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ABSENCE OF FLOWERING SHIFTS IN *ARCTOSTAPHYLOS* AND *CEANOTHUS* OVER THE PAST CENTURY OF CLIMATE WARMING

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ABSTRACT

Flowering phenology in five chaparral species was investigated using more than a century of data obtained from herbarium collections. Three species examined were from the genus *Arctostaphylos* (Ericaceae) and two from *Ceanothus* (Rhamnaceae). Collections of these species were examined relative to climate change data during the same time period. For all the species, no change in average flowering time occurred during the past century. Considerable variability was found in flowering phenology and this variability was explored using generalized linear (GLM) and generalized linear mixed models (GLMM) and different dimensions of temperature and precipitation timing. While the genera performed differently, both required combinations of precipitation, temperature, and their interactions to predict flowering date. *Arctostaphylos* responded the most to precipitation interactions, while *Ceanothus* responded the most to temperature interactions and the previous growing season's precipitation. In both genera, regression coefficients were combinations of both positive and negative variables, indicating that flowering dates are complex interactions among the different dimensions of precipitation and temperature.

Key words: chaparral, climate change, Ericaceae, generalized linear mixed models, phenology, precipitation, temperature, Rhamnaceae.

Plants adjust to seasonal changes in their environments by modifying the timing of developmental stages (Forrest and Miller-Rushing 2010; Piao et al. 2019; Dorji et al. 2020). Developmental processes like bud-break, flowering, and maturing of fruit track changes in their environments (Menzel and Fabrian 1999; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Badeck et al. 2004; Menzel et al. 2006). The environmental processes influencing their phenology are multiple, but in humid, temperate regions, temperature is usually designated a principal regulatory process, often as a chilling requirement or as a constraint, along with photoperiod as a control on temperature fluctuations at the atypical time period (Körner and Basier 2010). In semi-arid or arid regions, precipitation, with its contribution to soil moisture, becomes a significant and sometimes a principal influence on phenology, as long as other aspects of the environment are not a constraint (Beatley 1974; Kemp 1983; Bowers and Dimmett 1994; Gordo and Sanz 2005; Lesica and Kittelson 2010; Cleland et al. 2012; Mazer et al. 2015). For example, summer flowering in desert 'sky islands' was a response to the amount and timing of monsoonal rains (Crimmins et al. 2011).

Most studies have indicated an advance in flowering phenology, or earlier flowering, in reaction to current changes in climate due to warmer winters and springs (Menzel et al. 2006; Gordo and Sanz 2010; Cleland et al. 2012; Mazer et al. 2013). Others have found more complex responses, such as delays in spring phenology (Yu et al. 2010) or divergence of responses in plants of the same community (Sherry et al. 2007; Cleland et al. 2012; Kopp et al. 2020). Early spring flowering plants have responded more sensitively to warming and advanced their flowering compared to later blooming taxa (Park et al. 2019). Plants appear to be responding to multiple environmental influences, integrating those influences in sometimes unexpected responses (Peñeulas et al. 2004; Crimmins et al. 2010; Gordo and Sanz 2010).

California is experiencing increasing temperatures, while precipitation has fluctuated considerably, but has stayed roughly constant on average (Hayhoe et al. 2004; Dettinger 2005, 2016; Cayan et al. 2008) (Fig. 1). California already experiences extremely variable storm regimes (Ralph and Dettinger 2012), yet meteorological models indicate that this interannual-interdecadal variability will increase in the near future (Dettinger and Cayan 2014; Dettinger 2016; Gershunov et al. 2019). While climate change is quite apparent at higher latitudes, in western North America it has also become increasingly variable (Dettinger and Cayan 2014; Gershunov et al. 2019). If precipitation and temperature are important influences for plant phenology, phenological responses should respond to this environmental variability.

The objective of this study is to focus on a few woody species found in chaparral in the genera *Arctostaphylos* (Ericaceae) and *Ceanothus* (Rhamnaceae) and to investigate influences on their flowering phenology. Both genera are early bloomers and fall into a phenological class that is usually most sensitive to warming (e.g., Park et al. 2019). But flowering phenology is under the influence of a number of processes and in our Mediterranean climate, the amount and seasonality of water should influence flowering as much as temperature, especially in woody plants (Rathcke and Lacey 1985; Law et al. 2000; Grossiord et al. 2017). The first objective is to

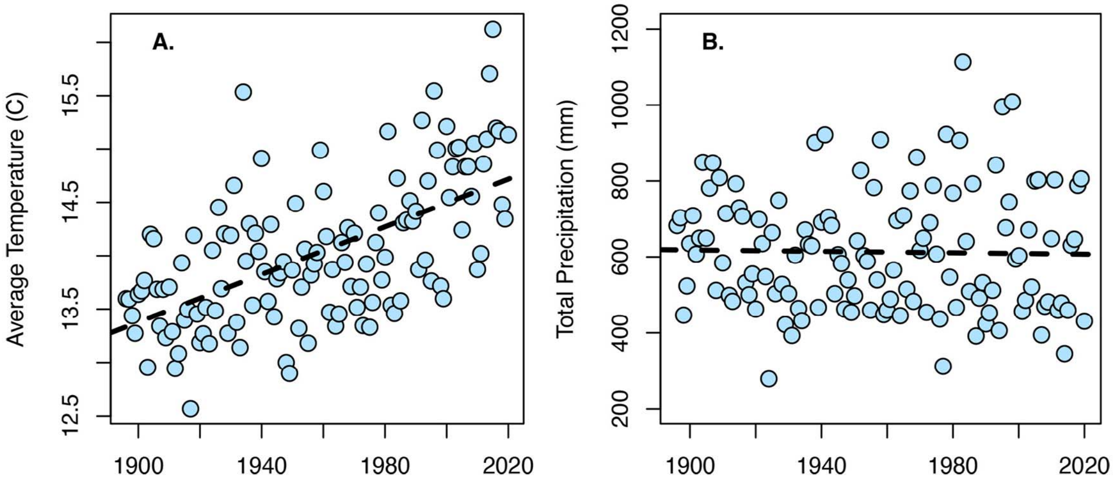

FIG. 1. Variation and trends in temperature and precipitation in California. A) Average temperature from 1886–2019; B) Total precipitation (mm) from 1886–2019. These data represent averages for each year based on data from the Western Regional Climate Center's (U.S.) WestWide Drought Tracker (https://wrcc.dri.edu/wwdt) that uses PRISM data (Abatzoglou et al. 2017).

assess whether species have responded to the past century's increase in winter/spring warming by advancing their flowering. A second objective is to determine the extent to which either temperature or precipitation during the growing season just before flowering is important, and whether there is an interaction between temperature and precipitation. Finally, in relatively seasonally dry habitats like California chaparral, one little explored issue is whether the prior year's precipitation might also have an influence. For example, a wet year should allow plants to produce and store more carbohydrates, potentially permitting earlier or more extensive flowering the following year, while a significant drought might limit resources in the next year and delay flowering.

METHODS

Species Selection

Arctostaphylos and *Ceanothus* were chosen as study taxa because of their overall distribution and dominance in the California Floristic Province, and because they differ in their typical flowering dates; *Arctostaphylos* species tend to flower between December and February, while *Ceanothus* species flower from March into April. Species of interest in this study included three species of *Arctostaphylos* (*A. glandulosa* Eastw. subsp. *glandulosa, A. andersonii* A.Gray, *A. hookeri* G.Don) and two species of *Ceanothus* (*C. cuneatus* (Hook.) Nutt.*, C. thyrsiflorus* Eschsch.). These taxa were chosen for several reasons, one was to examine broad-ranging taxa (*A. glandulosa, C. cuneatus*), along with more narrowly restricted coastal taxa (*A. andersonii, A. hookeri, C. thyrsiflorus*). Herbarium collections were used as the source of date of flowering, although a constraint was finding sufficient numbers of collections spread over a large number of years for plants in flower. A previous study determined that different lineages of *Arctostaphylos* species differed in phenology and the tetraploids also differed from one of those lineages (Parker et al. 2020). Therefore, species selected for this study represent those two lineages, plus the third is a tetraploid. The two *Ceanothus* species also represent the two large clades of this genus. Herbarium specimens have been found to be accurate with sufficient numbers for phenological work (Robbirt et al. 2011; Willis et al. 2017; Panchen et al. 2019).

Flowering Based on Collection Data

Flowering was the only phenological stage examined in this study spanning the years 1896–2020 using herbarium collections. If flowers were present, for each species the collection date and location data were recorded. In addition, collections were restricted to 0–1000 m elevation to ensure relatively similar phenological responses. Herbarium sheets were examined in person (California Academy of Sciences, CAS/DS); or digitally online (UC/JEPS, DAV, RSA/POM, and a few others using the Consortium of California Herbaria 2 database). Using these criteria, a large number of collections were analyzed (n = 311), specifically, for *C. thyrsiflorus* (n = 102); *C. cuneatus* (n = 71); *A. andersonii* (n = 28); *A. hookeri* (n = 34); *A. glandulosa* subsp. *glandulosa* (n = 76). Collections used are listed in Appendix 1.

Data Organization

The herbarium collection date was used as the sample date for flowering and converted to Day of Year (DOY) numbering. Because many *Arctostaphy-*

los species initiate flowering in the late fall-early winter and to restrict a single flowering season to be in a simple numerical sequence, collections dates were converted to a modified Day of Year (DOY) numbering scheme where October 1 corresponded to Day 1, and September 31 of the following year corresponded to Day 365 or 366, (equivalent to the 'Water Year' for the United States [USGS 2016]). Individual collections were excluded with dates earlier than 1896 due to the limitations of the environmental data set. The modified DOY scheme was also used for *Ceanothus* for consistency in statistical analyses.

Environmental Climate Data

Climate data were obtained from WestWide Drought Tracker (Abatzoglou et al. 2017), which uses data from the PRISM data set as a product of the Western Regional Climate Center (U.S.), the Desert Research Institute, and the University of Idaho. For the two broadly distributed taxa (*A. glandulosa* and *C. cuneatus*), latitude and longitude were extracted from the herbarium sheets; these were used to extract localized environmental data for each collection (nearest 4 × 4 km area). For the narrowly distributed taxa (*A. andersonii*, *A. hookeri*, *C. thyrsiflorus*), county averages encompassing their distribution range were used.

Previous studies indicate that precipitation and temperature for the growing season and immediately prior to flowering can influence flowering timing (Schlesinger et al. 1982; Keeley, 1987a). One study suggested that flowering in *Ceanothus*, at least, may be influenced by the previous growing-season's total precipitation (Keeley and Keeley 1988). Based on these earlier studies, several temperature and precipitation measures were used to study their relative influence on flowering. These represent a preliminary investigation and are not intended as to suggest a final resolution of abiotic influences on flowering in these two genera.

Rather than using calendar years that cut across two growing seasons, the water-year (October 1–September 31) was used as the growing season year. Based on the water-year, for each individual collection, five climatic data values were obtained. Two temperature values used in analyses represented deviations from "normal" average temperature as provided by WestWide Drought Tracker, which used a 20-yr record to determine the normal averages (1981–2000; Abatzoglou et al. 2017). Deviations indicate cooler or warmer periods based on the averages for the location of each individual collection and permit a single comparative value across collection sites. The first temperature variable obtained for each collection was the deviation from average annual temperature based on a 12-mo water-year period. A second temperature value extracted was the deviation for just the months prior to flowering (a 5-mo period, October–February, for *Arctostaphylos*; a 6-mo period, October–March, for *Ceanothus*).

Three precipitation values were extracted as well; these values represent precipitation as a % of normal average precipitation; paralleling the temperature values, the 'normal' average was based on a 20-yr record (1981–2000), and data extracted for this study were based on the water-year sequence of months. The first precipitation value extracted was the 12-mo water-year % of normal encompassing the flowering date. The second value was the % normal precipitation for the water-year months prior to flowering (October–February for *Arctostaphylos*; October–March for *Ceanothus*). In addition to these two values, a third value representing the % normal precipitation for the previous water-year was also obtained for each collection site and date.

Statistical Analyses

Flowering dates were initially probed using simple linear regression analysis against environmental variables using the *lm* function in R (version 3.5.3, R Foundation for Statistical Computing, Vienna, Austria). To address the long-term data set as a group for each genus, generalized linear mixed models (GLMM) tested the date of flowering against the individual climate variables or in combinations with and without interactions, resulting in 40 different models tested. In these models, the fixed variables were single or combinations of the five environmental variables extracted from WWDT/PRISM, and different species were considered random variables within each genus. The two genera were analyzed separately. The models used the *lme* function in R with from the *nlme* package. The Akaike information criterion (AIC) and Bayesian information criterion (BIC) were used to rank models. AIC and BIC estimate the relative quality of statistical models for a single data set; the lowest possible AIC or BIC indicates the best balance of model fit with generalizability. Residuals for the best model for each genus were graphed to examine whether the mean of the errors approximated zero, the distribution was normal, and the variation of errors appeared constant. The residuals were then specifically tested for normality using the Jarque-Bera Test (*jarqueberaTest* function) from the *fBasics* package. To analyze each species individually, generalized linear models were used (*glm* function in R), and were applied to the same 40 different models of individual climate variables or combinations; AIC was used to rank models in these analyses.

RESULTS

Temperature and Precipitation Trends

Temperatures have increased significantly on average over the last century in California (Abatzoglou et al. 2017) (Fig. 1a) (multiple $R^2 = 0.358$, adjusted $R^2 = 0.353$, $F_{1,123} = 68.62$. $P = 1.704e{-}13$), and the amount of variation among years has stayed

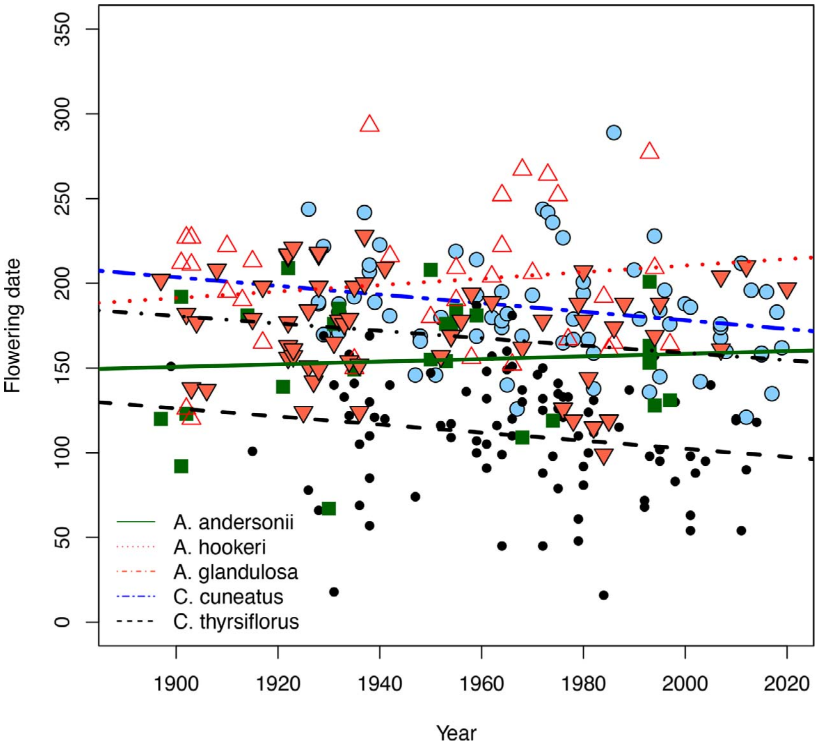

FIG. 2. Linear regressions of collection date for flowering individuals against time. No regression was statistically significant. Species symbols: *Arctostaphylos andersonii* are filled squares; *A. hookeri* are open triangles; *A. glandulosa* are downward and filled triangles; *Ceanothus cuneatus* are filled circles; *C. thyrsiflorus* are small, filled circles. Flowering date represents actual Day of Year for the two *Ceanothus* species. For *Arctostaphylos* species, due to flowering some years as early as November or December, a modified Day of Year (DOY+122) was used for this figure.

roughly constant. In contrast, precipitation has fluctuated considerably, but the average has changed little over the past century (Fig. 1b) (multiple $R^2 = 0.00043$, adjusted $R^2 = -0.0077$, $F_{1,123} = 0.053$. $P = 0.818$); although there is a trend for increased variability among years.

Linear Regressions

For all of these species, no trend in flowering phenology across the past century existed (Fig. 2). As could be predicted from the spread of data, r^2 results for these linear regressions were extremely low and ranged below 0.1. Linear regressions revealed that no species had significant relationships between flowering phenology and year, temperature departure from normal, % of normal precipitation, growing season temperature departure from normal, or growing season % of normal precipitation, and no linear relationship with the previous growing season's precipitation (Figs. 2–4).

Generalized Linear Mixed Models

In the GLMM models, simple single variable models for each genus performed poorly and rarely yielded statistically significant relationships between flowering phenology and the variables. The best performing models were combinations of fixed variables and often the more complex ones that included interactions among variables (Table 1) (Burnham et al. 2011). Graphing the residuals for the best model suggested the mean of the errors approximated zero, the distribution was normal, and the variation of errors appeared constant. Therefore model assumptions were met. The Jarque-Bera Test for normal distribution of the residuals confirmed the best model for each species contained normal distribution; the distribution is normal to approximately normal if the P-values are not significant x (*Arctostaphylos*: $\chi^2 = 3.4829$, $P = 0.1753$; *Ceanothus*: $\chi^2 = 0.5177$, $P = 0.7719$).

Examining the top ranked models for each genus (Table 1) indicated that both genera are responding to temperature and precipitation, but their responses differ. For *Arctostaphylos*, all models emphasized different dimensions of precipitation as the most influential variables; generally, models combined interactions of the previous year's total precipitation with current season's precipitation. One highly-ranked model included current season temperature as influential. Coefficients for the best models were examined to understand the pattern associated with these environmental factors (Table 2). Positive

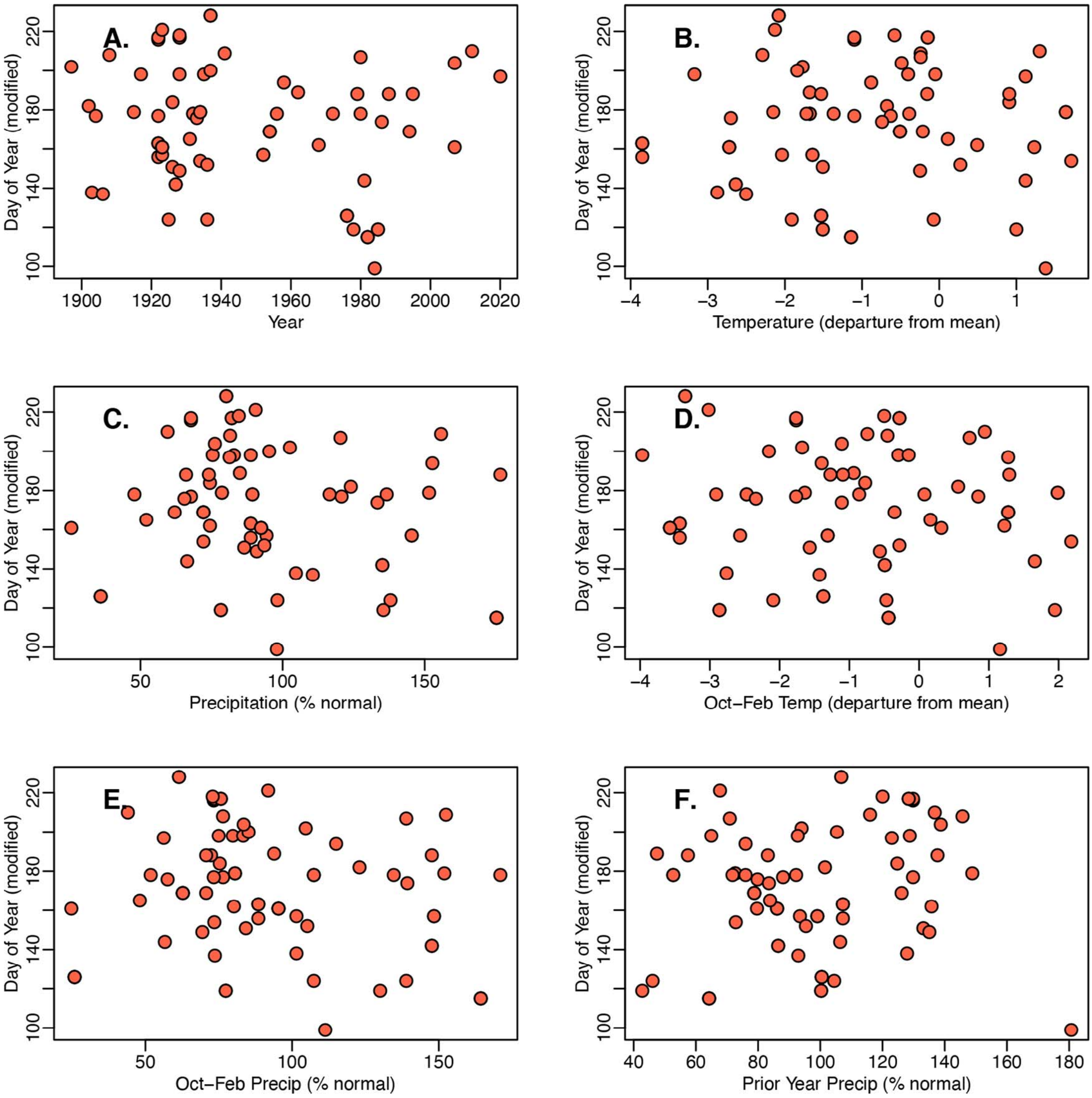

FIG. 3. Day of year flowering for *Arctostaphylos glandulosa* based on herbarium collections and various climatic factors. A modified flowering Day of Year (actual DOY+122) versus A) year of collection; B) departure from the mean average temperature for a given year; C) percentage of normal precipitation for a 12-mo period; D) departure from the mean average temperature for a 5-mo period before mean flowering; E) percentage of normal precipitation for a 5-mo period before mean flowering; F) percentage of normal precipitation for a 12-mo period prior to the year of collection.

coefficients will delay flowering while negative coefficients indicate earlier flowering. Because these are models with multiple variables, often a balance occurs between coefficients of the different climate variables supporting earlier and delayed flowering with the larger coefficients having greater impacts than smaller coefficients. Current season precipitation in the few months before flowering was usually the largest coefficient influencing flowering date. In the best model for *Arctostaphylos*, current season and prior season total precipitation were the most important influences and were positive, indicating delayed flowering. Total season precipitation and interactions between current growing season precipitation and that of the previous year were negative and would advance flowering earlier. Temperature was usually not a significant factor in most the top models, although current season average temperature was a component in two of the top three models.

For *Ceanothus* a different pattern emerges (Table 1). Most of the top models included variables representing temperature. Moreover, models lacking temperature variables usually were ranked lower than models that included temperature. Three of the

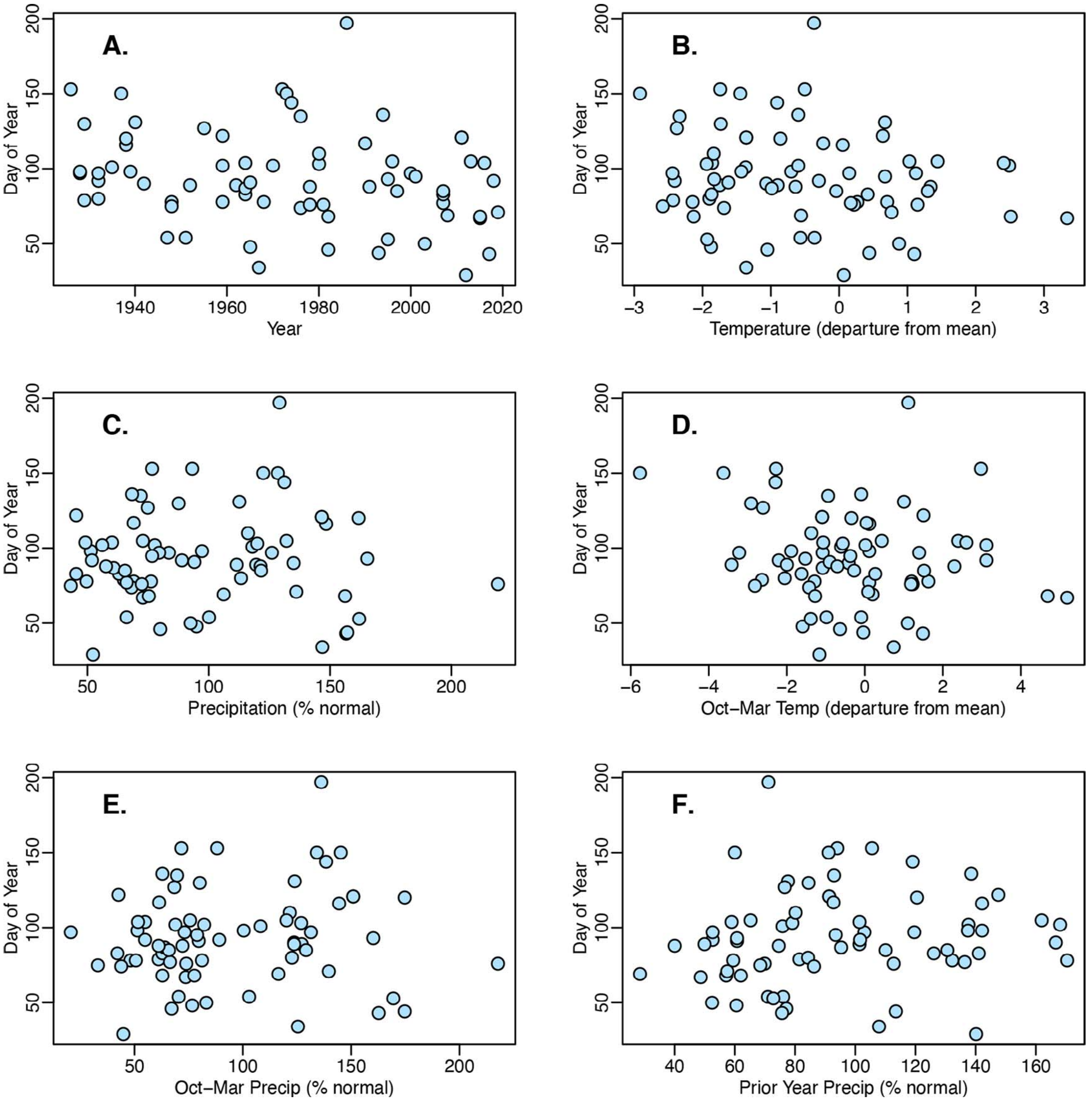

FIG. 4. Day of year flowering for *Ceanothus cuneatus* based on herbarium collections and various climatic factors. Flowering Day of Year versus A) year of collection; B) departure from the mean average temperature for a given year; C) percentage of normal precipitation for a 12-mo period; D) departure from the mean average temperature for a 6-mo period before mean flowering; E) percentage of normal precipitation for a 6-mo period before mean flowering; F) percentage of normal precipitation for a 12-mo period prior to the year of collection.

four highest ranking models incorporated total season average temperature; two included current growing temperature. In this analysis, only one of the four top models included coefficients that only reflected precipitation, that of both the current and previous growing seasons. Examining the coefficients of the best ranked *Ceanothus* model for the flowering date regression indicated two large coefficients (Table 2), with the average temperature for the entire biological year advancing flowering dates, while the current season's average temperature delayed flowering (the current season coefficient was not statistically significant). The balance between variations of these variables would either advance flowering, such as a colder winter and warmer spring, or potentially delay flowering, such as a warm winter and cooler spring to summer. In addition, one of the highest-ranking models included only precipitation from the previous growing season plus precipitation in the month preceding flowering. Other models that were ranked relatively high included both temperature and precipitation values in some combination.

Generalized linear models (GLM's) were applied to the same data set for each species separately

TABLE 1. THE TOP MODELS ASSESSED BY GENERALIZED LINEAR MIXED MODELS (GLMM) FOR FLOWERING IN *ARCTOSTAPHYLOS* AND *CEANOTHUS* SPECIES. Model = variables used in the model; AIC = Akaike information criterion; BIC = Bayesian information criterion. Models indicate the variables most strongly associated with the pattern of flowering phenology as represented in the herbarium collection data. All variables found in each model are indicated. The smallest value for either AIC or BIC represents a higher ranking. In general, models differing by 2–7 AIC units are considered statistically different (Burnham et al. 2011); the other models with larger values not shown. T = growing season (Oct–Sept) temperature departure from normal; P = growing season precipitation as a % of normal precipitation; Prior = previous growing season precipitation as a % of normal precipitation; T5m(T6m) = mean temperature departure from normal for the first 5(6) mo of the growing season (Oct–Feb[Mar]); P5m(P6m) = precipitation as a % of normal for the first 5(6) mo of the growing season (Oct–Feb[Mar]). Normal is calculated as the average of values from 1981–2000 by the National Climate Center.

Taxon	Model	AIC	BIC
Arctostaphylos	P + P5m + Prior + P:P5m + P:Prior + P5m:Prior + Prior:P5m:P	1374.409	1403.681
	P + P5m + Prior + P:P5m + P:Prior + P5m:Prior + Prior:P5m:P + T5m	1376.343	1408.543
Ceanothus	T + T6m	1710.747	1726.514
	T	1711.044	1723.657
	P6m + Prior	1711.044	1723.657
	T + T6m + T:T6m	1711.615	1730.535

(Table 3, Appendix 2). The overall results were similar with some important differences. *Arctostaphylos* species responded more to precipitation variables, while *Ceanothus* species responded more to temperature variables in these analyses as long as the prior season's precipitation was included. The models indicated some slight differences among the species. *Arctostaphylos andersonii* and *A. hookeri*, both restricted to colder maritime areas, had more high ranked models with responses to temperature variables than *A. glandulosa*. Similarly, both *Ceanothus* species had similar responses to the overall genus models, with the exception that the previous season's precipitation was found in every high ranked model. As in the GLMM models, coefficients that were significant were both negative and positive, indicating a complex response to these variables (Appendix 2).

DISCUSSION

For these chaparral species in *Arctostaphylos* and *Ceanothus*, flowering phenology has not paralleled historical temperature increases, an aspect of California's climate that has changed the most over the past century (Figs. 1, 2). Given that these plants are early flowering species, especially *Arctostaphylos*, they represent divergences from the pattern that has been found in most species (Cleland et al. 2012; Park et al. 2019). Because of the interannual variability inherent in California's climate, trends in temperature influences on these species may have been constrained by precipitation patterns. For example, patterns of biomass and composition in California's annual dominated grasslands are strongly influenced by precipitation and temperature interactions (e.g., Pitt and Heady 1978). For these shrub species, both precipitation and temperature variables combine in several ways in predicting the timing of flowering.

In *Arctostaphylos*, the prior year's total precipitation appeared to have the most frequent influence on flowering, but also this was associated with the current growing season's precipitation and sometimes temperatures. This pattern is congruent with what other researchers have found in short-term field studies (Baker et al. 1982; Keeley 1987a; Keeley and Keeley 1988). Flowering in *Ceanothus* species may respond to large fluctuations in precipitation between years (Baker et al. 1982; Schlesinger et al. 1982; Keeley 1987a), as indicated in one of the higher-ranking GLMM models and all of the GLM models for *Ceanothus* species. *Ceanothus*, however, for this

TABLE 2. COEFFICIENTS FOR THE TOP GLMM MODEL FOR EACH GENUS. Abbreviations as in Table 1.

Taxon	Model effect	Value	Std. error	DF	*t*-value	P-value
Arctostaphylos	(Intercept)	−18.091	102.267	128	−0.177	0.859
	P	−1.641	1.365	128	−1.202	0.232
	P5m	5.030	1.133	128	4.438	**0.0000**
	Prior	2.029	1.106	128	1.835	0.069
	P×P5m	−0.016	0.009	128	−1.816	0.072
	P×Prior	0.016	0.0149	128	1.105	0.271
	P5m×Prior	−0.053	0.012	128	−4.270	**0.0000**
	P×P5m ×Prior	0.0001	0.0001	128	1.754	0.082
Ceanothus	(Intercept)	143.835	26.700	169	5.387	**0.0000**
	T	−8.648	3.668	169	−2.357	**0.0195**
	T6m	3.924	2.603	169	1.507	0.134

TABLE 3. THE TOP FLOWERING MODELS ASSESSED BY GENERALIZED LINEAR MODELS (GLM) FOR *ARCTOSTAPHYLOS* AND *CEANOTHUS* SPECIES. Models indicate the variables most strongly associated with the pattern of flowering phenology as represented in the herbarium collection data. Models are presented ranked with the best models at the top as ranked by AIC. Abbreviations as in Table 1.

Taxon	Model	AIC
Arctostaphylos glandulosa	P + Prior + Prior:P	952.54
	P + Prior + Prior:P + T5m	953.26
	P + Prior + Prior:P + T	954.21
Arctostaphylos andersonii	T + T5m +P5m + P:P5m +T:P + T5m:P + T5m:P5m + T:P:P5m + T5m:P:P5m	354.92
	P5m + T + T5m +T:T5m + TP5m +T6m:P5m +T:T5m:P5m	384.20
Arctostaphylos hookeri	P + P5m + T + T5m + T:T5m + P:P5m +T:P + T:P5m + T5m:P + T5m:P5m +T:P:P5m + T5m:P:P5m +T:T5m:P +T:T5m:P5m +T:T5m:P:P5m	461.17
	P + P5m + T + T5m + P:P5m +T:T5m	475.88
Ceanothus cuneatus	Prior + P6m + T6m + T6m:P6m	843.77
	Prior + T + P6m + T:P6m	846.49
	Prior + T + P6m + Prior:T + Prior:P6m + T:P6m + Prior:T:P6m	846.97
Ceanothus thyrsiflorus	Prior + T + P6m + Prior:T + Prior:P6m + T:P6m + Prior:T:P6m	1740.20
	Prior + T + P6m + T:P6m	1750.10

flowering data set, also responds to temperature variables that in various forms are found in most of the best models predicting flowering date. The coefficients in the models of both genera often conflict in their influence on the timing of flowering suggests a more complicated response to seasonal variation in temperature and precipitation rather than a straightforward advancement of flowering as climate warms. These two genera appear to be responding to an ensemble of influences that interact, so far yielding essentially a lack of net phenological shift. While species from the same genus may respond differently from each other (Gerst et al. 2017), in this case, the few species investigated appear to respond similarly within each genus.

The lack of a flowering phenological response in these species to warmer temperatures over the last century is perhaps related to the marginal and variable precipitation patterns in California's climate. The models interpreting their responses presented here are unfortunately coarse-grained, and yet they are consistent with other studies (e.g., Baker et al. 1982; Keeley 1987a). In addition, with perennial, woody species, interactions among these environmental factors may also influence the timing of flowering. Plus, the strength of these interactions' influence on phenological timing may vary among years depending on an individual plant's physiological condition at the end of the summer rainless period. For example, an extensive drought or large fruit crop in the previous year may limit the amount of photosynthate available for the subsequent year's flowering regardless of otherwise favorable conditions for flowering, potentially shifting the timing of flower initiation (e.g., Baker et al. 1982; Schlesinger et al. 1982; Keeley 1987a, 1987b; Keeley and Keeley 1988). Keeley (1987a) and Keeley and Keeley (1988) proposed that prior year environmental conditions can influence the timing or abundance of flowering in subsequent years, especially by limitations on or enhancement of photosynthate, and the subsequent impact on production of dormant flowering buds. The higher-ranking models in this study indicate that prior-year precipitation influences the temporal flowering responses of both genera. Another among-year influence that can influence flower timing is supra-annual variation in fruit production; this is a general pattern in woody plants without dispersal mutualists or with seed predators as dispersal agents (Herrera et al. 1998), as is the case in these two genera (Warzecha and Parker 2014; Parker 2015).

The lack of phenological flowering responses to more than a century of temperature increase suggests phenological emphases in these two lineages that are comparable to those found in other woody plants of semi-arid habitats (Beatley 1974; Law et al. 2000; Preito et al., 2008; Crimmins et al. 2011; Grossiord et al. 2017). Both *A. glandulosa* and *C. cuneatus* are widely distributed and collections from different locations probably have experienced different climatic histories. While the other three taxa are more narrowly distributed and shared a more similar climatic history; their populations, however, are arrayed in their distribution in a variety of soils, soil depth, shading from trees, differential elevation effects of the coastal marine layer, and other factors that vary among populations in coastal areas. Parsing actual population responses would require more focused research, controlling for variation in elevation, topographical aspect, or other factors. These narrower constraints have been found to be significant for some developmental stages in these and other plants (Keeley 1987a, 1987b; Keeley and Keeley 1988; Maclean 2020).

The lack of phenological shifts may also represent a sampling issue: larger numbers of individuals for these species, plus additional species for each genus may reveal a different pattern. For example, both genera have species above the annual snow level and those species may respond more readily to trends in temperature. This limited study suggests the predicted increase in climatic variability in California will likely continue to constrain simple climatic responses in lower elevation woody taxa in the future (Gordo and Sanz 2010). Given the differential influences in their models, *Ceanothus* species may respond to future temperature warming well before *Arctostaphylos* species; *Ceanothus* species, for example, may have already started responding, but that response was statistically undetected due to relatively few collections over the last 20 yr. Future studies also may need to incorporate experimental conditions varying temperature and soil moisture patterns in common garden situations to determine how physiological conditions influence flowering in these genera in the context of varying combinations of temperature and precipitation.

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Appendix 1

The following are the specimens used in determining phenological states. The specific herbaria are listed using their abbreviations.

Arctostaphylos glandulosa subsp. ***glandulosa***: CAS27405, CAS27195, CAS38856, CAS38778, CAS507644, CAS27204, CAS38842, CAS38855, CAS179647, CAS179649, CAS216564, CAS179652, CAS179654, CAS179655, CAS164580, CAS163646, CAS163641, CAS163639, CAS201940, CAS171306, CAS171207, CAS178407, CAS194674, CAS504664, CAS162244, CAS189254, CAS200532, CAS193593, CAS186157, CAS188675, CAS164647, CAS228416, CAS216316, CAS216487, CAS239247, CAS239248, CAS269558, CAS268411, CAS475648, CAS242753, CAS269574, CAS269572, CAS318636, CAS371643, CAS371646, CAS374764, CAS374765, CAS385987, CAS385985, CAS394056, CAS475925, CAS475631, CAS994592. CAS493305, CAS475633, CAS484548, CAS557007, CAS1046547, CAS1046492, CAS1046546, CAS618248, CAS801083, CAS800138, CAS800128, CAS743271, CAS658266, CAS658264, CAS658267, CAS740374, CAS734062, CAS734050, CAS742090, CAS1007699, CAS951805; ***A. andersonii***: CAS49392. CAS91950, CAS214744, CAS86763, CAS86796, CAS86776, CAS86778, CAS392350, CAS392357, CAS122344, CAS212879, CAS504920, CAS202229, CAS219965, CAS301728, CAS219972, CAS219963, CAS219962, CAS220011, CAS355188, CAS392352, CAS392347, CAS392356, CAS557251, CAS392349, CAS557259, CAS557257, CAS475932, CAS621546, CAS731140, Parker&Vasey 119, Parker&Vasey 177, Parker&Vasey 464, Parker&Vasey 864, Parker&Vasey 866, Parker&Vasey 863; ***A. hookeri***: CAS91948, CAS91858, CAS466406, CAS27445, CAS88044, CAS27447, CAS141901, CAS141428, CAS138889, CAS134670, CAS38907, CAS557263, CAS17891, CAS13756, CAS38905, CAS194680, CAS74440, CAS220015, CAS301730, CAS239213, CAS475420. CAS382185, CAS358577, CAS475410, CAS402849, CAS557274, CAS475415, CAS475416, CAS475417, CAS475419, CAS475418, CAS740366, Parker&Vasey 88, Parker&Vasey 89, Parker&Vasey 86, Parker&Vasey 242, Parker&Vasey 555, Parker&Vasey 870; ***Ceanothus cuneatus***: AHUC102187, AHUC102188, CAS:BOT-BC:32726, CHSC055268, CHSC064367, CHSC077440, CHSC090088, DAV304685 , DAV304523, DAV304524, DAV304526, DAV304527, DAV304529, DAV304533, DAV304535, DAV304542, DAV304543, DAV304544, DAV304547, DAV304549, DAV304551, DAV304552, DAV304554, DAV304561, DAV304607, DAV304608, DAV304611, DAV304615, DAV304617, DAV304622, DAV304634, DAV304639, DAV304645, DAV304651, DAV304652, DAV304670, DAV304678, DAV304684, DAV324542, DAV324543, DAV324545, DAV392077, LOB110753, LOB110752, LOB110762, OBI124019, OBI161895, OBI161908, OBI161909, OBI161910, RSA0170332, RSA0208758, RSA0215365, SBBG167484, SBBG167491, SBBG167494, SBBG169632, SBBG169635, SBBG169649, SBBG169654, SBBG169656, SBBG171548, SBBG171564, SBBG171570, UCSB016098, UCSB016100, UCSB016108, UCSB016116, UCSB016152, UCSB016158, UCSB052313; ***Ceanothus thyrsiflorus***: SBBG169845, SBBG171199, OBI124438, LOB110808, SBBG168217, SBBG172582, UC18432, UC1281280, OBI124443, SBBG171174, OBI124409, SBBG171203, UCSB016534, SFV112236, OBI124446, SBBG167821, UCSB016535, UCSC100004896, SBBG169847, UC1071409, SBBG172584, OBI124459, OBI124452, SBBG171173, SBBG171178, CSLA014530, UC1505527, SDSU12875, SBBG171168, DAV304796, LOB110804, LOB110805, SJSU5720, OBI124426, UCSC100004888, SFV112237, SBBG171183, SDSU10424, LOB110807, SFV112235, OBI124428, OBI124430, OBI124455, UCSB016530, UCSB016531, OBI124457, SBBG171184, SBBG169837, CSLA014458, MACF032735, UCSB016517, UCSC100004905, UCSC100004917, DAV304784, SBBG171211, UCSB016528, OBI124434, DAV304792, SJSU5728, UCD36556, UCD112730, UCSC100004890, UCSC100004886, UCSC100004887, SFV112233, SBBG171153, DAV304787, OBI124449, SBBG171152, UCSC100004889, SFV112238, UCSC100004916, DAV304782, SBBG169840, UCSC100004909, SBBG171200, DAV304786, UCSC100004912, SBBG169152, OBI124431, SBBG171204, UCSC100004914, SBBG171177, DAV304793, UCSC100004910, UCSC100004915, UCSC100004898, DAV304824, DAV304785, SBBG168223, AHUC102291, SBBG168222, CSLA014532, UCSC100004897, SDSU10425, UCSB016526, SBBG168213, DAV304823, CSLA014538, SBBG171207, SBBG169937, DAV304789, UCSC100004834, SBBG172593.

Appendix 2

Coefficients for the Top GLM Model for Each Species.

Abbreviations as in Table 1 in the main text. The colon separating variables indicates interactions between or among those variables. Asterisks indicate degree of statistical significance: * = 0.05; ** = 0.005; *** = 0.0005.

Species	Coefficient	Estimate	Std. Error	z value	P value
Arctostaphylos glandulosa	(Intercept)	5.425e+00	1.068e−01	50.789	<2e−16 ***
	P	−3.899e−03	1.020e−03	−3.822	0.000133 ***
	Prior	−2.406e−03	1.103e−03	−2.181	0.029198 *
	P:Prior	3.500e−05	1.101e−05	3.179	0.001476 **
Arctostaphylos andersonii	(Intercept)	3.763e+00	4.500e−01	8.364	<2e−16 ***
	T	3.351e+00	9.059e−01	3.699	0.000217 ***
	T5m	−8.553e+00	2.253e+00	−3.797	0.000147 ***
	P	1.848e−03	5.838e−03	0.317	0.751574
	P5m	3.137e−02	1.309e−02	2.397	0.016538 *
	T:T5m	−2.198e+00	1.420e+00	−1.548	0.121722
	P:P5m	−2.124e−04	7.353e−05	−2.888	0.003878 **
	T:P	−4.621e−02	1.231e−02	−3.753	0.000175 ***
	T:P5m	−1.481e−02	1.447e−02	−1.024	0.306071
	T5m:P	6.847e−02	2.032e−02	3.370	0.000752 ***
	T5m:P5m	1.092e−01	3.281e−02	3.330	0.000869 ***
	T:P:P5m	2.677e−04	1.131e−04	2.366	0.017962 *
	T5m:P:P5m	−9.273e−04	2.522e−04	−3.677	0.000236 ***
	T:T5m:P	6.256e−03	7.888e−03	0.793	0.427697
	T:T5m:P5m	4.393e−02	2.393e−02	1.836	0.066362 .
	T:T5m:P:P5m	−2.906e−04	1.672e−04	−1.738	0.082202 .
Arctostaphylos hookeri	(Intercept)	5.774e+00	1.242e−01	46.500	<−2e−16 ***
	T	−1.118e−01	2.383e−02	−4.690	2.73e−06 ***
	T5m	4.126e−02	2.236e−02	1.845	0.065 .
	P	−9.797e−03	1.526e−03	−6.422	1.35e−10 ***
	P5m	−2.890e−03	1.572e−03	−1.838	0.066 .
	T:T5m	−1.101e−02	9.455e−03	−1.165	0.244
	P:P5m	6.825e−0	5 1.188e−05	5.743	9.31e−09 ***
Ceanothus cuneatus	(Intercept)	5.1233020	0.0354029	144.714	<2e−16 ***
	T6m	0.0325149	0.0127056	2.559	0.01049 *
	P6m	0.0001846	0.0002231	0.827	0.40798
	Prior	0.0007372	0.0002610	2.824	0.00474 **
	T6m:P6m	−0.0004966	0.0001234	−4.024	5.71e−05 ***
Ceanothus thyrsiflorus	(Intercept)	4.551e+00	1.226e−01	37.129	<2e−16 ***
	T	−2.939e−01	1.139e−01	−2.579	0.009895 **
	P6m	3.505e−03	1.382e−03	2.536	0.011218 *
	Prior	2.486e−03	1.215e−03	2.046	0.040725 *
	T:P6m	3.258e−03	1.332e−03	2.445	0.014471 *
	T:Prior	3.865e−03	1.138e−03	3.398	0.000680 ***
	P6m:Prior	−4.897e−05	1.365e−05	−3.588	0.000334 ***
	T:P6m:Prior	−4.805e−05	1.301e−05	−3.694	0.000221 ***