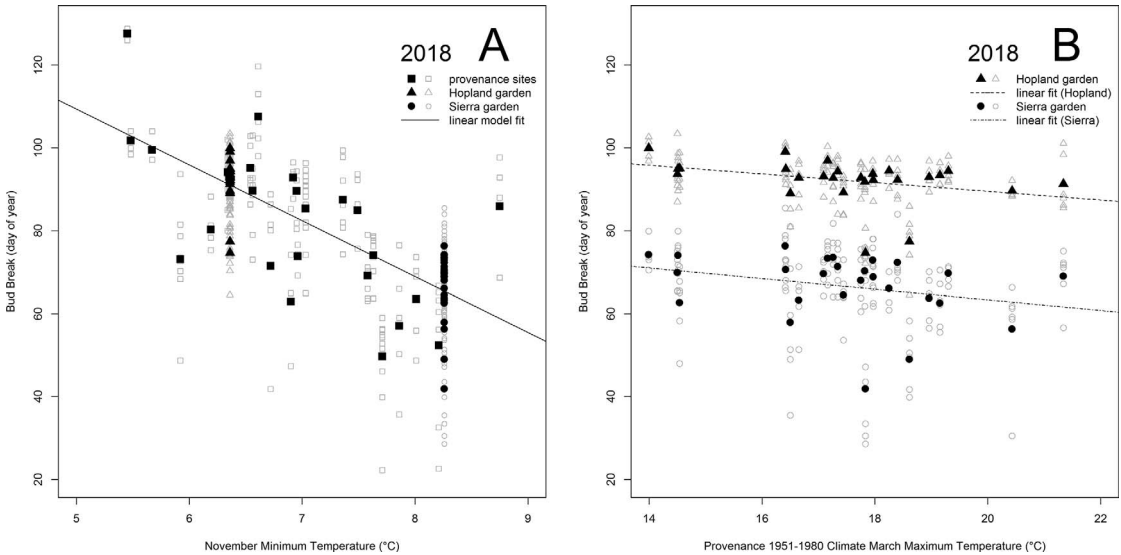


FIG. 5. 2018 bud break phenology for *Quercus douglasii*. (A) Bud break for all surveyed trees across two common gardens and 24 provenance field sites as a response to minimum temperature the previous November. (B) Bud break in the two common gardens (Hopland and Sierra Foothills) as a response to 1951–1980 climate March maximum temperature at the original acorn collection provenance sites. Open shapes in grey represent individual trees, while closed shapes are population means.

and September precipitation in a combined model (Table 2). Warmer November and March minimum temperatures experienced in the current water year advance bud break date by about 8 and 3 d per degree-Celsius, respectively, while warmer March maximum temperatures in the historical climate advance bud break by an additional day per degree-Celsius. These variables together explain 51.5% of the total observed phenological variation across all sites ($F = 209.6$ on 5 and 979 df, $P << 0.0001$). However, previous warnings about the effects multicollinearity among variables should still be applied here, despite VIF values < 2.0 .

DISCUSSION

Using an established common garden experiment planted from acorn collections across the range of *Quercus douglasii* (Blue Oak), with trees growing at two locations and more than 25 yr old at the time of the study, we found significant effects of both environment (common garden location and year)

and population level genetics (acorn provenance site) on the timing of spring bud break (Table 1). The genetic \times environmental interaction effect in the model is significant, but very weak, meaning that individuals responded uniformly based on their genetic background and the local environment. The remaining residual variation, similar in size to the provenance genetic effect, may be largely due to individual genetic variation among trees from the same provenance, though the effect of microsite soil and moisture variability within the common gardens is likely to be important as well. A large role for environmentally-driven phenotypic plasticity in phenology is expected (García-Mozo et al. 2002; Parmesan and Yohe 2003; Vitasse et al. 2009), while the significant genetic effect we found demonstrates a role of local evolutionary forces in shaping the phenological timing of blue oak as well.

Previous studies of oaks in both North America and Europe have reported high within population phenotypic variation across a range of traits; while a consistent local genetic effect can sometimes also be

TABLE 2. MULTIPLE REGRESSION RESULTS OF SELECTED CLIMATE AND WEATHER VARIABLES ON DATE OF BUD BREAK ACROSS BOTH GARDENS AND ALL PROVENANCE FIELD SITES FOR 2017 AND 2018. Historical climate (1951–1980) at the acorn provenance site represents a genetic component of variation in this model while the water year variables represent an environmental component. Adjusted $R^2 = 51.45\%$, $P << 0.0001$.

	Parameter Estimate	Standard Error	<i>t</i> -value	P-value
March max temp (1951–1980)	−1.0646	0.2291	−5.646	3.845×10^{-6}
March precip (1951–1980)	0.0586	0.0147	3.868	1.169×10^{-4}
September precip (1951–1980)	0.4700	0.0754	6.234	6.744×10^{-10}
November min temp (water year)	−8.0369	0.4142	−18.963	1.461×10^{-68}
March min temp (water year)	−2.7827	0.2653	−10.525	1.283×10^{-24}

identified, its importance varies widely (Derory et al. 2010; Ramírez-Valiente et al. 2010; Cavender-Bares and Ramírez-Valiente 2017). Previous results even from this same common garden experiment illustrate how the magnitude of genetic effects may depend on what aspect of phenotype is studied. Shoot growth over the first 4 yr in the common gardens was found to be strongly influenced by provenance site (McBride et al. 1997), but more recent ecophysiological work on the same trees found no variation among provenances in their susceptibility to vascular embolism (Skelton et al. 2019).

Comparison with the study of Wright et al. (2021) published in this special issue is especially interesting. Using a common garden design similar to ours, they found significant genetic effects of provenance climate on the spring phenology in Valley Oak (*Quercus lobata*). Their analysis focused on bioclim summary variables (rather than monthly climate) and did not include bioclim_8, which is most similar to the March maximum temperature that we identified as a significant climate predictor. However, both maximum temperature of the warmest month (bioclim_5) and elevation, which is strongly associated with spring temperature, had effects consistent with our findings for Blue Oaks. They also found that a climate history of precipitation in both the wet season (bioclim_13) and dry season (bioclim_14) delayed phenology, which is again consistent with our findings for the genetic effects associated with March and September precipitation.

In our study, the environmental component of phenological variation across all sites could largely be explained by minimum temperatures in the months preceding bud break, especially November and March (Figs. 4A and 5A), while the genetic component, as revealed in common garden conditions, was in part associated with climate history at the provenance locations. A composite climate effect in regression models with only common garden trees explained 12.9% of the bud break variation, which compares well with the 16.4% explained by provenance site as a categorical variable in ANOVA. No single monthly climate variable was found to explain a major portion of this genetic effect, but March maximum temperature was consistently significant, though alone it only explained a small amount of the observed phenological variation (Figs. 4B and 5B).

The magnitude of the effect of temperature forcing on spring phenology we report in these oaks (Table 2) is similar to figures that have previously been reported for oaks in the Mediterranean region (Sanz-Pérez et al. 2009) and northern European temperate forest trees, including *Quercus robur* L. (Roberts et al. 2015). Between 5 and 10 d of phenological advance per degree-Celsius of temperature increase is commonly found. However, we must note again that, despite VIF in all our models < 2.0 (indicating very low multicollinearity), parameter estimates remained sensitive to exactly which monthly temperature and precipitation variables we included together

in a model. As a result, we do not believe that the parameter estimates for the effects of November or March minimum temperature in our models and reported here should be considered definitive. Instead, the responses we highlight involving these particular months point to a more general importance of low temperature, in both fall and spring, as an environmental influence on phenological timing in Blue Oaks. A summary statistic like monthly minimum temperature is ultimately not likely to be the direct environmental factor influencing the timing of phenology. Similar to geographic proxies that are often used (e.g., elevation or latitude), monthly minimum temperatures are correlated with mechanistically proximate factors. Variable selection and parameter estimates in models will depend on the strength and interactions involved in those correlations.

We did not find that winter cold temperatures advanced the timing of bud break (i.e. chilling hours). In fact, the relationship between winter temperature and spring phenology was negative, so that colder temperatures in winter delayed bud break just as they did in spring. This finding agrees with previously reported results in European oaks from both Mediterranean and continental climates (García-Mozo et al. 2002; Roberts et al. 2015; Wilkinson et al. 2017). Oaks do not seem to require chilling-hour accumulation during dormancy to set buds as seen for some other temperate forest trees (e.g., birch or hawthorn). Instead, temperature has a uniform forcing effect, with warmer temperature advancing bud break throughout the entire dormant season.

Our results suggest that the debate over assisted gene flow versus using local seed sources should not in fact be a major concern in the case of Blue Oaks, at least when considering spring phenology with its important implications for pollination success, freeze-damage, productivity, and herbivory. While a significant signal of local adaptation in phenological timing was observed, there was a high variation among trees collected from the same provenance site, often encompassing almost the total variation observed across all provenance sites (Figs. 4B and 5B, open shapes). Thus, while climate-informed assisted gene flow seems unlikely to disrupt patterns of local adaptation, it also may not be particularly beneficial in the case of Blue Oaks. Local populations of Blue Oak have been shown to harbor large amounts of genetic variation (Rice et al 1997; Papper unpublished data) and this within-population genetic variation, together with the microsite variation within both gardens and provenance sites, likely explains much of the residual phenological variation that was not explained in this study. If the local phenological variation within sites is comparable to variation across the species' entire range, as it seems to be, that existing local variation already provides the potential to allow populations to track changing climate and assisted gene flow would add little to

their adaptive potential. This agrees with results found in other oaks, for which within population variation has been suggested as important for seedling establishment (González-Rodríguez et al. 2012). The critical question is whether cycles of seedling recruitment, maturation, and mortality will be able to keep pace with the rate of changing climate. This process can be aided by restoration efforts, with or without involving assisted gene flow. For restoration purposes, the most important recommendation may simply be to plant more acorns, in order to better capture the adaptive potential of whatever population is chosen as a seed source. The advantage of assisted gene flow should be seen as only a somewhat increased probability of planting well-adapted genotypes, in which case fewer acorns may be necessary. This could warrant consideration in terms of cost- and labor-saving in restoration projects.

By building on the legacy of the two established common garden plantings, combined with new field work tracking phenological activity and high-resolution monthly temperature and precipitation model data from PRISM/BCM, we have been able to tease out a significant component of genetic phenological adaptation in Blue Oaks and associate it with the temperature and precipitation history of the provenance sites that provided acorns for the common garden plantings. This study illustrates a powerful combination of data sources with the potential to be replicated in many other cases. A rich legacy of mature common garden plantings, involving a variety of woody species, can be found languishing, largely unknown, across California and outside the state. The availability of modeled climate data has the potential to make these gardens very valuable if the seed source locations are or can be established, as they were in this case. Broad efforts should be made to document and catalog historical common garden plantings such as these and collate whatever data is available about them, so that they can be utilized in a new generation of research informing climate adaptation strategies.

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