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ANALYSIS OF A PLANT'S RESPONSE TO CLIMATE CHANGE FACTORS THROUGH THE USE OF HERBARIUM RECORDS: *COLLINSIA VIOLACEA* NUTT. (PLANTAGINACEAE)

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ABSTRACT

Climate change has resulted in various changes to the phenology of species, and some of these changes have been documented through the use of herbarium specimens. Understanding how plants react to changes in the environment can give scientists insight into how plants have been responding and will respond to the continuing consequences of climate change as well as how to approach biodiversity conservation. In this study, herbarium records of *Collinsia violacea* Nutt. ranging from 1895 to 2014 were utilized to show the trends of the first and peak flowering dates with regard to various geographic and climatic variables using regression analysis. The results from simple linear regression analyses showed a trend of the flowering times for first and peak flowering dates occurring earlier over the years; however, the relationship was not significant. The multiple linear regression full model for first flowering indicated increases in latitude, longitude, and mean monthly temperatures were associated with delayed flowering while increases in monthly minimum and maximum temperatures were associated with earlier flowering. The full model for peak flowering showed that peak flowering was delayed with increases in latitude, longitude, and maximum monthly temperature. The reduced models, with highly correlated variables removed, indicated significant delays in first flowering and peak flowering with increases in latitude, longitude, and mean monthly temperature, but no significant relationship between monthly precipitation and flowering time. Further research is needed to fully understand the implications of these changes.

INTRODUCTION

The average global temperature has increased 1.1℃ since 1880 and is projected to continue to increase (IPCC 2014). This increase in temperature has resulted in loss of sea ice, intense temperature changes, shifts in the geographic ranges of plants and animals, and changes to the phenology of plants (NASA 2022). Plant phenology is defined as the timing of species' phenophases (e.g., leaf-out, flowering, and fruiting) and provides an indication of change due to internal and external factors (Keatley and Hudson 2010; Morellato et al. 2013; Parmesan and Hanley 2015). Plant phenology can be affected by a wide range of variables including temperature, precipitation, and day length. The effects of

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the ongoing changes to the climate have become apparent in plants over the years. Changes of plant phenology can vary based on the species (Calinger et al. 2013; Pearson 2019). Spring is important in terms of phenological events, as many plants start showing signs of emergence from the winter (Keatley and Hudson 2010). Phenological observations have been used for centuries to allow for the understanding of our environment (Keatley and Hudson 2010). A wealth of long-term data is held within herbaria globally and can be utilized to document changes in plant phenology (Davis et al. 2015; Jones and Daehler 2017; Hufft et al. 2018; Pearson 2019). With herbarium specimens being digitized globally, researchers can now easily access them to conduct large scale studies.

Numerous studies have shown the utility of using herbarium specimens to investigate climate change impacts (Davis et al. 2015; Jones and Daehler 2017). Previous studies have primarily focused on the effects of temperature on flowering times; however, there have been mixed results. Lima et al. (2021) found that climate change has caused inconsistent patterns in flowering and fruiting times across different species. Calinger et al. (2013) and Gallagher and Leishman (2009) found that the increase in temperature caused by climate change has caused plants to flower at an earlier date. Pearson (2019) found that spring flowering species flowered 1.8 - 2.3 days earlier per 1°C increase in spring temperatures. However, Sherry et al. (2011) found that warm temperatures delayed flowering by 6.2 days.

In this study, we used herbarium specimens (Jones and Daehler 2017; Hufft et al. 2018) to assess the impacts of year as well as specific geographic and climatic factors (latitude, longitude, elevation, precipitation, mean temperature, and maximum and minimum temperatures) on the flowering time of *Collinsia violacea* Nutt., an Oklahoma native spring flowering plant.

Collinsia violacea is native to the United States with a center of distribution in Missouri, Arkansas, Oklahoma, and Kansas (USDA, NRCS 2024). It is on the state endangered species list in Illinois, with an isolated population in Shelby County (Taft et al. 2009). According to NatureServe (2024), it is critically imperiled in Illinois, with a rank of S1; imperiled in Texas, with a rank of S2; and vulnerable in Kansas, with a rank of S3. As there are various factors that could affect the decline of this species, it is important to monitor it to determine if there are any trends among the Illinois population and populations native to other states. In Oklahoma, *C. violacea* grows mainly in the eastern half of the state (USDA, NRCS 2024) and is commonly found in "sandy or rocky soils, dry open areas, and woodlands" (Flora of North America Editorial Committee 2019). *Collinsia violacea* has also been collected in Comanche County in southwestern Oklahoma. While western Oklahoma is drier than the eastern half of the state, these *C. violacea* specimens were collected in wetter microhabitats near creeks and draws in or near the Wichita Mountains Wildlife Refuge (Hoagland et al. 2022). Flowering begins in late March and can last until early June. It can multiply quickly and easily by reseeding, sometimes forming large colonies. As seedlings develop in late fall, they can survive harsh winters and start budding in early March (Arkansas Native Plant Society 2022).

Oklahoma is home to over 3,700 plant taxa, including subspecies and varieties, mainly due to variation in the state’s climate and physiographic and geological features. Temperature and precipitation of Oklahoma decrease along a gradient from east to west. The eastern area of the state is very moist due to the Gulf of Mexico, while the western area is significantly drier (Tyrl et al. 2017). Average annual precipitation in Oklahoma can range from as much as 56 inches in the southeast and decrease to 16 inches in the northwest (Arndt 2003). Average annual temperature ranges from approximately 16°C (62°F) in the southeast to approximately 14°C (58°F) in the northwest (Arndt 2003). The average growing season ranges from 225 to 230 days in the southern part of the state and decreases to 175 to 195 days in the panhandle. Oklahoma is often described as flat; however, its topographical features include rolling hills, narrow canyons, mesas, and deep ravines (Tyrl et al. 2017). The elevation of Oklahoma ranges from 88 m (289 ft) to 1,516 m (4975 ft) (Arndt 2003). Additionally, Oklahoma soils are very diverse, ranging from sand to clay to loam (Tyrl et al. 2017). According to Frankson et al. (2022), Oklahoma temperatures have increased 0.6°F since the early 1900s, and are predicted to have an "unprecedented" increase this century. Although they indicate there is no clear trend in changes in precipitation, they note that increased temperatures will lead to increased evaporation and drought intensity.

We utilized digitized herbarium records dating back to the 1890s to analyze the phenological response of *C. violacea* to climate change. Our null hypothesis was that there is no significant relationship between flowering time of *C. violacea* in Oklahoma and our selected variables.

METHODS

Digitized herbarium specimens of *C. violacea* collected from Oklahoma were used to investigate the effects of year and the effects of geographic and climatic factors on flowering phenology. Specimen records of *C. violacea* were downloaded from the Southeast Regional Network of Expertise and Collections Database (SERNEC 2022) and access to images of specimens housed in the Robert Bebb Herbarium (OKL) at the University of Oklahoma, Norman, OK, was requested. There was a total of 684 collected specimens in the original dataset. Specimen records without images were excluded before evaluating phenophase. Flowering phenology was evaluated based on pre-flowering (no flower buds open), first flowering (at least 25% of flower buds open), peak flowering (at least 50% of the flower buds open), and last flowering (the terminal flower buds on branches open) (Haggerty et al. 2013). After determining the phenophase of each specimen, we excluded those without a clear locality, exact collection date, specimens with a phenophase of pre-flowering or last flowering, and specimens without roots present. This resulted in a total of 253 specimens for first flowering ranging from 1895 to 2014 and a total of 252 specimens for peak flowering ranging from 1913 to 2009. No specimens were assigned to the last flowering category.

In addition to the Oklahoma *C. violacea,* we investigated the Illinois *C. violacea* specimens. As there is a limited population in Illinois, there was a total of 18 collected specimens in the Illinois dataset. We requested rare species viewer permissions in SERNEC to access images of the Illinois specimens. Phenophase assessment was identical to that used for the Oklahoma *C. violacea.* After determining the phenophase of each specimen, we excluded one specimen because it was categorized with a phenophase of last flowering. This resulted in a total of eight specimens for first flowering ranging from 1947 to 1971 and a total of nine specimens for peak flowering ranging from 1947 to 1971.

The collection locality information on each herbarium specimen label was utilized to georeference decimal degree coordinates. Specimens were georeferenced using GEOLocate (Rios et al. 2005) to obtain latitude and longitude. With the decimal degree coordinates, the historical climate data were collected using the PRISM model provided by the PRISM Climate Group (2015). The climate variables included the average monthly temperature (°F), average monthly maximum and minimum temperatures (°F), and average monthly precipitation (in) for the month the specimen was collected. In addition to the climate data, elevation (ft) data of four km resolution were obtained for each specimen. The collection date of each specimen was converted to the day of the year (DOY), with Jan 1 representing day one.

Statistical analyses were performed using R version 4.2.2 (R Core Team 2022). Linear regression (with a significance level of 0.05) was performed to determine whether there was a relationship between the collection DOY and the year. First flowering and peak flowering phenophases were combined and analyzed to determine if any general relationships were present. Then each phenophase was analyzed separately to determine whether a relationship was present for first and peak flowering. The regression equation slopes were evaluated as indicators of changes in flowering times. Negative slope values indicated the species was exhibiting earlier flowering dates, while positive slope values indicated delayed flowering dates (Primack et al. 2004; Haggerty et al. 2013; Jones and Daehler 2017). To determine whether there was a relationship between the day of the year (response variable) and the potential explanatory variables of year, elevation, latitude, longitude, precipitation, mean temperature , and maximum and minimum temperatures (Park and Mazer 2018) multiple linear regression analyses were conducted, using the combined flowering dataset and then on the individual phenophase datasets. Prior to the multiple regression analyses, simple linear regression was run for each variable against day of year. Multiple regression was then run for each of the three datasets using all variables except those that were not significant based on the simple linear regression. Then to determine whether any variables were correlated with one another, a Pearson correlation test was performed. Reduced models were run with the highly correlated (Pearson correlation coefficient ≥ 0.70) variables removed. Finally, we compared the multiple regression models using the *performance* function in the R package performance (Ludecke et al. 2021) to determine the best fit model based on the obtained Akaike Information Criterion (AIC) values.

RESULTS

Five hundred and five herbarium specimens of Oklahoma *C. violacea* were examined, ranging from 1895 to 2014. Of the 505 specimens, 253 specimens were categorized as first flowering and 252 specimens were categorized as peak flowering.

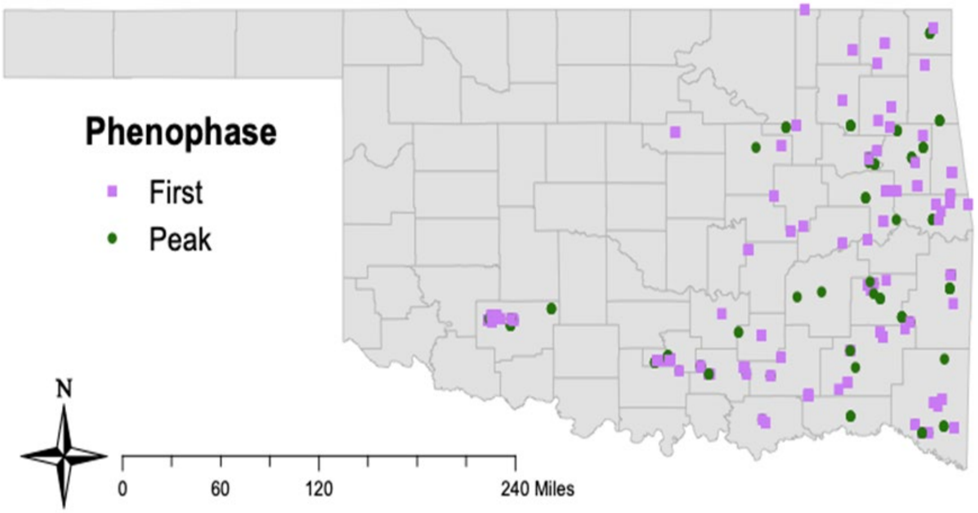


Figure 1 Distribution of herbarium records of *Collinsia violacea* Nutt. in Oklahoma from 1895 to 2014

They were scattered throughout the eastern region of Oklahoma, with a few locations (representing 70 specimens) from the southwestern part of the state (Figure 1). The frequency of specimens in the first flowering phenophase varied among years, but there was a good representation of the species around the 1930s, 1940s, and 1970s. The frequency distribution of specimens in the peak flowering phenophase was somewhat

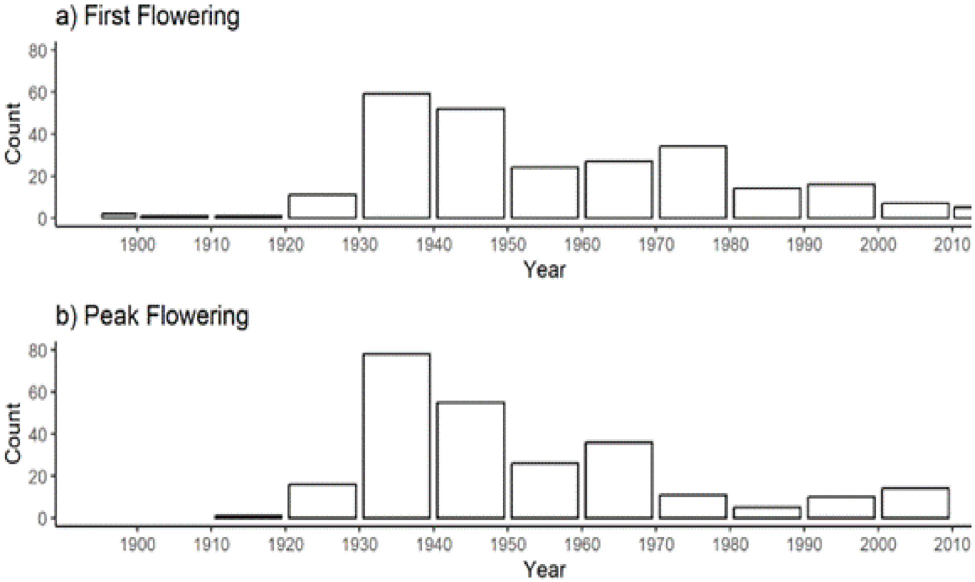


Figure 2 Counts of Oklahoma *Collinsia violacea* Nutt. specimens based on year of specimen collection. a) specimens in first flowering phenophase. b) specimens in peak flowering phenophase.

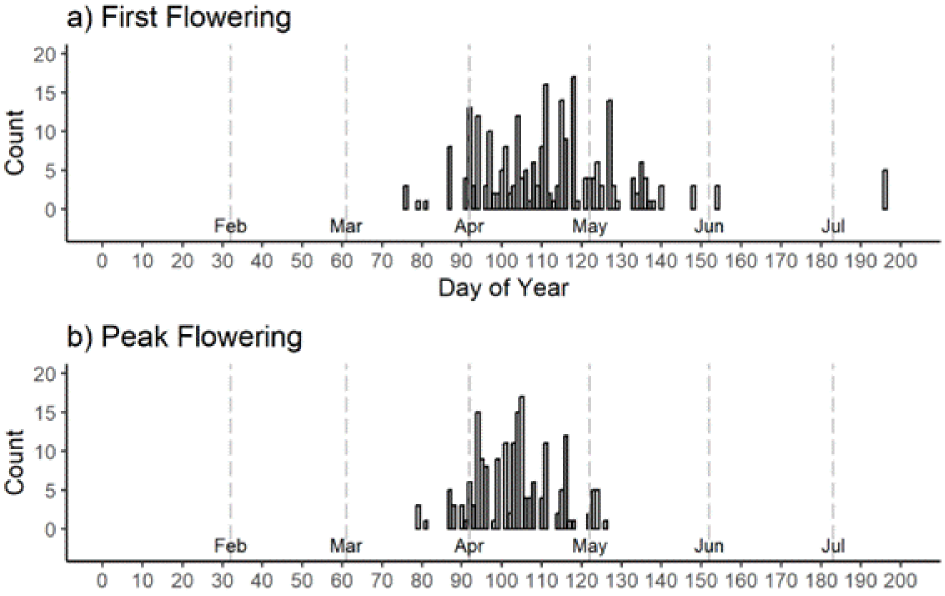
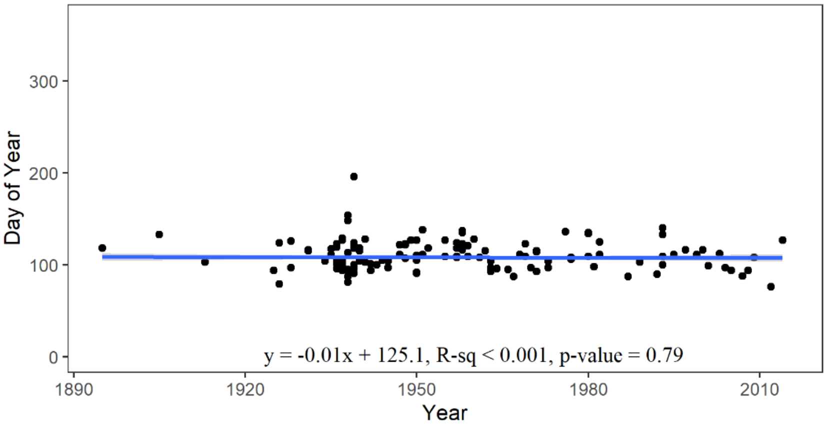


Figure 3 Counts of Oklahoma *Collinsia violacea* Nutt. specimens based on day of the year of specimen collection. a) specimens in first flowering phenophase. b) specimens in peak flowering phenophase. Grey dashed lines represent the first day of a month.

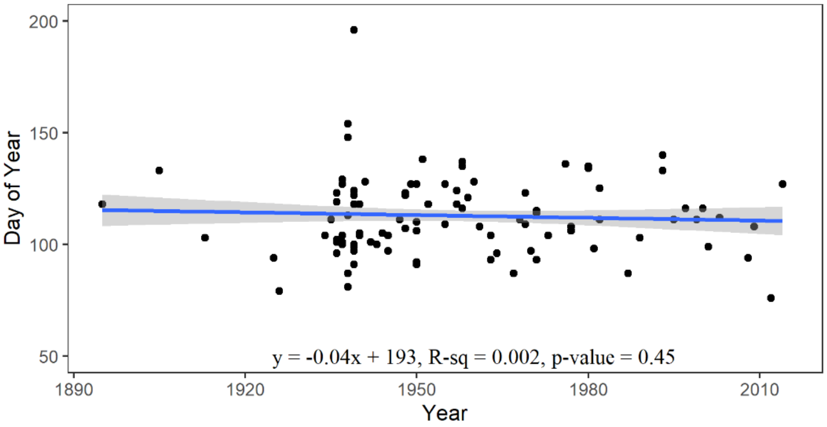
scattered but there was a large number of specimens from the mid-1930s to 1960s (Figure 2). The dates of collection of the species were similar for both first and peak flowering ranging around April (Figure 3).

Linear regression of day of year and year for both first and peak phenophases

a) First and Peak Flowering



b) First Flowering



c) Peak Flowering

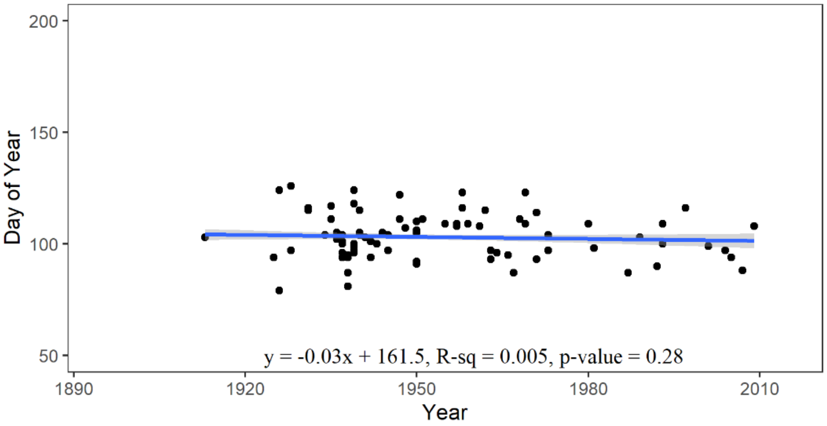


Figure 4 Scatterplots displaying trend of each phenophase on day of the year of collection versus year of collection for Oklahoma *Collinsia violacea* Nutt. a) combination of first and peak flowering, b) first flowering, and c) peak flowering.

combined resulted in a statistically insignificant negative relationship with a slope of -0.01 (Figure 4a; $R^2 < 0.001$, $p = 0.79$). Linear regression of first flowering phenophase also resulted in a negative association, with a slope of -0.04 (Figure 4b; $R^2 = 0.002$, $p = 0.45$, 95% CI = -0.147, 0.065). The slope indicates that the Oklahoma *C. violacea* plants in the first flowering phenophase were collected, on average, about 0.04 days earlier per year over the sampled time period, but the regression was not significant. Linear regression of peak flowering phenophase had a negative relationship with a slope of -0.03 (Figure 4c; $R^2 = 0.005$, $p = 0.28$, 95% CI = -0.084, 0.023), indicating that the Oklahoma *C. violacea* plants in the peak flowering phenophase were collected, on average, about 0.03 days earlier per year, but this regression was not significant.

Simple linear regression using each explanatory variable individually showed all variables excluding year to be statistically significant for all three datasets (Table 1). For all three datasets, the individual variable regression coefficients were negative for year and elevation; all other variables had positive regression coefficients (Table 1). As year was not significant alone, we removed this variable prior to proceeding with the multiple regression analyses.

Multiple regression retaining all variables for the combined phenophases dataset found only latitude ($p < 0.001$) and longitude ($p < 0.001$) statistically significant. This model explained 49% of the variation in flowering and both significant variables had positive regression coefficients (adjusted $R^2 = 0.49$; Table 2). For the first flowering dataset multiple regression retaining all variables found all variables (latitude $p = 0.02$, longitude $p < 0.001$, minimum temperature $p = 0.02$, mean temperature $p = 0.02$, maximum temperature $p = 0.02$) except precipitation and elevation statistically significant while explaining 55% of the variation in first flowering (adjusted $R^2 = 0.55$; Table 2). Of these significant variables, minimum temperature and maximum temperature had negative regression coefficients and the remaining significant variables had positive regression coefficients (Table 2). The peak flowering dataset analysis found latitude ($p < 0.001$), longitude ($p = 0.04$), and maximum temperature ($p = 0.05$) statistically significant and these had positive regression coefficients (Table 2).

The Pearson correlation test showed elevation, minimum temperature, and maximum temperature to be highly correlated with many variables, thus these three variables were removed and multiple regression was run again on the three datasets using the remaining variables as reduced models. For the combined phenophases dataset, the reduced variable multiple regression explained 49% of the variation in day of year. In this model latitude ($p < 0.001$), longitude ($p < 0.001$), and mean temperature ($p < 0.001$) were statistically significant while precipitation ($p = 0.76$) was not significant (Table 2). For the first flowering phenophase, the reduced variable model explained 54% of the variation. Latitude ($p = 0.01$), longitude ($p < 0.001$), and mean temperature ($p < 0.001$) were again statistically significant and precipitation ($p = 0.18$) was not significant. The reduced variable model explained 31% of the variation of flowering times for the peak flowering phenophase. In this model latitude ($p < 0.001$), longitude ($p < 0.001$), and mean temperature ($p < 0.001$) were statistically significant while precipitation ($p = 0.57$) was not significant. In all three reduced models, all significant variables had positive regression coefficients. In the multiple regression model performance comparisons, the reduced variable models only slightly performed better for the combined phenophases dataset (AIC = 3,893.54; Table 2) and the peak flowering dataset (AIC = 1,732.6; Table 2). The full model retaining all the explanatory variables performed slightly better for the first flowering dataset (AIC = 2,024.6) than the reduced model (AIC = 2,025.1).

Table 1 Simple linear regression coefficient results for individual variables showing significant (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) and non-significant changes in flowering day over the years 1895-2014. Significant results in **bold**.

Phenophase Dataset	Year	Latitude (DD)	Longitude (DD)	Precipitation (in)	Minimum Temperature (°F)	Mean Temperature (°F)	Maximum Temperature (°F)	Elevation (ft)
All Flowering	-0.009	**6.00*****	**4.35*****	**1.17*****	**2.03*****	**2.09*****	**1.34*****	**-0.01*****
	$R^2 = 0.0001$	**$R^2 = 0.09$**	**$R^2 = 0.13$**	**$R^2 = 0.03$**	**$R^2 = 0.41$**	**$R^2 = 0.39$**	**$R^2= 0.24$**	**$R^2 = 0.06$**
First Flowering	-0.04	**7.11*****	**5.90*****	**1.61*****	**2.30*****	**2.43*****	**2.28*****	**-0.01*****
	$R^2 = 0.002$	**$R^2 = 0.09$**	**$R^2 = 0.15$**	**$R^2 = 0.04$**	**$R^2 = 0.47$**	**$R^2 = 0.46$**	**$R^2 = 0.39$**	**$R^2 = 0.06$**
Peak Flowering	-0.03	**4.43*****	**2.59*****	**0.47***	**0.90*****	**0.83*****	**0.35*****	**-0.006*****
	$R^2 = 0.005$	**$R^2 = 0.13$**	**$R^2 = 0.15$**	**$R^2 = 0.02$**	**$R^2 = 0.14$**	**$R^2 = 0.11$**	**$R^2 = 0.05$**	**$R^2 = 0.09$**

Table 2 Multiple linear regression coefficients results showing significant (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) and non-significant changes in flowering day over the years 1895-2014 and with various geographic and climatic variables; significant results in **bold**.

	Phenophase Dataset	Adjusted R^2	Latitude (DD)	Longitude (DD)	Precipitation (in)	Minimum Temperature (°F)	Mean Temperature (°F)	Maximum Temperature (°F)	Elevation (ft)	AIC (weights)
Full Models	All Flowering	**0.49*** **	**3.27*** **	**3.18*** **	-0.13	0.86	0.82	0.26	0.002	3894.0 (<0.001)
			t = 4.40	**t = 4.66**	t = -0.49	t = 1.82	t = 1.48	t = 1.63	t = 1.08	
	First Flowering	**0.55*** **	**2.75* **	**4.91*** **	-0.79	**-28.84* **	**60.17* **	**-29.12* **	0.003	2024.6 (<0.001)
			t = 2.34	**t = 4.52**	t = -1.82	**t = -2.30**	**t = 2.41**	**t = -2.34**	t = 1.01	
	Peak Flowering	**0.32*** **	**3.81*** **	**1.42* **	0.07	0.26	0.38	**0.21* **	-0.001	1734.1 (<0.001)
			t = 5.27	**t = 2.10**	t = 0.29	t = 0.65	t = 0.85	**t = 2.01**	t = -0.49	

	Phenophase Dataset	Adjusted R^2	Latitude (DD)	Longitude (DD)	Precipitation (in)	Minimum Temperature (°F)	Mean Temperature (°F)	Maximum Temperature (°F)	Elevation (ft)	AIC (weights)
Reduced Models	All Flowering	**0.49*** **	**3.73*** **	**2.57*** **	0.07		**1.94*** **			3893.5 (<0.001)
			t = 5.38	**t = 5.81**	t = 0.31		**t = 17.83**			
	First Flowering	**0.54*** **	**2.85** **	**4.13*** **	-0.51		**2.24*** **			2025.1 (<0.001)
			t = 2.63	**t = 5.45**	t = -1.35		**t = 14.16**			
	Peak Flowering	**0.31*** **	**3.8*** **	**1.62*** **	0.11		**0.86*** **			1732.6 (<0.001)
			t = 5.55	**t = 4.09**	t = 0.57		**t = 6.37**			

Seventeen Illinois *Collinsia violacea* herbarium specimen images were examined, all collected within Shelby County. The dataset did not provide a good representation of the species, as the range of collection dates was very limited. The species was only collected in May, and it is unknown whether it only flowers in May at this location. We examined linear regression as well as multiple linear regression of the dataset; however, because the sample size was small, we did not obtain valid results.

DISCUSSION

Many studies have hypothesized that climate change would cause some species of plants to start flowering at an earlier date. This prediction has been supported by various studies, but others have indicated that flowering times of plants can be delayed (Calinger et al. 2013; Gallagher and Leishman 2009; Pearson 2019; Sherry et al. 2011). Species' distributions are based on biotic and abiotic factors. *Collinsia violacea* is commonly found across the central US (Missouri, Arkansas, Oklahoma, and Kansas). Habitats in which the plant was collected include shady banks, sandy soils, wet soils, loam, and wooded hills. Previous studies found that habitats can affect plant phenology (Croat 1975, Bazzaz 1979, Wallace and Painter 2002).

Collinsia violacea specimens collected in Oklahoma were from throughout the eastern region, with a few collected in the western region. This distribution is due to the habitats and the climate in the different regions of Oklahoma. In the far western region, shortgrass prairie is present. In the middle region, tallgrass and mixed grass prairie are present and the forest type habitats dominate the eastern region (Tyrl et al. 2017). The distribution of *C. violacea* was expected as the species prefers to grow in wooded areas. The eastern region normally experiences more precipitation than the west, resulting in a humid climate (Tyrl et al. 2017). However, upon closer analysis, a majority of the collected specimens were found in drier microhabitats of the wet eastern region. Although there were very few specimens collected in the west, there was a cluster of collections of the species in Comanche County (Hoagland et al. 2022). Although it is part of the drier western area, the specimens were collected near creeks and wet microhabitats.

Collectors may have a bias as to which phenophase the species is in when collecting it, seeking out only one specific phenophase of the plant (Willis et al. 2017). As we were concerned about the potential bias present, we resolved this problem by dividing the dataset by phenophase and separately analyzing each subset with the same method used to analyze the entire dataset. In each subset, although the results of the regressions for year and DOY were not significant, we found the same trend toward earlier flowering times, indicating that the bias toward collection of a specific phenophase did not affect the results.

In this study of Oklahoma *C. violacea*, the year and DOY linear regression analyses for both the first flowering and peak flowering dates showed a non-significant trend toward earlier flowering. We conclude that early and peak flowering times have not significantly changed over the approximately 120 years represented by the analyzed specimens. Simple linear regressions showed significant relationships between day of year for first and peak flowering phenophases and all geographic and climatic variables. A full multiple linear regression model with all variables showed that first flowering was significantly delayed (positive regression coefficients) with increases in latitude, longitude, and monthly mean temperature, and it was significantly earlier (negative regression coefficients) with increases in monthly minimum and maximum temperatures. Peak flowering was significantly delayed with increases in latitude, longitude, and monthly maximum temperature. Our reduced multiple linear regression model, with highly correlated variables removed, showed significant delays in flowering time for both first flowering and peak flowering phenophases with increases in latitude, longitude, and mean monthly temperature. Global average temperatures as well as Oklahoma temperatures are expected to increase (IPCC 2014; Frankson et al. 2022). If minimum and maximum temperatures are the best predictors of first flowering for *C. violacea*, then in the future we expect that flowering will begin earlier. However, if mean temperature is the best predictor of first flowering for *C. violacea*, then we would expect a delay in the future. Although precipitation might also vary in the future with climate change, our multiple linear regressions showed no significant relationships between day of year of first or peak flowering and monthly precipitation.

Regarding this specific study, in the future, we could incorporate soil factors, or factors such as precipitation and temperatures one to three months prior to collection (Calinger et al. 2013; Rawal et al. 2015; Matthews and Mazer 2016) that were not considered in this study to determine whether they would have an influence on the species' flowering dates. Expanding the study to include herbarium specimens from the rest of this species' range would allow assessment of flowering over the entire range.

The contradictory results for some of the climate variables may be because we used averaged climate variables for the month the specimen was collected or because we tested only the possibility of linear responses to our selected variables. Non-linear plant responses have been found in other studies of phenological responses to climatic variables (Hudson et al. 2009; Iler et al. 2013). Additional non-linear testing using generalized additive modeling (Hudson et al. 2009) or piece-wise regression (Iler et al. 2013) approaches could assess the possibility of non-linear responses to our selected variables.

Many plant species may face extinction as climate change progresses. The population of *C. violacea* in Illinois is declining (Taft et al. 2009; Taft and Smith 2012) and is on the state endangered species list (Illinois Natural Heritage 2023). The population is separated from the established populations found throughout Missouri, Arkansas, Oklahoma, and Kansas, being about 200 km from the nearest population found in Jefferson County, Missouri (Taft and Smith 2012). It is unknown whether animals or humans were involved in the dispersal of the species resulting in an isolated population in Illinois, or whether populations of the species that were linked from Illinois to Missouri could have gone extinct due to disturbances in their environment. We were not able to analyze the linear regression and multiple linear regression results for the Illinois dataset as there was not a large enough sample size for a reliable regression summary. Future studies could specifically investigate the Illinois *C. violacea* phenology patterns, as well as look at the species across its entire range and compare the results based on each state to compare and contrast whether there is a delay in flowering or earlier flowering.

As climate change continues to be a driving force in affecting our environment, plants will be forced to continue to adapt to these changes. We have seen that some plants have continued to evolve to cope with the changes by altering their flowering time, allowing us to document the changes. But there is a limit to how much plants can adapt to the changes to their environment. Hamann et al. (2018) documented some species of plants that had altered their flowering times but experienced a decrease in seed production and plant fitness due to climate change. Species that cannot keep up with the changes and adapt will be at risk for extinction. Therefore, it is important that we continue to research the phenology of plants to predict how they may respond in the future.

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LITERATURE CITED

Arkansas Native Plant Society. 2022. Know Your Natives - Violet Blue-Eyed Mary. https://anps.org (1 January 2022).

Arndt, D. 2003. The Climate of Oklahoma. https://cig.mesonet.org/climateatlas/doc60.html (1 December 2022).

Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10:351-371.

Calinger, K.M., S. Queenborough, and P.S. Curtis. 2013. Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters* 16:1037–1044.

Croat, T.B. 1975. Phenological behavior of habitat and habitat classes on Barro Colorado Island (Panama Canal zone). *Biotropica* 7:270-277.

Davis, C.C., C.G. Willis, B. Connolly, C. Kelly, and A.M. Ellison. 2015. Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany* 102:1599–1609

Flora of North America Editorial Committee. 2019. Flora of North America North of Mexico. Vol. 17: Magnoliophyta: Tetrachondraceae to Orobanchaceae. New York (NY): Oxford University Press.

Frankson, R., K.E. Kunkel, L.E. Stevens, S.M. Champion, B.C. Stewart, J. Nielsen-Gammon. 2022. Oklahoma State Climate Summary 2022. NOAA Technical Report NESDIS 150-OK. NOAA/NESDIS, Silver Spring, MD. https://statesummaries.ncics.org/chapter/ok/.

Gallagher, R. and M. Leishman. 2009. Phenological trends among Australian alpine species: using herbarium records to identify climate-change indicators. *Australian Journal of Botany* 57:1-9.

Hamann, E., A.E. Weis, and S.J. Franks. 2018. Two decades of evolutionary changes in *Brassica rapa* in response to fluctuations in precipitation and severe drought. *Evolution* 72:2682-2696.

Haggerty, B., A. Hove, and S. Mazer. 2013. A Primer on Herbarium-based Phenological Research. https://cpp.msi.ucsb.edu/sites/cpp.usanpn.org/files/pdfs/A%20primer%20on%20herbarium-based%20phenological%20research%20for%20web.pdf (November 2021).

Hoagland, B. W., A. Buthod, I. Butler, P. Callahan-Crawford, W. Elisens, A. Udasi, and R. Tyrl. 2022. Oklahoma Vascular Plants Database. *Collinsia violacea* specimen search. http://www.oklahomaplantdatabase.org/ (1 December 2022).

Hudson, I.L., S.W. Kim, and M.R. Keatley. 2009. Climatic influences on the flowering phenology of four Eucalypts: a GAMLSS approach. 18th World IMACS/MODSIM Congress, Cairns, Australia 13-17 July 2009. http://mssanz.org.au/modsim09/G2/hudson_il.pdf (21 December 2023).

Hufft, R.A., M.E. DePrenger-Levin, R.A. Levy, and M.B. Islam. 2018. Using herbarium specimens to select indicator species for climate change monitoring. *Biodiversity Conservation* 27:1487-1501.

Iler, A.M., T.T. Hoye, D.W. Inouye, and N.M. Schmidt. 2013. Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B* 368: 20120489.

Illinois Natural Heritage. 2023. Checklist of Illinois Endangered and Threatened Animals and Plants. https://naturalheritage.illinois.gov/content/dam/soi/en/web/naturalheritage/documents/illinoisendangeredandthreatenedspecies.pdf (19 December 2023).

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland.

Jones, C.A. and C.C. Daehler. 2017. Herbarium specimens can reveal impacts of climate change on plant phenology: a review of methods and applications. *PeerJ* 6:e4576.

Keatley, M.R. and I.L. Hudson. 2010. Introduction and Overview. In: Hudson, I.L. and M.R. Keatley, eds. *Phenological Research: Methods for Environmental and Climate Change Analysis*. Dordrecht (Netherlands): Springer.

Lima, D.F., J. Mello, I.T. Lopes, R.C. Forzza, R. Goldenberg, and L. Freitas. 2021. Phenological responses to climate change based on a hundred years of herbarium collections of tropical Melastomataceae. *PloS one* 16:e0251360.

Ludecke, D., M.S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software* 6:3139.

Matthews, E.R. and S.J. Mazer. 2016. Historical changes in flowering phenology are governed by temperature *x* precipitation interactions in a widespread perennial herb in western North America. *New Phytologist* 210:157-167.

Morellato, L.P.C., M.G.C. Camargo, and E. Gressler. 2013. A review of plant phenology in South and Central America. In: Schwartz, M.D., ed. *Phenology: An Integrative Environmental Science*, 2nd ed. Dordrecht (Netherlands): Springer.

NASA. 2022. World of Change: Global Temperatures Earth Observatory. https://earthobservatory.nasa.gov/world-of-change/decadaltemp.php (1 December 2022).

NatureServe. 2024. NatureServe Network Biodiversity Location Data accessed through NatureServe Explorer [web application]. NatureServe, Arlington, Virginia. https://explorer.natureserve.org/ (5 February 2024).

Park, I.W. and S.J. Mazer. 2018. Overlooked climate parameters best predict flowering onset: assessing phenological models using the elastic net. *Global Change Biology* 24:5972-5984.

Parmesan, C. and M.E. Hanley. 2015. Plants and climate change: complexities and surprises. *Annals of Botany* 116:849-864.

Pearson, K.D. 2019. Spring- and fall-flowering species show diverging phenological responses to climate in the Southeast USA. *International Journal of Biometeorology* 63:481-492.

Primack, D., C. Imbres, R.B. Primack, A.J. Miller-Rushing, and P. Del Tredici. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91:1260-1264.

PRISM Climate Group. 2015. Oregon State University. https://prism.oregonstate.edu (1 January 2022).

R Core Team 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rawal, D.S., S. Kasel, M.R. Keatley, and C.R. Nitschke. 2015. Herbarium records identify sensitivity of flowering phenology of Eucalypts to climate: implications for species response to climate change. *Austral Ecology* 40:117-125.

Rios, N.E., H.L. Bart Jr., C. Sturgill, S. Park, D. Abibou, A. Ranipeta, S. Belame, S. Huang, J. Boutte, A. Tseng, and N. Spears. 2005. GEOLocate – Software for georeferencing natural history data. https://www.geo-locate.org/web/WebGeoref.aspx (1 January 2022).

Southeast Regional Network of Expertise and Collections (SERNEC). 2022. *Collinsia violacea* specimen search. http://sernecportal.org/portal/collections/list.php (1 December 2022).

Sherry, R.A., X. Zhou, S. Gu, J.A. Arnone, D.W. Johnson, D.S. Schimel, P.S.J. Verberg, L. Wallace, and Y. Luo. 2011. Changes in duration of reproductive phases and lagged phenological response to experimental climate warming. *Plant Ecology & Diversity* 4:23-35.

Taft, J.B., J.O. Dawson, and B.M. Flores. 2009. Restoration in terrestrial plant communities- examples from the prairie-forest transition zone. *Canaries in the Catbird Seat* 30:229-249.

Taft, J.B. and E.L. Smith. 2012. A field test of regeneration in an isolated population of violet Collinsia (*Collinsia violacea*). *Ecological Restoration* 31:57-62.

Tyrl, R.J., T.G. Bidwell, R.E. Masters, R.D. Elmore, and J.R. Weir. 2017. Oklahoma's Native Vegetation Types. Oklahoma State University. https://extension.okstate.edu/fact-sheets/oklahomas-native-vegetation-types.html (1 November 2022).

USDA, NRCS. 2024. The PLANTS Database. National Plant Data Team, Greensboro, NC. http://plants.usda.gov/plants (5 February 2024).

Wallace, R.B. and R.L.E. Painter. 2002. Phenological patterns in a southern Amazonian tropical forest: implications for suitable management. *Forest Ecology and Management* 160:19-33.

Willis, C.G., E.R. Ellwood, R.B. Primack, C.C. Davis, K.D. Pearson, A.S. Gallinat, J.M. Yost, G. Nelson, S.J. Mazer, N.L. Rossington, T.H. Sparks, and P.S. Soltis. 2017. Old plants, new tricks: phenological research using herbarium specimens. *Trends in Ecology and Evolution* 32:531-546.