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Title

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Permalink

<https://escholarship.org/uc/item/1rs1z375>

Journal

New Phytologist, 210(1)

ISSN

0028-646X

Authors

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Publication Date

2016-04-01

DOI

10.1111/nph.13751

Peer reviewed

Historical changes in flowering phenology are governed by temperature × precipitation interactions in a widespread perennial herb in western North America

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Received: 11 August 2015

Accepted: 8 October 2015

New Phytologist (2015)

doi: 10.1111/nph.13751

Key words: climate, elevation, herbarium records, latitude, longitude, minimum temperature, *Trillium ovatum* (Pacific trillium).

Summary

- For most species, a precise understanding of how climatic parameters determine the timing of seasonal life cycle stages is constrained by limited long-term data. Further, most long-term studies of plant phenology that have examined relationships between phenological timing and climate have been local in scale or have focused on single climatic parameters. Herbarium specimens, however, can expand the temporal and spatial coverage of phenological datasets.
- Using *Trillium ovatum* specimens collected over > 100 yr across its native range, we analyzed how seasonal climatic conditions (mean minimum temperature (T_{\min}), mean maximum temperature and total precipitation (PPT)) affect flowering phenology. We then examined long-term changes in climatic conditions and in the timing of flowering across *T. ovatum*'s range.
- Warmer T_{\min} advanced flowering, whereas higher PPT delayed flowering. However, T_{\min} and PPT were shown to interact: the advancing effect of warmer T_{\min} was strongest where PPT was highest, and the delaying effect of higher PPT was strongest where T_{\min} was coldest. The direction of temporal change in climatic parameters and in the timing of flowering was dependent on geographic location. T_{\min} , for example, decreased across the observation period in coastal regions, but increased in inland areas.
- Our results highlight the complex effects of climate and geographic location on phenology.

Introduction

Phenology is the study of the timing of seasonal life cycle stages (*phenophases*), such as the flowering and fruiting of plants, the migration of birds and mammals, and the emergence of insect pollinators and pests. Shifts in the timing of phenophases are a well-documented response to climate change (Menzel *et al.*, 2006; Parmesan, 2006), and these shifts can have profound and immediate effects on the interactions of species (Visser & Both, 2005; Both *et al.*, 2006; Ozgul *et al.*, 2010; McKinney *et al.*, 2012), as well as longer term effects on the abundance and distribution of species (Moller *et al.*, 2008; Chuine, 2010; Miller-Rushing *et al.*, 2010; Willis *et al.*, 2010; Cleland *et al.*, 2012), and on ecosystem function and services (Richardson *et al.*, 2010). For flowering plants, the timing of reproductive phenophases is particularly important, as it can influence the strength of mutualistic or antagonistic interactions between plants and their pollinators, seed dispersers, herbivores and seed predators (Elzinga *et al.*, 2007; Yang & Rudolf, 2010; Forrest, 2015; Rafferty *et al.*, 2015).

In order to identify the causes and consequences of recent or historical shifts in phenology and to predict future climate

change-induced shifts, large-scale efforts to document contemporary plant and animal phenology are underway (Schwartz *et al.*, 2012). These efforts include national-level programs, such as the USA National Phenology Network and Project BudBurst, as well as regional programs, such as the California Phenology Project (Haggerty *et al.*, 2013; Denny *et al.*, 2014; Mazer *et al.*, 2015). Two primary goals of these projects are to maximize the quantity and accessibility of high-quality phenological data with respect to the frequency and duration of monitoring, the numbers of species targeted for monitoring and the variety of geographic locations monitored, and to link inter-annual and geographic variation in phenology to local climatic conditions.

Despite these efforts, our current understanding of plant phenology and its relationships with climatic parameters is constrained by a dearth of historical data against which contemporary observations can be compared. This gap can be mitigated by accessing phenological information preserved in natural history collections, and this approach has been particularly effective for the examination of patterns of plant reproductive phenology using herbarium specimens (Primack *et al.*, 2004; Lavoie & Lachance, 2006; Miller-Rushing *et al.*, 2006; Gallagher *et al.*, 2009; Gaira *et al.*, 2011; Robbirt *et al.*, 2011; Hart *et al.*,

2014; Park, 2014). Most of the herbarium-based phenological studies to date have examined local patterns of plant phenology and have used natural history collections to expand the temporal range of phenological observations at a given location or within a relatively small region. However, herbarium collections can also expand the spatial range of historical datasets (e.g. Park, 2012). Datasets that are geographically widespread and that represent many decades can comprise greater variation in both phenological and climatic data than datasets based on single locations or shorter term surveys. Further, with datasets representing a broad geographic range – which can be provided by herbarium specimens – larger scale relationships among geographic, climatic and temporal variables, and plant phenophases, can be identified and quantified.

In this study, we examined the herbarium records of *Trillium ovatum* to build a dataset representing flowering dates (including both day of year (DOY) and year) and locations across the entire native range of this species. *T. ovatum* is particularly valuable for herbarium-based phenological research because the flowering status of sampled plants is unambiguous: plants typically produce a single stem per year and stems produce only one flower (older plants have been found occasionally to produce more than one stem; Jules & Rathcke, 1999; Ream, 2011). With this dataset, we ask four questions related to how flowering phenology varies across climatic, geographic and temporal gradients. (1) Which climatic variables (e.g. minimum temperature, maximum temperature and cumulative precipitation) and which seasonal time periods (three 3-month windows from January to May, before flowering) best explain the variation in the day of the year on which *T. ovatum* specimens are collected in flower? (2) Can we detect interactions between temperature and precipitation in their effects on the flowering phenology of *T. ovatum*? For example, where precipitation is not limiting, we expect that temperature will have a stronger effect than where precipitation is limiting. (3) When controlling statistically for geographic location (i.e. latitude, longitude and elevation, which affect seasonal temperatures and precipitation), can we detect long-term temporal change in the climatic variables that affect flowering phenology? (4) Finally, controlling statistically for geographic parameters, can we detect a long-term inter-annual change in the onset date of spring flowering over the past 122 yr? The application of multivariate models to historical climatic data and herbarium-derived phenological records provides a way to detect a suite of novel interactions between rainfall and temperature that affect the estimated onset of flowering, and between geographic variables and collection year that affect local climatic conditions.

Materials and Methods

Study organism

Trillium ovatum Pursh (Western Trillium; Melianthaceae) is a long-lived perennial herb that is common in mesic coniferous and mixed coniferous–deciduous forests in western North America. Its range extends from northern California in the USA to southern British Columbia and Alberta in Canada (USDA,

NRCS, 2014; Fig. 1). *Trillium ovatum* flowers in spring, with reproductive individuals producing a single flower per stem. Individual flowers last *c.* 22 d (Jules & Rathcke, 1999), providing a reasonable estimate of the flowering onset date given the wide range in specimen collection dates across the geographic range of the species (mean collection DOY = 122; range = 32–239).

Herbarium data

Trillium ovatum is well represented in herbaria throughout its range and produces showy flowers, making it a good candidate for study via preserved herbarium specimens. We obtained loans from five California herbaria, including Rancho Santa Ana Botanic Garden Herbarium (RSA), University of California, Riverside (UCR), Santa Barbara Botanic Garden (SBBG), and the Jepson Herbarium (JEPS) and the University Herbarium (UC) at University of California, Berkeley. Because *T. ovatum* produces a single, relatively large flower per stem, its phenological status is also simple to observe via photographs; consequently, we were able to expand the size and geographic coverage of our dataset by downloading specimen images through the Consortium of Pacific Northwest Herbaria website (<http://www.pnwherbaria.org>). These specimens are housed in the following herbaria: H.J. Andrews Experimental Forest (HJAEF), Stillinger Herbarium at University of Idaho (ID), Montana State (MONT), Pacific Luthern University (PLU), Reed College (REED), Rocky Mountain Herbarium at University of Wyoming (RM) and Western Washington University (WWB).

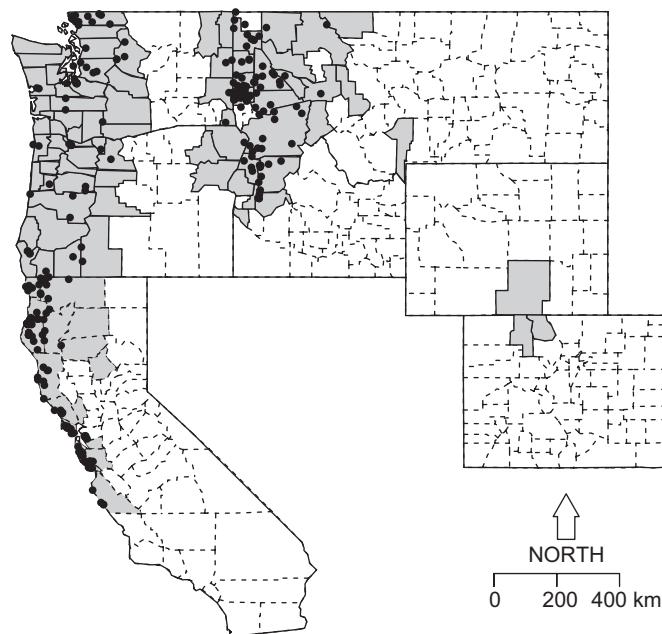


Fig. 1 Collection locations of flowering *Trillium ovatum* specimens ($n = 289$). Black dots are collection locations, which are overlaid on the county-level geographic range information obtained from the USDA PLANTS database (USDA, NRCS, 2014; *Trillium ovatum* occurs in the counties that are shaded gray).

We examined each specimen and recorded its collection date (day, month and year), collection location (latitude, longitude and elevation) and phenological status (flowering or not). Specimens that were missing detailed label information (e.g. the exact day, month and year of collection) were excluded. Many specimen labels did not include geographic coordinates, but provided a detailed description of the collection location (e.g. a county and road name). These specimens were geo-referenced using online tools (e.g. GEOLocate: <http://www.museum.tulane.edu/geolocate/>) and US Geological Survey topographic maps. We estimated the elevation for each collection location using georeferenced coordinates. Specimens for which the labels provided insufficient location information to enable the assignment of GPS coordinates or elevations were rejected. Finally, if there was more than one stem preserved on an herbarium sheet, only one datum was recorded. Our final dataset included 289 flowering specimens that met these criteria.

Climatic data

The link between temperature and plant phenology is well documented (Menzel *et al.*, 2006; Parmesan, 2006; Gallagher *et al.*, 2009; and references therein), but fewer studies have examined the degree to which precipitation drives phenological variation and how temperature and precipitation may interact to influence phenology (but see Crimmins *et al.*, 2011 and Mazer *et al.*, 2015). Because our study area covers a large geographic range and climate stations are available at few of our sample locations, we accessed climatic data for our study area from the PRISM dataset (PRISM Climate Group, 2013). The PRISM dataset includes 4 km gridded data for the conterminous USA, interpolated from point station data; PRISM data are readily available online and have been used frequently in phenological research (Crimmins *et al.*, 2011; Park, 2014; Mazer *et al.*, 2015). For the georeferenced location of each specimen, we downloaded monthly climatic data for the year of collection. For each collection event (a combination of the collection location and date), we obtained monthly mean maximum temperature (T_{\max}), mean minimum temperature (T_{\min}) and total precipitation (PPT) (the three climatic variables provided by the PRISM dataset). We then generated composite seasonal climatic parameters representing the T_{\max} , T_{\min} and PPT during three 3-month windows preceding the collection date of *T. ovatum* specimens: JFM (January, February and March), FMA (February, March and April) and MAM (March, April and May).

Statistical analysis

Effects of temperature and rainfall on flowering date We constructed multiple linear regression models to detect the effect of each site- and year-specific climatic variable on the flowering DOY. For each specimen, we calculated the flowering DOY as the number of days after 1st January (e.g. 1st April is day 90) on which it was collected. We first constructed saturated models, which included (for each specimen's georeferenced location) the three seasonal climatic parameters (T_{\min} , T_{\max} and PPT) and

their interactions during each of the 3-month windows (JFM, FMA or MAM); in these models, DOY was the response variable, and T_{\min} , T_{\max} , PPT and the interactions among them were the independent variables. Each seasonal window (JFM, FMA and MAM) was analyzed separately. Because the first year represented in the PRISM dataset is 1895, collection events before 1895 were not used in any analysis that included climatic data ($n = 282$) for analyses that included climate data. Precipitation values were log transformed to achieve normality. We identified a minimal adequate model through backward elimination, in which non-significant predictors ($P > 0.05$) were removed in successive steps (Crawley, 2007). A stepwise approach to multiple regression analysis is frequently used in phenological research studies (Keatley *et al.*, 2002; Moller *et al.*, 2008; Hulme, 2011; Mazer *et al.*, 2015), and has the benefit of identifying the independent variables that have the strongest influence on phenology (Roberts, 2009). The statistically significant regression coefficients associated with the independent variables were examined to determine whether DOY was advanced or delayed in response to higher temperatures and/or precipitation. The relative sensitivity of DOY to each of the three seasonal windows was also examined to determine whether flowering DOY was more sensitive to winter or to spring conditions.

Statistically significant two-way interaction terms were examined graphically to reveal how the effect of one factor (e.g. T_{\min}) on DOY was dependent on the value of a second (i.e. interacting) factor (e.g. PPT). We used the equation estimated by the linear model to generate three lines, each of which plotted the predicted DOY against a range of values for the first climatic variable in the interaction term whilst using one of three values of the second climatic variable in the interaction term: the minimum value, mean value and maximum value. All other significant predictors were included in the equation at their mean value. For example, we used the equation of the linear model to illustrate the effects of T_{\min} on DOY using the minimum, mean and maximum values of PPT (see Fig. 2a). We similarly created three lines in which the predicted DOY was plotted against a range of values for the second climatic variable in the significant interaction term, where each line used one of three values of the first climatic variable in the interaction (again, the minimum, mean and maximum values; see Fig. 2b).

Temporal changes in temperature and rainfall We analyzed data comprising each specimen's latitude, longitude, elevation, year of collection and climatic parameters to quantify the relationship between the seasonal climatic parameters that were identified as significant predictors of flowering phenology in the previous analysis (as the dependent variables) and the collection year, controlling for variation in climate that is associated with latitude, longitude and elevation. We used an analytical approach similar to the previous analysis of flowering dates and climatic variables. We built multiple linear regression models, using a seasonal climatic parameter (e.g. mean T_{\min} in JFM) as the response variable, and collection year (treated as a continuous variable), geographic parameters (latitude, longitude and elevation) and their interactions as independent variables. In this model,

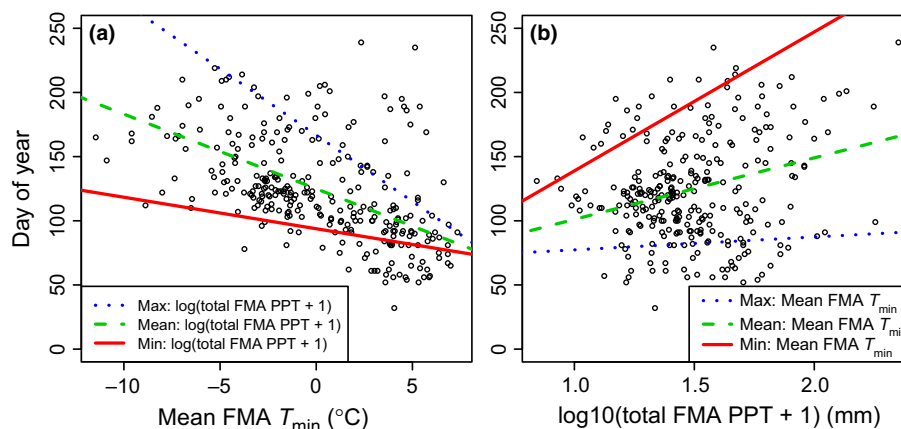


Fig. 2 Effect of the interactions between February–March–April (FMA) climatic variables (mean T_{\min} ($^{\circ}\text{C}$) and total precipitation (PPT) (mm)) on the day of year (DOY). Predicted DOY values were plotted as a function of FMA climatic variables, based on the equation estimated from the linear model (Table 1b). (a) Predicted DOY values as a function of mean T_{\min} . The dotted blue line represents the predicted DOY at the maximum value of $\log(\text{total FMA PPT} + 1)$, the dashed green line represents the predicted DOY at the mean value of $\log(\text{total FMA PPT} + 1)$ and the solid red line represents the predicted DOY at the minimum value of $\log(\text{total FMA PPT} + 1)$. (b) Predicted DOY values as a function of total precipitation. The dotted blue line is the predicted DOY at the maximum value of mean FMA T_{\min} , the dashed green line is the predicted DOY at the mean value of mean FMA T_{\min} and the solid red line is the predicted DOY at the minimum value of mean FMA T_{\min} . The lines are superimposed on the actual data to illustrate the bounds of the data.

significant effects of collection year on the response variable were interpreted as a significant long-term temporal trend, and the values of the statistically significant regression coefficients associated with year, latitude, longitude and elevation were examined to determine whether each of the climatic variables increased (or decreased) over time (independent of geographic location) or in association with geographic location (independent of temporal effects).

Where significant interactions between two variables were detected, we again used a graphical approach to visualize how the effects of one factor were dependent on the value of a second factor. We graphed the predicted values of the seasonal climatic parameters against a range of values for the first variable contributing to the interaction term and, for each of three separate lines, one of three levels of the second variable contributing to the interaction term (the minimum value, mean value and maximum value of the second variable). For example, the interacting effects on FMA T_{\min} of collection year and longitude were examined by graphing predicted FMA T_{\min} against collection year using each of three longitude values (the westernmost, mean and easternmost longitude values represented by the specimens; see Fig. 3a).

Long-term temporal changes in flowering date We used multiple linear regression to quantify the relationship between flowering phenology (DOY) and collection year. To control for environmental effects on DOY associated with geographic location rather than temporal changes in climate, we created a regression model with flowering DOY as the response variable and collection year, geographic variables (latitude, longitude and elevation) and their interactions as independent variables. The sign of the regression coefficient associated with collection year was examined to determine whether the DOY was significantly delayed or advanced (earlier) over time, controlling for

environmental variation (climatic or biotic) associated with geographic location that may have also influenced DOY. In addition, the regression coefficients associated with latitude, longitude and elevation were examined to corroborate the prediction that DOY would be delayed at higher latitudes and elevations and to detect, if present, an association between flowering DOY and longitude.

All statistical analyses were performed in R (R Development Core Team, 2013).

Results

Our dataset spanned a 122-yr period from 1888 to 2009. The mean collection DOY was 122 (3^{rd} May) + SD = 40.29 (range = 32–239; SE = ± 2.37 ; Fig. 4).

Effects of seasonal temperature and rainfall on flowering date

Temperature and precipitation in both winter and spring influenced flowering DOY. For each of the three seasonal windows, there were significant effects of mean T_{\min} , PPT or their interaction on flowering DOY (Table 1). In none of the models did mean T_{\max} have a significant effect on DOY. The climate models account for 34–36% of the variation in flowering DOY.

Flowering DOY was advanced (earlier) where January–March mean T_{\min} was warmer, and delayed (later) where January–March PPT was higher. For the February–April and March–May climate windows, the main effects of T_{\min} and precipitation were similar, but there was also a significant interaction between mean T_{\min} and PPT. The advancing effect of warmer mean T_{\min} was stronger where PPT was higher (Fig. 2a shows this interaction for the FMA window), and the

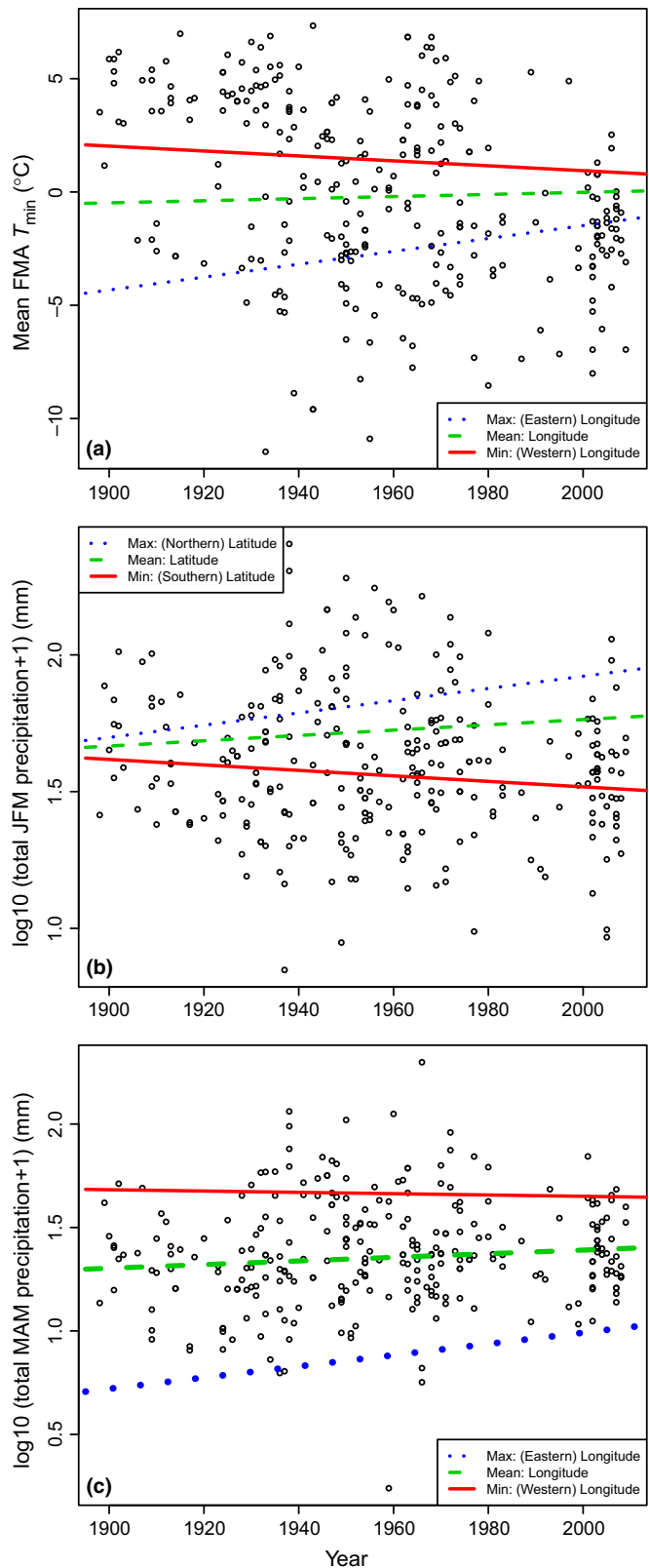


Fig. 3 Effect of the interactions between year and geographic variables on seasonal climatic variables. Predicted values of the climatic variables were plotted as a function of year based on the equations estimated from the linear models (Table 2). The lines are superimposed on the actual data to illustrate the bounds of the data. (a) The effect of the interaction between year and longitude on mean February–March–April (FMA) T_{\min} ($^{\circ}\text{C}$). The dotted blue line is the predicted mean T_{\min} at the maximum value of longitude (in decimal degrees); these are the eastern-most collection locations. The dashed green line is the predicted mean T_{\min} at the mean value of longitude. The solid red line is the predicted mean T_{\min} at the minimum (western-most) longitude value. (b) The effect of the interaction between year and latitude on total January–February–March (JFM) precipitation (mm). The dotted blue line is the predicted total precipitation at maximum values of latitude (i.e. northern sites), the dashed green line is the predicted total precipitation at the mean value of latitude and the solid red line is the predicted total precipitation at the minimum value of latitude (i.e. southern-most sites). (c) Effect of the interaction between year and longitude on total March–April–May (MAM) precipitation (mm). The dotted blue line is the predicted total precipitation at the maximum value of longitude (eastern locations), the dashed green line is the predicted total precipitation at the mean value of longitude and the solid red line is the predicted total precipitation at the minimum value of longitude (western-most locations).

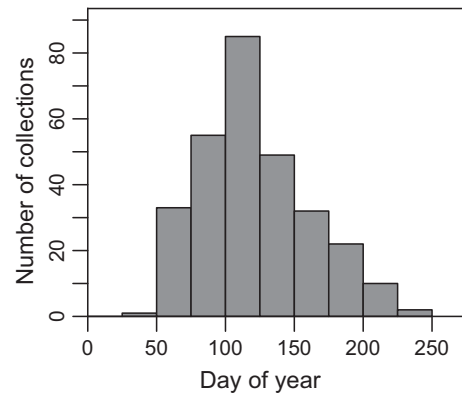


Fig. 4 Frequency distribution of day of year (DOY) on which flowering *Trillium ovatum* herbarium specimens were collected ($n = 289$). The mean collection DOY is 122 (3rd May).

Temporal changes in temperature and rainfall

We detected long-term temporal changes in mean T_{\min} and PPT, independent of variation associated with geographic location. Across all three seasonal windows, there were significant independent effects of year, elevation, latitude, longitude and their interactions on mean T_{\min} and PPT (Tables 2, 3). The models account for 74–81% of the variation in T_{\min} and 41–52% of the variation in precipitation.

The model of January–March mean T_{\min} as influenced by the geographic variables detected significant interactions between each pair of geographic parameters (e.g. elevation \times latitude; elevation \times longitude; latitude \times longitude; Table 2a), indicating complex effects of geography on winter minimum temperatures. The effects of elevation on mean T_{\min} , for example, were dependent on latitude and longitude. By contrast, the effect of geographic parameters on mean T_{\min} in the FMA and MAM windows was primarily attributed to the main effects, with lower T_{\min} values associated with higher latitudes (more northern sites), higher elevations and

delaying effect of increased precipitation was stronger where mean T_{\min} values were lower (Fig. 2b shows this interaction for the FMA window).

Table 1 Summary of multiple linear regressions conducted to detect significant effects of seasonal climatic variables (mean maximum temperature (T_{\max}), mean minimum temperature (T_{\min}), total precipitation (PPT)) and their interaction on the day of year (DOY) of the collection of flowering *Trillium ovatum* specimens

(a) Independent variables: seasonal climatic conditions in January–March				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
T_{\min}	1	134 223	126.81	< 0.001
Log(PPT + 1)	1	56 951	53.81	< 0.001
Error	279	295 309		
R^2				0.34
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	24.56	12.88	1.81	0.06
T_{\min}	−4.76	0.42	−11.26	< 0.001
Log(PPT + 1)	57.34	7.82	7.34	< 0.001
(b) Independent variables: seasonal climatic conditions in February–April				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
T_{\min}	1	139 875	136.52	< 0.001
Log(PPT + 1)	1	40 368	39.40	< 0.001
$T_{\min} \times \log(\text{PPT} + 1)$	1	6592	6.43	0.01
Error	279	284 832		
R^2				0.36
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	53.05	11.85	4.48	< 0.001
T_{\min}	1.95	3.05	0.64	0.52
Log(PPT + 1)	48.38	7.86	6.16	< 0.001
$T_{\min} \times \log(\text{PPT} + 1)$	−5.23	2.06	−2.54	0.01

more easterly (inland) sites (Table 2b,c). In all three seasonal windows, there was a significant interaction between year and longitude: T_{\min} increased over time at inland (eastern) sites, whereas T_{\min} decreased at coastal (western) sites (Fig. 3a illustrates this relationship for the FMA seasonal window).

The sign and statistical significance of the regression coefficients in the models of precipitation as influenced by geographic parameters differed among the 3-month focal windows (Table 3). The negative coefficients associated with longitude, however, indicate that precipitation consistently declined from western to eastern collection localities. The models detected at least one interaction among geographic variables in each seasonal window, although PPT generally decreased with higher elevation and higher latitudes. Temporal trends in precipitation were complex. In the JFM window, there was a significant interaction between year and latitude; at northern latitudes, precipitation increased over time, whereas at southern latitudes, precipitation decreased over time (Fig. 3b). In the MAM window, there was a significant interaction between year and longitude: PPT increased across the observed period at eastern (inland) sites, whereas PPT decreased

Table 1 (Continued)

(c) Independent variables: seasonal climatic conditions in March–May				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
T_{\min}	1	107 169	104.08	< 0.001
Log(PPT + 1)	1	28 438	27.62	< 0.001
$T_{\min} \times \log(\text{PPT} + 1)$	1	7587	7.37	< 0.001
Error	279	286 245		
R^2				0.36
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	25.08	13.61	4.34	< 0.001
T_{\min}	2.39	3.19	0.75	0.45
Log(PPT + 1)	55.31	9.50	5.82	< 0.001
$T_{\min} \times \log(\text{PPT} + 1)$	−6.14	2.26	−2.71	< 0.001

We report the minimal adequate model, identified through backward elimination of predictor variables (see text for details of model selection procedure). Each model tests for the effects on DOY of climatic variables during a different 3-month window preceding specimen collection; independent variables represent conditions in: (a) January–March; (b) February–April; and (c) March–May. Parameter estimates are the regression intercepts and coefficients; values significantly < 0 indicate that flowering times occur earlier with increasing temperature or precipitation, whereas values significantly > 0 indicate that flowering times are delayed with increasing temperature or precipitation. Interaction terms are discussed in the text.

R^2 values and significant P values (< 0.05) are shown in bold to facilitate comparison across tables.

at western (coastal) sites (Fig. 3c). The FMA window was the only season in which there was no temporal trend in precipitation (Table 3b).

Long-term temporal changes in flowering date

Collection year and geographic variables explained 48% of the variation in flowering DOY. The effect of year on flowering date, however, was dependent on geographic location. The model detected two significant three-way interaction terms that included year and geographic parameters (year \times elevation \times latitude and year \times elevation \times longitude) and several two-way interaction terms between year and geographic parameters (Table 4). For example, a significant two-way interaction between year and elevation indicated that the long-term direction of the change in flowering DOY was dependent on elevation. The only significant main effect detected was that of elevation on DOY, with advanced flowering dates associated with high elevations.

Discussion

Effects of temperature and rainfall on flowering date

Flowering DOY is associated with winter and spring mean T_{\min} and PPT. Higher spring T_{\min} is associated with earlier flowering phenology, and greater spring precipitation is associated with delayed flowering. Advanced flowering phenology as

Table 2 Summary of multiple linear models conducted to detect effects of year, elevation, latitude, longitude and their interactions on mean minimum temperature (T_{\min}) during three 3-month windows (January–March, February–April and March–May) preceding the collection date of each sampled *Trillium ovatum* specimen

(a) Response variable: mean T_{\min} (January–March)				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Year	1	94.38	20.92	< 0.001
Elevation	1	805.30	178.54	< 0.001
Latitude	1	272.23	60.35	< 0.001
Longitude	1	349.78	77.55	< 0.001
Elevation × latitude	1	1.03	0.22	0.63
Year × longitude	1	60.46	13.40	< 0.001
Elevation × longitude	1	0.08	0.01	0.89
Latitude × longitude	1	8.01	1.88	0.18
Elevation × latitude × longitude	1	19.94	4.42	0.04
Error	272	1226.87		
R^2				0.81
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	−1206.00	405.00	−2.859	0.004
Year	0.70	0.19	3.634	< 0.001
Elevation	−0.56	0.26	−2.179	0.03
Latitude	−5.35	5.65	−0.96	0.34
Longitude	−9.93	3.36	−2.826	0.005
Elevation × latitude	0.01	0.01	2.165	0.03
Year × longitude	0.006	0.001	3.508	< 0.001
Elevation × longitude	−0.005	0.002	−2.162	0.03
Latitude × longitude	−0.04	0.05	−0.894	0.37
Elevation × latitude × longitude	0.0001	0.00004	2.16	0.03
(b) Response variable: mean T_{\min} (February–April)				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Year	1	9.37	2.81	0.09
Elevation	1	748.85	224.70	< 0.001
Latitude	1	149.14	44.75	< 0.001
Longitude	1	196.23	58.88	< 0.001
Year × longitude	1	32.47	9.74	0.002
Error	276	919.84		
R^2				0.80
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	−986.60	302.10	−3.26	0.001
Year	0.49	0.15	3.17	0.002
Elevation	−0.004	0.0002	−14.99	< 0.001
Latitude	−0.26	0.04	−6.69	< 0.001
Longitude	−8.27	2.53	−3.27	0.001
Year × longitude	0.004	0.001	3.12	0.002

a response to increased spring temperatures has been reported for many species in temperate regions (Menzel *et al.*, 2006; Miller-Rushing *et al.*, 2007; Beaubien & Hamann, 2011;

Table 2 (Continued)

(c) Response variable: mean T_{\min} (March–May)				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Year	1	0.27	0.19	0.75
Elevation	1	642.44	234.53	< 0.001
Latitude	1	72.43	25.93	< 0.001
Longitude	1	55.85	20.32	< 0.001
Year × longitude	1	16.51	5.12	0.01
Error	276	757.40		
R^2				0.74
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	−685.40	274.60	−2.798	0.01
Year	0.34	0.14	2.461	0.01
Elevation	−0.003	0.0002	−15.301	< 0.001
Latitude	−0.18	0.04	−5.138	< 0.001
Longitude	−5.83	2.30	−2.539	0.01
Year × longitude	0.003	0.001	2.453	0.01

Table 2(a) reports the independent effects of each dependent variable and their interactions on T_{\min} from January to March; Table 2(b) reports the effects of these variables on T_{\min} from February–April; Table 2(c) reports the effects of these variables on T_{\min} from March–May. Parameter estimates are the regression intercept and coefficients of each independent variable. R^2 values and significant P values (< 0.05) are shown in bold to facilitate comparison across tables.

Panchen *et al.*, 2012). Although phenological responses to precipitation have been less well studied, it appears that the phenological response to precipitation may be less consistent than that with temperature. Some authors have found no effect of precipitation on flowering phenology (Abu-Asab *et al.*, 2001), whereas others have found that increased precipitation results in delayed flowering (Von Holle *et al.*, 2010; Mazer *et al.*, 2013) or earlier phenophase onset dates (Crimmins *et al.*, 2010; Lambert *et al.*, 2010).

In the current study, multiple linear regression models also detected a significant interaction between mean T_{\min} and PPT during late winter and spring (the February–April and March–May windows) affecting flowering DOY. In these windows, the advancing effect of warmer mean T_{\min} was stronger where PPT was higher (Fig. 2a). One proximal explanation for this pattern is that flowering phenology more closely tracks minimum temperatures where precipitation is not limiting. Another interpretation is that, where PPT is relatively high, DOY is delayed (cf. the effects of precipitation as a main effect) and, accordingly, there is greater potential for higher temperatures to advance DOY towards earlier values without risking reproductive failure. Advancing DOY in response to increasing temperature may not be possible where DOY is already relatively early without risking floral failure as a result of late winter or early spring frost events. These interpretations are not mutually exclusive and may both contribute to the interaction. In any case, the ultimate evolutionary or physiological mechanisms underlying these interactions cannot

Table 3 Summary of multiple linear models conducted to detect the effects of year, elevation, latitude and longitude on mean total precipitation during three 3-month windows (January–March, February–April and March–May) preceding the collection date of each sampled *Trillium ovatum* specimen

(a) Response variable: log(precipitation + 1) (January–March)				
Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Year	1	0.16	4.99	0.03
Elevation	1	3.46	104.24	< 0.001
Latitude	1	0.09	2.65	0.11
Longitude	1	8.04	241.90	< 0.001
Year × latitude	1	0.16	4.94	0.03
Latitude × longitude	1	0.31	9.59	0.002
Error	275	9.14		
R ²				0.52
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	−24.77	15.89	−1.575	0.12
Year	−0.01	0.004	−2.021	0.04
Elevation	0.0002	0.00002	10.210	< 0.001
Latitude	0.32	0.35	0.900	0.37
Longitude	−0.37	0.10	−3.880	< 0.001
Year × latitude	0.0002	0.0001	2.224	0.03
Latitude × longitude	0.007	0.002	3.097	0.002

(b) Response variable: log(precipitation + 1) (February–April)

Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Elevation	1	3.02	93.63	< 0.001
Latitude	1	0.35	10.91	0.001
Longitude	1	6.21	192.53	< 0.001
Elevation × latitude	1	0.21	6.40	0.01
Error	276	8.90		
R ²				0.49
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	−9.88	1.15	−8.61	< 0.001
Elevation	−0.0006	0.0003	−1.86	0.06
Latitude	0.006	0.004	1.37	0.17
Longitude	−0.08	0.006	−13.88	< 0.001
Elevation × latitude	0.00002	0.000008	2.53	0.01

be deduced from these patterns alone; to our knowledge, this is the first report of such a pattern in any wild species.

The temperature × precipitation interaction is also a result of the delaying effect of precipitation being stronger where T_{\min} values are colder, suggesting that future changes in precipitation in the western USA will have greater effects on the flowering time of *T. ovatum* in cooler locations (in Fig. 2b, the positive slope of the line representing the minimum value of mean T_{\min} (solid red) is steeper than the slope of the lines representing the mean and maximum values of mean T_{\min} (dashed green and dotted blue)); based on the patterns detected here, any reductions in precipitation will advance flowering, particularly where the climate is relatively cool.

Table 3 (Continued)

(c) Response variable: log(sum precipitation + 1) (March–May)

Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Year	1	0.22	5.62	0.02
Elevation	1	3.75	93.93	< 0.001
Latitude	1	1.52	38.05	< 0.001
Longitude	1	5.29	132.49	< 0.001
Elevation × latitude	1	0.24	6.07	0.01
Year × longitude	1	0.17	4.25	0.04
Error	275	10.99		
R ²				0.40
Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	−78.98	33.13	−2.38	0.01
Year	0.04	0.02	2.13	0.03
Elevation	−0.0007	0.0004	−1.79	0.07
Latitude	0.02	0.005	3.83	< 0.001
Longitude	−0.64	0.28	−2.33	0.02
Elevation × latitude	0.00002	0.00001	2.46	0.01
Year × longitude	0.0003	0.0001	2.06	0.04

Table 3 reports the independent effects of year, elevation, latitude and longitude on total precipitation from (a) January–March; (b) February–April; and (c) March–May. Parameter estimates are the regression intercepts and coefficients for each independent variable.

R² values and significant P values (< 0.05) are shown in bold to facilitate comparison across tables.

This result was unexpected; where T_{\min} values are low, flowering is relatively late. Therefore, the delaying effect of high precipitation is strongest where flowering is *already* delayed. By contrast, we might expect that variation in precipitation would have the strongest effect on the onset of flowering in *T. ovatum* where T_{\min} is highest and flowering is relatively early, that is, precipitation would have a delaying effect where plants are flowering early and there is greater potential for phenology to be delayed. One possible explanation for the observed pattern is that, under cooler conditions, precipitation may freeze and be deposited as snow, requiring additional time for snow to melt and for soils to warm before plants are able to initiate growth and reproduction. Under warmer climatic conditions, by contrast, the effect of precipitation on flowering time is not as strong. Given that very few studies have documented interactions between T_{\min} and precipitation (but see Fu *et al.*, 2014), a better understanding of phenological responses to precipitation is needed if we are to model and forecast phenological changes more effectively, particularly in water-limited ecosystems.

Finally, climatic conditions during the later seasonal windows (FMA and MAM) explained slightly more variation in the flowering phenology of *T. ovatum* than the earlier window. Previous studies have found that the flowering phenology of some taxa is more sensitive to climatic conditions in certain months or seasons than in others (Hart *et al.*, 2014; Mazer *et al.*, 2015), but the mechanism driving this pattern is unclear. In our study, sensitivity to the later seasonal windows

Table 4 Summary of multiple linear regression models conducted to detect effects of year, elevation, latitude, longitude and their interactions on the day of year (DOY) of the collection of flowering specimens of *Trillium ovatum*

Analysis of variance				
Source	df	Sum of squares	F ratio	P value
Year	1	4621	5.24	0.02
Elevation	1	153 943	58.28	< 0.0001
Latitude	1	11 422	6.49	0.001
Longitude	1	25 570	29.04	< 0.0001
Year × elevation	1	505	0.57	0.45
Year × latitude	1	2120	2.41	0.12
Elevation × latitude	1	2157	2.45	0.12
Year × longitude	1	397	0.45	0.50
Elevation × longitude	1	130	0.15	0.70
Latitude × longitude	1	1313	1.49	0.22
Year × elevation × latitude	1	6115	6.94	0.009
Year × elevation × longitude	1	5244	5.96	0.02
Error	276	243 016		
R^2				0.48

Parameter estimates				
Term	Estimate	SE	t ratio	Prob > t
Intercept	9305	12 460	0.75	0.46
Year	−6.36	6.52	−0.98	0.33
Elevation	−49.37	18.26	−2.70	0.007
Latitude	19.53	71.62	0.27	0.79
Longitude	64.32	93.41	0.69	0.49
Year × elevation	0.025	0.009	2.70	0.007
Year × latitude	0.02	0.03	0.64	0.52
Elevation × latitude	0.31	0.12	2.66	0.008
Year × longitude	−0.046	0.05	−0.95	0.34
Elevation × longitude	−0.297	0.12	−2.45	0.02
Latitude × longitude	0.484	0.40	1.22	0.22
Year × Elevation × latitude	−0.0002	0.00006	−2.64	0.009
Year × Elevation × longitude	0.0002	0.00006	2.44	0.02

Parameter estimates are the regression coefficients for each variable. R^2 values and significant P values (< 0.05) are shown in bold to facilitate comparison across tables.

may be caused by the individuals in our study that flowered relatively late (e.g. a flowering DOY > 150, or 30th May; Fig. 2); these plants may be more sensitive than earlier flowering individuals to the more recent climatic conditions (e.g. those observed in FMA and MAM).

One limitation of the current study is that the models included only contemporaneous temperature and rainfall (i.e. climatic parameters experienced in the same set of months). Mazer *et al.* (2015) found that, for some Californian native woody species, the effects on a phenophase's DOY of T_{min} during 1 month were dependent on the level of rainfall in another month. For example, precipitation in one winter month influenced an individual plant's sensitivity to T_{min} experienced in a subsequent month. The examination of the effects of non-synchronous combinations of temperature and rainfall was beyond the scope of the current study, but the variance in DOY explained by multivariate models might be increased by including such interactions.

Temporal changes in temperature and rainfall

Seasonal T_{min} values varied across the > 100 yr of observation (1895–2009) in our climatic dataset, but the direction of change was dependent on the location of observation. Observations from the western coastal portion of *T. ovatum*'s range revealed that minimum temperatures have decreased across the observation period, whereas, in the eastern inland portion of the range, minimum temperatures have increased. Lebassi *et al.* (2009) reported similar patterns for summer temperature over a 50-yr observation period (from 1948 to 2004) in California: summer temperatures have become cooler at low-elevation coastal sites, which are open to marine air penetration, whereas summer temperatures at inland sites have increased in recent years. Likewise, the temporal changes in precipitation are complex, with the direction of change depending on location. In the January–March window, long-term temporal changes in PPT were dependent on latitude, whereas, in March–May, the temporal change in precipitation was dependent on longitude. To our knowledge, the fact that temporal trends in temperature and/or precipitation vary regionally has not previously been accounted for in studies of the responses of species to climate change, and is an important consideration for any widespread species, in which long-term phenological patterns in one part of its range may differ from those in another part of its range as a result of regional variation in the direction or magnitude of climate change.

Climate models for the Pacific Northwest generally predict warmer and similar to slightly wetter conditions in the future; the climate models available in The Nature Conservancy's online climate wizard tool (<http://www.climatewizard.org/>; accessed 9 November 2014), for example, predict warmer springs (March–May) and relatively little change in precipitation in the Pacific Northwest by the 2080s (Girvetz *et al.*, 2009). We found that warmer spring T_{min} values were associated with advanced flowering and the delaying effect of precipitation was more pronounced where T_{min} values were lower. If the climate predictions hold true for this region, we expect the inter-annual trend in the flowering phenology of *T. ovatum* to shift towards earlier flowering in the upcoming decades.

Long-term temporal changes in flowering date

Given the complexity of long-term temporal changes in climatic variables that affect flowering phenology, it is not surprising that the long-term temporal trend in flowering date was similarly complex and location dependent. Surprisingly, few studies have emphasized the importance of considering location- or region-specific trends in phenology (but see Cocu *et al.*, 2005, who found location-specific trends in aphid phenology across Europe), perhaps because most studies have been limited to local or regional scales.

Interestingly, the model including geographic variables and collection year explained a larger proportion of the variation in flowering date than any of the models with seasonal climatic variables (48% (Table 4) vs 34–36% (Table 1)). Although geographic parameters are a good proxy for (and probably capture most)

variation in climate, other abiotic factors that affect phenology are also likely to vary geographically and may account for the additional explained variance (e.g. day length, duration of the warmest part of the day, soil nutrients or temperatures, and the intensity of herbivory). Moreover, each season may explain some portion of the variance in flowering DOY, independent of other seasons, a possibility not explored here (as each three-month window was modeled independently). Finally, biotic factors, such as the timing of pollinator availability and abundance, could determine the optimum flowering time in different regions. If so, natural selection could result in local adaptation and differentiation among populations in flowering time that is somewhat independent of local climatic conditions.

Using natural history collections as a data source

The geographic distribution of *T. ovatum* is well represented by the specimens included in our dataset (Fig. 1). Although herbarium specimens have been used to extend the temporal coverage of phenological datasets (Primack *et al.*, 2004; Robbirt *et al.*, 2011; Panchen *et al.*, 2012), here we show that they can also expand geographic coverage, which allowed us to describe relationships with geographic variables and to capture a wider range of climatic conditions. Many natural history collections are now being digitized, making information contained within them more accessible, and allowing researchers to document phenological information without physically visiting herbaria or requesting loan specimens (Park, 2012, 2014).

As shown here, data derived from natural history collections can be used to detect phenological relationships with climate and provide a reference point for comparison with future phenological research. *Trillium ovatum* is a focal species for two national-scale phenological monitoring programs in the USA, the USA National Phenology Network (www.usanpn.org) and Project Budburst (<http://budburst.org/>), and we expect that contemporary phenological data across its native range will be increasingly accessible via these online platforms. These herbarium-derived data and results represent a 122-yr time series that will provide a baseline on which to interpret phenological data that are reported to these programs in the future.

Acknowledgements

The authors gratefully acknowledge University of California, Santa Barbara (UCSB) student interns, who invested considerable time and effort in the examination of hundreds of herbarium specimens; Danica Taber for her assistance in data management and organizing undergraduate schedules; and Kimberly Crispin for retrieving PRISM data. The authors also thank the herbaria that loaned specimens, particularly Dr Jennifer Thorsch, and UCSB Cheadle Center For Biodiversity and Ecological Restoration for hosting the borrowed specimens and for providing space to work with them. The authors acknowledge funding from the National Park Service Climate Change Response Program (Cooperative Agreement H8C07080001).

Author contributions

E.R.M. and S.J.M. planned and designed the research. E.R.M. acquired the herbarium loans, supervised student interns and managed the data. E.R.M. led the data analysis, and E.R.M. and S.J.M. discussed all analyses, results and interpretations. E.R.M. led the writing and preparation of the manuscript. E.R.M. and S.J.M. contributed to the editing of the manuscript.

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