UC Santa Barbara
UC Santa Barbara Previously Published Works

Title

Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem

Permalink

Journal

ISSN

Authors

Mazer, Susan J
Gerst, Katharine L
Matthews, Elizabeth R
et al.

Publication Date

DOI

Peer reviewed

Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem

Susan J. Mazer,[1],† Katharine L. Gerst,[2,3] Elizabeth R. Matthews,[1,4] and Angela Evenden[5]

[1]*Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[2]*USA National Phenology Network, National Coordinating Office, 1955 East Sixth Street, Tucson, Arizona 85721 USA*
[3]*School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721 USA*
[4]*National Capital Region Network, Inventory and Monitoring Program, National Park Service, Center for Urban Ecology, 4598 MacArthur Boulevard NW, Washington, D.C. 20007 USA*
[5]*National Park Service, Pacific West Region and Californian Cooperative Ecosystem Studies Unit, University of California, Berkeley, California 94720 USA*

Abstract. Phenology is the study of seasonal biological events such as flowering, leaf-out, insect emergence, and animal migration. Long-term observational studies at numerous temperate zone sites have found that the timing of phenological events responds to temporal variation in climate. To assess the phenological effects of climatic variation on California's flora, The California Phenology Project (CPP) was established in 2010 to develop and to test monitoring protocols and to create tools to support long-term phenological monitoring and education in several California national parks. The CPP uses standardized protocols developed in collaboration with the USA National Phenology Network (USA-NPN) to track the phenological status of 30 plant species across key environmental gradients (e.g., latitude, elevation, and precipitation). To date, over 860K phenological records collected by trained citizen scientists, natural resource managers, and park interns participating in the CPP have been contributed to the National Phenology Database. Observations recorded up to twice per week during the first 40 months of monitoring by the CPP were of sufficiently high resolution to detect associations between local climatic conditions and the onset of targeted phenophases. Here, we present analyses of four of the most intensively-monitored species: *Baccharis pilularis* (Asteraceae), *Quercus lobata* (Fagaceae), *Sambucus nigra* (Caprifoliaceae), and *Eriogonum fasciculatum* (Polygonaceae). We examined the effects of monthly climate parameters during a four month window (December to March), including mean minimum temperatures (Tmin), total monthly precipitation, and their interactions, on the onset dates of four phenophases per species. Stepwise regressions explained a high proportion (30–99%) of the variation in the onset date of each phenophase. Species and phenophases differed, however, with respect to the strength and the direction of the relationship between each month's conditions (Tmin and/or precipitation) and the timing of vegetative and reproductive phenophases. Given the high climatic variation represented among the monitored sites and among years (2011–2013), it was possible to detect significant associations between local, recent winter conditions and the onset dates of subsequent phenophases, although interactions between monthly conditions were also common. These patterns permit preliminary predictions regarding how these species will respond to future winter warming and intensifying drought.

† E-mail: mazer@lifesci.ucsb.edu

INTRODUCTION

In the continental United States, observational studies have been conducted in several seasonal communities to track inter-annual changes in phenology. In most species, the dates of breaking leaf buds (the emergence of new leaves at the onset of spring) and flowering appear to respond to inter-annual variation in mean annual or seasonal temperature. Moreover, the magnitude and direction of this response differs among species or higher taxa within and across locations (Crimmins et al. 2010, Davis et al. 2010, Cleland et al. 2012, Cook et al. 2012a, 2012b, Wolkovich et al. 2012, Davies et al. 2013, Mazer et al. 2013). In most species, warmer temperatures are associated with earlier onset dates of breaking leaf buds and flowering; however, other species respond to warmer temperatures by delaying these phenological transitions, potentially because they require a sufficiently long and deep winter chill before initiating new growth and reproduction (Zhang et al. 2007, Polgar et al. 2013). Among those species that advance their phenological schedules in response to warming, earlier-flowering taxa generally exhibit larger responses (Munguía-Rosas et al. 2011, Mazer et al. 2013).

In the long-term studies cited above, the earliest dates on which new phenophases (e.g., breaking leaf buds or open flowers) were observed on any plant were recorded at each site (Mazer et al. 2013). Individual plants were not selected at random for monitoring, nor were they marked for repeated monitoring in successive years. As a result, the onset dates recorded were not necessarily representative of each species and could have been significantly biased by outliers that exhibited the earliest phenological transitions (cf. Miller-Rushing et al. 2008). One approach to long-term phenological monitoring that mitigates these limitations is to map and label multiple randomly sampled individuals of focal species within a community, and to visit them frequently to record their phenological status, thereby obtaining precise dates for targeted phenological transitions. For such individuals, inter-annual changes in phenological onset dates that are associated with changes in temperature or precipitation would necessarily be environmentally (as opposed to genetically) induced, and the mean phenological responses among randomly sampled conspecific individuals would be more representative of the species monitored. While a similar approach has been used to study inter-annual variation in the timing of phenological transitions for cultivated taxa (e.g., studies of the common lilac, *Syringa vulgaris*, have repeatedly monitored genetically identical individuals planted at geographically widespread sites; Schwartz et al. 2012), to our knowledge this approach has not been used to study phenological patterns of wild plants. Here, we report the phenological patterns exhibited by four intensively monitored taxa, along with the relationships between the onset dates of their observed phenological stages, or phenophases, and local climatic conditions.

Despite recent studies in the U.S. documenting species' responses to climate and the consequences of these responses (e.g., Inouye 2008, Willis et al. 2010, Cleland et al. 2012, McKinney et al. 2012), relatively little phenological information is available from water-limited ecosystems. In addition, few studies investigate the degree to which precipitation acts as a driver of phenological variation in arid and semi-arid ecosystems (but see Crimmins et al. 2010, 2011, Gordo and Sanz 2010, Dunnell and Travers 2011, de Oliveira et al. 2015). Currently, phenological models that predict ecosystem responses to climate change are primarily based on responsiveness to temperature (Richardson et al. 2010, Diez et al. 2012, Jeong et al. 2013); incorporating phenological responses to precipitation will be critical as these models become more sophisticated and applied to non-temperate regions.

In 2010, the California Phenology Project (CPP; http://www.usanpn.org/cpp) was established at seven California national park units in coastal, desert, foothill, and montane sites. The primary goals of the CPP were to design and to initiate phenological monitoring programs at each park, using a standardized set of protocols designed by the USA National Phenology Network (USA-NPN; http://www.usanpn.org; Denny et al. 2014), and to use the short-term results of these

programs to detect climatic sources of geographic variation in phenological onset dates that could be used as a preliminary proxy for the effects of future climate change on the phenological behavior of the focal species.

The results presented here address the following questions: (1) Are there significant associations between phenological onset dates and local mean monthly minimum temperatures (Tmin) or total monthly precipitation during winter months? (2) In a water-limited ecosystem, are the onset dates of vegetative and reproductive phenophases more sensitive to local precipitation or Tmin? (3) Within species, do different phenophases respond similarly to the same environmental variables? (4) Are there qualitative differences among taxa and phenophases with respect to the direction of their phenological responses (advances vs. delays) to increases in winter monthly Tmin or winter monthly precipitation?

MATERIALS AND METHODS

In 2010, with funding from the National Park Service (NPS) Climate Change Response Program, the authors worked with park staff to design and implement a phenological monitoring program in seven NPS units in California (Joshua Tree National Park [NP], Santa Monica Mountains National Recreation Area [NRA], Sequoia and Kings Canyon National Parks, Golden Gate NRA, Lassen Volcanic NP, John Muir National Historic Site [NHS], and Redwood National Park). Multiple individuals of each of 30 species were selected for regular monitoring in one or more parks (total number of individuals = 770; mean number of individuals per species = 25.7 [range 5–126]; Matthews et al. 2013). The selected species included iconic, locally dominant, easily accessible, and widespread taxa; most were woody (or long-lived perennials) so that it would be possible to track individuals for many years. Following the selection of individual plants and sites for monitoring (Matthews et al. 2013, 2014), a series of workshops was held at each park to train park staff, seasonal interns, visitors and community members in the methods used to record the phenological status of CPP species.

Site selection

At each park, we established a hierarchy of locations and sites for monitoring. First, we selected four to six species for monitoring in each park, with the constraint that these species must be represented by individual plants accessible enough to enable frequent monitoring (i.e., sufficiently close to trails or visitor centers). In addition to the national parks targeted for study, the CPP established several partnerships outside of the parks where CPP species were monitored. Taxa analyzed here were monitored at three of these places (Pepperwood Preserve, Santa Rosa, CA; Kenneth S. Norris Rancho Marino Reserve, Cambria, CA; and Sedgwick Ranch Reserve, Santa Ynez, CA; the latter two are part of the University of California Natural Reserve System). Second, at each park (or reserve), we identified several *locations* (e.g., segments of hiking trails or visitors centers) where two to four of the species selected for monitoring were common. Third, we selected multiple *sites* at each location, where each site included 1–9 healthy individuals of one or more of the focal species within a ~20-m radius, and adjacent sites were ~50–200 m apart. The locations where each of the species in the present study was monitored are shown in Fig. 1.

Frequency of monitoring

The phenological status of each individual plant was recorded up to twice per week using the protocols of the USA-NPN (Denny et al. 2014). Plants were monitored during the phenologically active periods of each species from March 2011 to the present; the data presented here extend through April 2014. Data were contributed to the National Phenology Database (NPDb) through its on-line interface, *Nature's Notebook*; data were accessed from the database in May 2014 (USA National Phenology Network 2014).

Data and analyses

Phenological observations and data set.—The protocols of the USA-NPN specify that at each visit to an individual plant, observers record whether the plant exhibits any of the phenophases targeted for that species (e.g., breaking leaf buds, open flowers, or ripe fruits). The status of each plant observed on a given date with
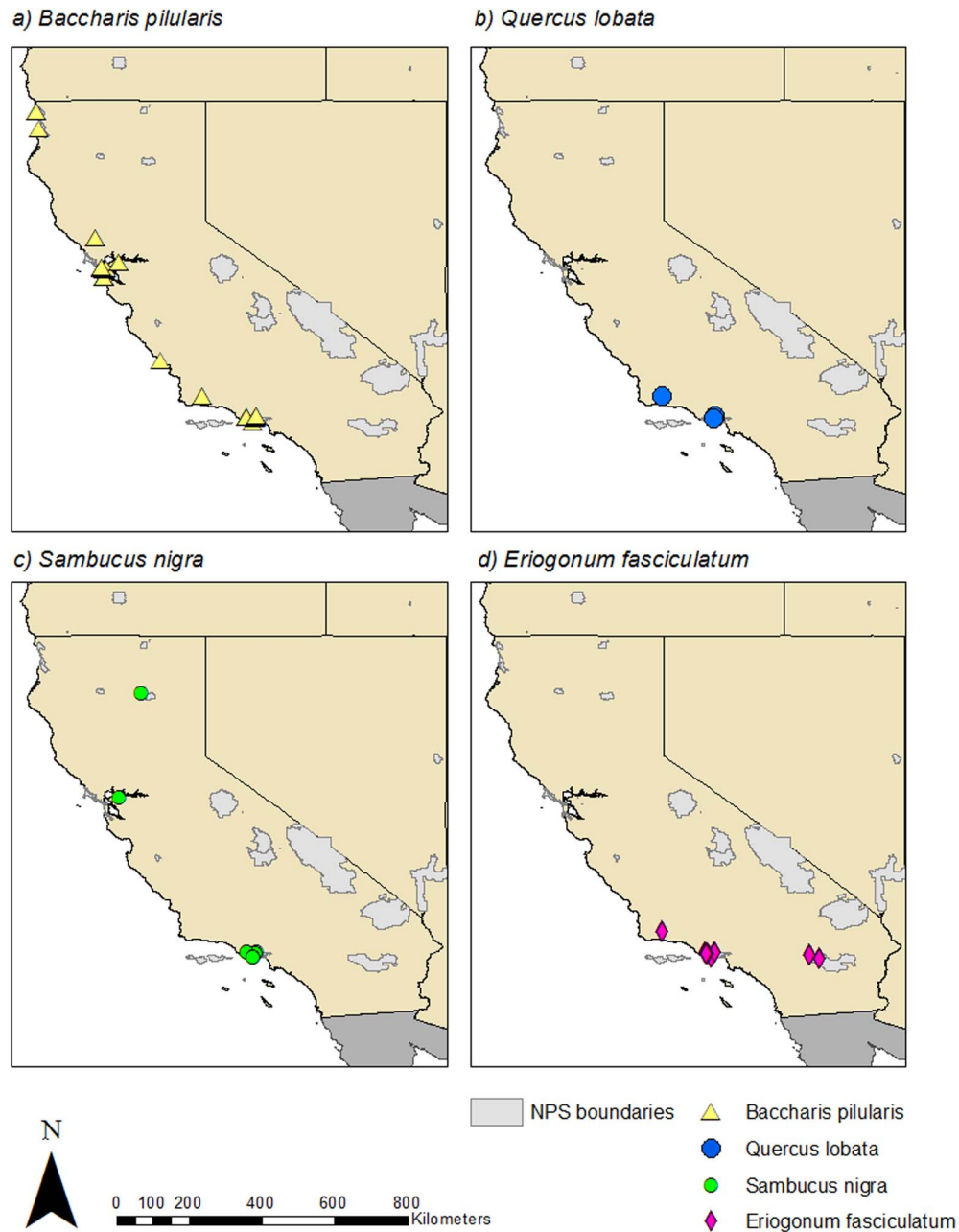
Fig. 1. Locations of the sites where each of the four focal species examined here were monitored.

respect to each phenophase's presence is recorded as a "Yes" or "No". The records associated with each individual and phenophase status enable the identification of day of the year (DOY: 1–366) on which the phenophase was first recorded as a "Yes".

For some phenophases in *B. pilularis*, onset dates began before December 31 of one calendar year and extended beyond January 1 of the subsequent year. For these phenophases, the values of the DOY were adjusted so that the dates of onset would increase continuously from the first DOY to the last. This was achieved by adding 365 to the values of all DOY after

December 31 until the tail end of the phenological cycle was reached. In this way, the "phenological year" was shifted to accommodate phenophase onset dates that occurred prior to January 1. The "phenological year" of any phenophase could thereby be defined as beginning at the lower tail of its unimodal distribution and ending at the opposite end of the distribution regardless of when in the calendar year the first onset date fell.

The estimated onset date for a given phenophase was estimated to be the date of the first "yes" for the phenological year. The precision of the estimated date of onset is determined by the length of the interval during which the status of the phenophase changed from being absent (e.g., when the observer records a "No" when seeking its presence) to present (e.g., when a "Yes" is recorded). In this study, we used only dates of onset that were preceded by ≤7 days since the most recent "No"; the dates of onset are therefore precise within 7 days or less. The mean onset dates for each species and site were calculated where data from more than one conspecific individual were available per site; if data representing only one individual was available, the site's value was represented by this individual's onset date.

In much of California, where a Mediterranean climate prevails, the growing season comprises the period between the onset of fall or winter rains and the cessation of rains in mid- or late spring. During this period of sporadic rainfall events, many individual plants exhibited multiple episodes of breaking leaf buds and/or flowering within a growing season. For the current study, for each individual, we excluded all but the *first* onset date in a given phenological year.

Among the 30 taxa monitored in the participating parks and other CPP sites, we selected four well-monitored taxa for analysis: *Quercus lobata* (valley oak, a deciduous tree; n = 28 individuals); *Sambucus nigra* (blue elderberry, a deciduous treelet; n = 31); *Eriogonum fasciculatum* (California buckwheat, an evergreen shrub; n = 83); and *Baccharis pilularis* (coyotebrush, a dioecious evergreen shrub; n = 126). At each site, 1–9 plants per species were monitored, depending on the species, phenophase, and year of observation. Across all four species, the number of sites per

park ranged from 1 to 17, depending on the phenophase and year (Table 1). Among all four species, the total number of site means available for analysis (including all site × year combinations) ranged from 17 to 59 (Table 2).

Climatic data.—For each site we used the PRISM dataset (http://www.prism.oregonstate.edu/explorer/) to extract mean monthly Tmin and total monthly precipitation from 2010 to 2014 for the winter months, December through March. We chose to track the effects of Tmin rather than mean monthly maximum temperatures (Tmax) because, in the temperate zone, the former is increasing with climate change more rapidly than Tmax (Karl et al. 1993, Easterling et al. 1997, Lu et al. 2006). To determine how recent climatic conditions experienced by the species in this study compare to historical conditions, we examined 30-year normals (PRISM data; 1971–2000) at eight widely distributed locations included in this study (Appendix: Table A1).

Analysis: detecting associations between climate and onset dates.—For each species and year of observation, the site means for the first onset dates of each phenophase were used as response variables in stepwise regressions to identify climate parameters that explained the highest proportion of variance in the DOY of the focal phenophases. Where a site was monitored for multiple years (2011–2014), the site mean for each year was included in the data set, generating some pseudoreplication. This pooling of data, however, enabled us to take advantage of both spatial and temporal variation in climate, increasing the range of variation in each of the independent variables. Stepwise regressions included the following variables as main effects as well as all two-way and three-way interaction terms: Tmin(December), Tmin(January), Tmin(February), Tmin(March), Precipitation(December), Precipitation(January), Precipitation(February), and Precipitation(March). Values for precipitation were log-transformed for *B. pilularis* to improve normality, but raw values for precipitation were used in the analyses of the other species (transformation did not improve normality). For each species and phenophase, the model that resulted in the minimum corrected Akaike Information Criterion (AICc) was selected. Where higher order terms were retained by the AIC approach but were statistically non-significant, they were excluded from the model and the

Table 1. Number of sites monitored for each species (n = number of individuals contributing to an onset date), phenophase, park or reserve, and year in the dataset analyzed here. Site means for the first date of onset of each phenophase were used in all analyses; each site included 1–9 individuals of each species for which the first onset date was recorded within ≤7 days of its occurrence.

Species and phenophase	National Park or Reserve	No. sites			
		2011	2012	2013	2014
Baccharis pilularis (n = 126)†					
Young leaves	Golden Gate NRA	2	3	2	
	John Muir NHS		2	1	
	Pepperwood Preserve			1	
	Redwood National Park		2		
	Santa Monica Mountains NRA	6	6	11	
	Sedgwick Ranch Reserve		2	2	
Flowers or flower buds	Golden Gate NRA	11	13	2	
	John Muir NHS		2	1	
	Kenneth S. Norris Rancho Marino Reserve			1	
	Pepperwood Preserve			1	
	Redwood National Park	3	3		
	Santa Monica Mountains NRA	4	8	6	
	Sedgwick Ranch Reserve		2	2	
Fruits	Golden Gate NRA	7	2	3	
	John Muir NHS		2	1	
	Kenneth S. Norris Rancho Marino Reserve			1	
	Pepperwood Preserve			1	
	Redwood National Park	2			
	Santa Monica Mountains NRA	5	9	6	
	Sedgwick Ranch Reserve		2	2	
Pollen release	Golden Gate NRA	12	5	3	
	John Muir NHS		2	1	
	Pepperwood Preserve			2	
	Redwood National Park	1	3		
	Santa Monica Mountains NRA	3	1	5	
	Sedgwick Ranch Reserve		2	2	
Quercus lobata (n = 28)					
Breaking leaf buds	Santa Monica Mountains NRA	2	8	10	10
	Sedgwick Ranch Reserve			1	1
Flowers or flower buds	Santa Monica Mountains NRA		7	6	8
	Sedgwick Ranch Reserve		1	1	1
Open flowers	Santa Monica Mountains NRA		8	6	8
	Sedgwick Ranch Reserve			1	1
Pollen release	Santa Monica Mountains NRA		7	6	8
	Sedgwick Ranch Reserve			1	1
Sambucus nigra (n = 31)					
Breaking leaf buds	John Muir NHS		1	1	1
	Lassen Volcanic NP	1			
	Santa Monica Mountains NRA	5	10	10	3
Leaves	John Muir NHS		1		1
	Lassen Volcanic NP	1			
	Santa Monica Mountains NRA	5	7	7	4
Flowers or flower buds	John Muir NHS		1	1	
	Santa Monica Mountains NRA		8	9	1
Open flowers	John Muir NHS		1	1	
	Santa Monica Mountains NRA		8	6	1
Fruits	John Muir NHS		1	1	
	Lassen Volcanic NP	1			
	Santa Monica Mountains NRA	3	9	8	1
Ripe fruits	John Muir NHS		1	1	
	Santa Monica Mountains NRA	3	10	7	1
Eriogonum fasciculatum (n = 83)					
Young leaves	Joshua Tree NP		5	1	
	Santa Monica Mountains NRA	3	12	17	6
	Sedgwick Ranch Reserve		3	3	3
Flowers or flower buds	Joshua Tree NP		6		
	Santa Monica Mountains NRA		8	18	3
	Sedgwick Ranch Reserve		2		
Open flowers	Joshua Tree NP		7		
	Santa Monica Mountains NRA		9	15	1

Table 1. Continued.

Species and phenophase	National Park or Reserve	No. sites			
		2011	2012	2013	2014
	Sedgwick Ranch Reserve			3	
Fruits	Joshua Tree NP		8	1	
	Santa Monica Mountains NRA		8	12	4
	Sedgwick Ranch Reserve			3	2
Ripe fruits	Joshua Tree NP		6		
	Santa Monica Mountains NRA		7	16	4
	Sedgwick Ranch Reserve			3	2

 † For *Baccharis pilularis*, data for each "phenological year" span January 1st and therefore include portions of two calendar years: 2011–2012, 2012–2013, 2013–2014. For all other species, data are for one-year spans.

regression was run again (except for non-significant two-way interactions, which were retained if the three-way interaction was significant). Eliminating the higher-order non-significant interactions did not reduce the R^2 value but the re-run analyses sometimes detected significant main effects for variables that were not initially statistically significant. The regression coefficients estimated in the final models (presented here) were examined to detect differences among phenophases or months in the direction of the effects of higher Tmin or higher precipitation on the phenological onset dates. All analyses were performed in JMP Pro v. 11.0.0 (2013; SAS Institute, Cary, North Carolina, USA).

RESULTS

Geographic and temporal variation in climate and onset dates

 Of the locations where recent climatic conditions were compared to 30-year normals, most were warmer and drier between 2011 and 2014 (see Appendix: Table A1), but there were several exceptions. 2012 was wetter than normal at Golden Gate NRA, Redwood National and State Parks, and Lassen Volcanic National Park; and 2011 was cooler than normal at most locations. The years of 2012–2013 were also comparatively cool years at Golden Gate NRA, the Sedgwick Ranch Reserve and Santa Monica Mountains NRA. Across these locations, from 2011 to 2013, annual cumulative precipitation estimated by PRISM varied from 45.70 to 1831.38 mm and annual mean monthly Tmin varied from −0.46°C to 13.78°C (Appendix: Table A1).

 Across the sites monitored from 2011–2014, monthly Tmin and precipitation varied by one or more orders of magnitude (Fig. 2 shows conditions at sites where *B. pilularis* was monitored), providing a wide range of conditions across which to test for influences on phenophase onset dates. Across these sites, January Tmin varied more than that of the other three months (based on the SD and range), while March precipitation varied more across sites than December–February.

Table 2. Mean onset day of year (DOY) (sample size = the number of site × year combinations) of observed phenophases. Mean values are derived from the means from each site in each phenological year. An ellipsis ("...") indicates either phenophases that are not targeted for a given species due to its habit (USA-NPN species-specific phenophase protocols depend on life history and growth form), phenophases for which the analyses are not presented due to low sample sizes, or phenophases that were not analyzed due to difficulty in identifying the start and end dates of each "phenological year."

Species	Breaking leaf buds	Young leaves	Leaves	Flowers and flower buds	Open flowers	Pollen release	Fruit	Ripe fruit
Baccharis pilularis	...	296.0 (40)	...	239.9 (59)	...	259.5 (42)	292.9 (39)	...
Quercus lobata	80.3 (32)	...	...	78.2 (24)	77.5 (24)	78.1 (23)	...	...
Sambucus nigra	216.1 (32)	...	183.12 (26)	101.8 (20)	124.6 (17)	...	175.4 (24)	200.5 (23)
Eriogonum fasciculatum	...	130.3 (53)	...	84.1 (37)	120.2 (35)	...	118.3 (38)	137.3 (38)
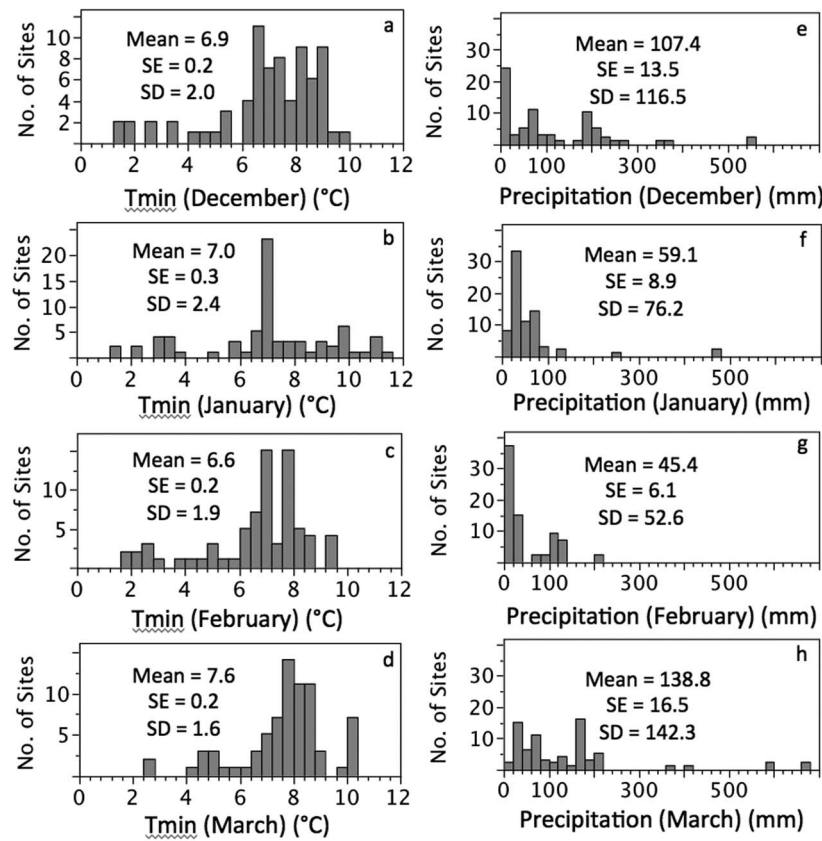
Fig. 2. Frequency distribution of mean minimum monthly minimum temperature (a–d) and monthly precipitation (e–h) during the winter months among sites where *Baccharis pilularis* was monitored during three phenological years (2011–12, 2012–13, and 2013–14). All site × year combinations are included (n = 74); each phenophase was monitored at a subset of these combinations (see Table 3 for number of sites monitored per phenophase).

Associations between DOY of phenophase onset and the preceding winter monthly conditions

Baccharis pilularis (coyotebrush).—The regression models explained 30–90% of the variance in the DOY of the coyotebrush phenophases reported here (Table 3). Vegetative phenology was strongly associated with winter precipitation but not with monthly Tmin. High precipitation in both February and March was associated with delayed leaf production.

Onset dates of flowering and fruiting in coyotebrush were regularly influenced by the mean Tmin of winter months, but the direction and strength of the effect of Tmin differed among phenophases and months (Table 3). While there was greater variation among sites in January Tmin than in the Tmin of the other months (Fig.

2), this did not result in a stronger association between January Tmin and the DOY of each phenophase relative to other months. For example, December Tmin had stronger (and opposite) effects on the DOY of pollen release and fruit ripening than January Tmin. In addition, at sites where December Tmin was relatively high, flowering was advanced, but higher January Tmin was associated with later flowering. Similarly, pollen release occurred earlier at sites with relatively high December, February, or March Tmin and later at sites with higher January Tmin. Across sites and years, high December Tmin was associated with earlier fruit ripening, while high January and February Tmin were associated with delayed fruit ripening.

The influence of winter precipitation on

Table 3. Summary of stepwise regressions to detect significant associations between the date of onset of vegetative and reproductive phenophases and winter monthly climatic parameters among monitored sites and years in *Baccharis pilularis*. The adjusted R^2 value is the proportion of variance in the DOY of the onset of a phenophase explained by the model, adjusted for the degrees of freedom; it provides an R^2 that is comparable across models that differ in the number of parameters. PPT refers to monthly precipitation; Tmin refers to mean monthly minimum daily temperature. Significant p-values ($\alpha < 0.05$) are shown in boldface; marginally non-significant p-values ($0.05 < p < 0.1$) are shown in italics.

Source	df	Sums of squares	F ratio	Regression coefficient	p-value	R^2	Adj R^2
Young leaves							
PPT(February)	1	21169	3.06	60.73	*0.0887*		
PPT(March)	1	58727	8.50	114.26	**0.0061**		
PPT(Feb)×PPT(Mar)	1	62531	9.05	−255.08	**0.0048**		
Model	3	107954	5.21		**0.0043**		
Error	36	248865					
Total	39	356819				0.30	0.24
Flowers or flower buds							
Tmin(December)	1	66707	28.05	−40.15	**<0.0001**		
Tmin(January)	1	90519	38.06	31.90	**<0.0001**		
PPT (Dec)	1	734	0.31	10.00	0.5809		
Tmin(Dec) × Tmin(Jan)	1	4121	1.73	−2.20	0.1939		
Tmin(Dec) × PPT(Dec)	1	40223	16.91	51.10	**<0.0001**		
Tmin(Jan) × PPT(Dec)	1	10231	4.30	−20.15	**0.0431**		
Tmin(Dec) × Tmin(Jan) × PPT(Dec)	1	11520	4.84	5.84	**0.0323**		
Model	5	151904	9.12		**<0.0001**		
Error	53	121298					
Total	58	273202				0.56	0.50
Pollen release							
Tmin(December)	1	12637	14.56	−66.23	**0.0007**		
Tmin(January)	1	12401	14.28	103.68	**0.0007**		
Tmin(February)	1	1715	1.98	−42.10	0.1705		
Tmin(March)	1	6720	7.74	−49.71	**0.0094**		
PPT(December)	1	10028	11.55	−89.79	**0.0020**		
PPT(February)	1	48701	56.09	514.25	**<0.0001**		
PPT(March)	1	47862	55.13	−604.55	**<0.0001**		
Tmin(Dec) × Tmin(Feb)	1	44509	51.26	−49.25	**<0.0001**		
Tmin(Feb) × Tmin(Mar)	1	50124	57.73	55.56	**<0.0001**		
PPT(Dec) × PPT(Feb)	1	51157	58.92	−503.80	**<0.0001**		
PPT(Dec) × PPT(Mar)	1	25635	29.53	746.10	**<0.0001**		
PPT(Feb) × PPT(Mar)	1	54361	62.61	−1104.21	**<0.0001**		
Model	12	185614	17.82		**<0.0001**		
Error	29	25178					
Total	41	210793				0.88	0.83
Ripe fruits							
Tmin(December)	1	7260	12.58	−47.87	**0.0019**		
Tmin(January)	1	2127	3.69	13.30	*0.0686*		
Tmin(February)	1	8738	15.14	65.64	**0.0008**		
PPT(December)	1	4300	7.45	47.09	**0.0125**		
PPT(January)	1	5229	9.06	125.41	**0.0067**		
PPT(March)	1	4169	7.22	−82.78	**0.0138**		
Tmin(Dec) × Tmin(Jan)	1	19	0.03	1.09	0.8551		
Tmin(Dec) × Tmin(Feb)	1	9535	16.52	−44.91	**0.0006**		
Tmin(Dec) × PPT(Jan)	1	28994	50.25	−357.76	**<0.0001**		
Tmin(Dec) × PPT(Mar)	1	12315	21.34	161.36	**0.0001**		
Tmin(Jan) × Tmin(Feb)	1	20939	36.29	30.40	**<0.0001**		
Tmin(Jan) × PPT(Jan)	1	30287	52.49	294.70	**<0.0001**		
Tmin(Jan) × PPT(Mar)	1	22562	39.10	−180.37	**<0.0001**		
Tmin(Feb) × PPT(Dec)	1	3051	5.29	17.52	**0.0318**		
Tmin(Dec) × Tmin(Jan) × Tmin(Feb)	1	12301	21.32	−5.78	**0.0001**		
Tmin(Dec) × Tmin(Jan) × PPT(Jan)	1	11459	19.85	−32.82	**0.0002**		
Model	7	106189	11.50		**<0.0001**		
Error	31	12117					
Total	38	118305				0.90	0.82

Table 4. Summary of stepwise regressions to detect significant associations between the date of onset of vegetative and reproductive phenophases and winter monthly climatic parameters among monitored sites and years in *Quercus lobata*. The Adjusted R^2 value is the proportion of variance in the DOY of the onset of a phenophase explained by the model, adjusted for the degrees of freedom; it provides an R^2 that is comparable across models that differ in the number of parameters. PPT refers to monthly precipitation; Tmin refers to mean monthly minimum daily temperature. Significant p-values ($\alpha < 0.05$) are shown in boldface; marginally non-significant p-values ($0.05 < p < 0.1$) are in italics.

Source	df	Sums of squares	F ratio	Regression coefficient	p-value	R^2	Adj R^2
Breaking leaf buds							
Tmin(March)	1	1251	11.41	30.22	**0.0026**		
PPT(December)	1	2869	26.15	3.75	**<0.0001**		
PPT(February)	1	2549	23.24	−18.75	**<0.0001**		
PPT(March)	1	2402	21.90	11.74	**0.0001**		
Tmin(Mar) × PPT(Dec)	1	2170	19.78	−2.55	**0.0002**		
Tmin(Mar) ×PPT(Mar)	1	2150	19.60	−3.34	**0.0002**		
PPT(Dec) × PPT(Feb)	1	2399	21.87	−0.46	**0.0001**		
PPT(Dec) × PPT(Mar)	1	2496	22.76	0.24	**<0.0001**		
Model	8	123429	140.67		**<0.0001**		
Error	23	2523					
Total	31	125952				0.98	0.97
Flowers or flower buds							
Tmin(December)	1	10	0.36	19.40	0.5561		
Tmin(January)	1	8	0.29	17.98	0.5958		
PPT(January)	1	471	17.64	−4.21	**0.0008**		
PPT(March)	1	156	5.85	−4.63	**0.0287**		
Tmin(Dec) × Tmin(Jan)	1	1767	66.20	14.27	**<0.0001**		
Tmin(Dec) × PPT(Jan)	1	3592	134.59	−3.24	**<0.0001**		
Tmin(Jan) × PPT(Jan)	1	10749	402.71	5.51	**<0.0001**		
Tmin(Dec) × Tmin(Jan) × PPT(Jan)	1	554	20.75	0.52	**0.0004**		
Model	8	79385	371.77		**<0.0001**		
Error	15	400					
Total	23	79786				0.99	0.99
Pollen release							
Tmin(January)	1	2343	44.84	138.06	**<0.0001**		
PPT(December)	1	65	1.25	−1.05	0.2809		
PPT(March)	1	1001	19.15	−3.16	**0.0005**		
Tmin(Jan) × PPT(Dec)	1	1683	32.21	5.00	**<0.0001**		
Tmin(Jan) × PPT(Mar)	1	868	16.60	2.47	**0.0010**		
PPT(Dec) × PPT(Mar)	1	46	0.87	0.03	0.3648		
Tmin(Jan) × PPT(Dec) × PPT(Mar)	1	2057	39.36	0.16	**<0.0001**		
Model	7	9318	25.47		**<0.0001**		
Error	15	784					
Total	22	10102				0.92	0.89
Recent fruit drop							
Tmin(December)	1	97218	67.89	36.05	**<0.0001**		
Model	1	97218	67.89		**<0.0001**		
Error	20	28639					
Total	21	125857				0.77	0.76

reproductive phenology similarly differed among phenophases in coyotebrush. The DOY of flowering was independent of precipitation, but high precipitation in December and March was associated with early pollen release, and high precipitation in February appeared to delay it. In contrast, fruit ripening was delayed by high precipitation in December and January, whereas high March precipitation appeared to accelerate it.

The influence of interactions (particularly Tmin × Precipitation) also appears to be pheno-phase-specific. In *B. pilularis*, the reproductive phenophases appear to be more strongly affected by such interactions than leaf production.

Quercus lobata (valley oak).—The stepwise regression models explained 77–99% of the variation in the DOY of the valley oak phenophases reported here (Table 4). Vegetative phenology was most consistently associated with precipitation, while reproductive phenophases were influenced by winter monthly Tmin, precipitation, or both. For both vegetative and reproductive traits, the direction and strength of the effects

differed among months (Table 4). Warm March conditions appeared to delay vegetative bud break, and sites with warm December and January conditions exhibited delayed flowering. Similarly, sites with high January Tmin exhibited delayed pollen release and those with high December Tmin exhibited delayed fruit drop. The effects of monthly Tmin on the DOY for flowers or flower buds were non-significant as main effects (although they contributed to several interaction terms; Table 4).

Sites where precipitation was relatively high in December and in March exhibited delayed vegetative bud break, while sites with relatively wet February conditions exhibited earlier bud break. Increased January and March precipitation advanced the appearance of flowers and flower buds, while December and March precipitation was associated with earlier pollen release. The timing of recent fruit drop was not significantly influenced by winter precipitation.

Interactions between monthly conditions influenced all four phenophases in valley oak, but their identity and strength differed among phenophases. Fruit drop was the only phenophase for which there was not a significant interaction term.

Sambucus nigra (blue elderberry).—The regression models explained 77–98% of the variation in the DOY of the phenophases reported here (Table 5). Vegetative phenology was strongly associated with winter monthly Tmin, but, unlike the other species examined here, there was no association between precipitation and the DOY of bud break. By contrast, blue elderberry's reproductive phenophases were influenced by both Tmin and precipitation. For all phenophases, the direction and strength of the statistical effects of monthly winter conditions on DOY differed among months (Table 5). Sites where Tmin was relatively high in December exhibited delayed leaf bud break, while sites with relatively high February Tmin exhibited earlier bud break. The stepwise regressions detected no significant effects of any monthly Tmin or precipitation on the DOY of flowers or flower buds, or of open flowers (thus statistical results not reported here).

March Tmin affected the onset of fruiting in blue elderberry; sites with relatively high March Tmin fruited early. Sites with high precipitation in January or February exhibited delayed fruit-ing, with January precipitation exhibiting a much stronger influence (based on regression coefficients: 18.05 vs. 3.03 and on F-ratios: 58.23 vs. 25.87, respectively; Table 5). The relationship between winter monthly Tmin and the DOY for ripe fruits differed dramatically between months. High Tmin in December and February were associated with earlier DOY (regression coefficients = −457.40 and −73.98, respectively); high Tmin in January was associated with delayed DOY (regression coefficient = 510.22). Similarly, the DOY for recent fruit drop was inconsistently affected by winter monthly Tmin. Sites with high December Tmin exhibited delayed fruit drop while sites with high March Tmin exhibited relatively early fruit drop. Sites with high March precipitation exhibited a small but significant advancement of fruit drop.

With the exception of leaf bud break, all blue elderberry phenophases appeared to be influenced by interactions between monthly Tmin and precipitation.

Eriogonum fasciculatum (California buckwheat).—The stepwise regression models explained 70–82% of the variation in the DOY of the phenophases reported here (Table 6). Vegetative phenology was strongly associated with precipitation only, while reproductive phenophases were associated with winter monthly mean Tmin, monthly precipitation, or both.

Sites where precipitation was relatively high in December or in March exhibited delayed young leaf production (Table 6). Sites with high March Tmin produced flowers or flower buds later than sites with cooler March conditions. High January precipitation appeared to advance flowering, while high February precipitation appeared to delay it. The relationship between winter monthly conditions and the timing of the appearance of fruits was significant only for February precipitation; sites with high February precipitation produced fruit slightly but significantly earlier than sites with low February precipitation. The DOY for the appearance of ripe fruits was associated only with March Tmin; sites with warmer March conditions ripened their fruits later than sites with cool March conditions. Winter rainfall influenced fruit ripening in California buckwheat only through its interaction with Tmin or precipitation in other months. With the exception of the DOY of young leaves,

Table 5. Summary of stepwise regressions to detect significant associations between the date of onset of vegetative and reproductive phenophases and winter monthly climatic parameters among monitored sites and years in *Sambucus nigra*. The Adj R^2 value is the proportion of variance in the DOY of the onset of a phenophase explained by the model, adjusted for the degrees of freedom; it provides an R^2 that is comparable across models that differ in the number of parameters. PPT refers to monthly precipitation; Tmin refers to mean monthly minimum daily temperature. Significant p-values ($\alpha < 0.05$) are shown in boldface; marginally non-significant p-values ($0.05 < p < 0.1$) are shown in italics.

Source	df	Sums of squares	F ratio	Regression coefficient	p-value	R^2	Adj R^2
Breaking leaf buds							
Tmin(December)	1	92814	30.18	49.42	**<0.0001**		
Tmin(February)	1	40908	13.30	−39.42	**0.0013**		
Tmin(March)	1	5691	1.85	−16.13	0.1864		
Tmin(Dec) × Tmin(Feb)	1	4075	1.33	10.33	0.2610		
Tmin(Dec) × Tmin(Mar)	1	6971	2.27	11.85	0.1452		
Tmin(Feb) × Tmin(Mar)	1	44053	14.32	−39.43	**0.0009**		
Tmin(Dec) × Tmin(Feb) × Tmin(Mar)	1	30483	9.91	−1.60	**0.0044**		
Model	7	254124	11.80		**<0.0001**		
Error	24	73813					
Total	31	327937				0.77	0.71
Fruits							
Tmin(March)	1	11998	14.59	−18.43	**0.0015**		
PPT(January)	1	47878	58.23	18.05	**<0.0001**		
PPT(February)	1	21275	25.87	3.03	**0.0001**		
Tmin(Mar) × PPT(Jan)	1	47546	57.82	9.51	**<0.0001**		
Tmin(Mar) × PPT(Feb)	1	22887	27.83	1.23	**<0.0001**		
PPT(Jan) × PPT(Feb)	1	13720	16.69	−0.28	**0.0009**		
Tmin(Mar) × PPT(Jan) × PPT(Feb)	1	28382	34.52	−0.36	**<0.0001**		
Model	7	172739	30.01		**<0.0001**		
Error	16	13156					
Total	23	185895				0.93	0.90
Ripe fruits							
Tmin(December)	1	28915	143.94	−457.40	**<0.0001**		
Tmin(January)	1	33126	164.91	510.22	**<0.0001**		
Tmin(February)	1	1258	6.26	−73.98	**0.0254**		
PPT(December)	1	33390	166.22	10.73	**<0.0001**		
Tmin(Dec) × Tmin(Jan)	1	21700	108.03	54.49	**<0.0001**		
Tmin(Dec) × PPT(Dec)	1	31044	154.54	−8.65	**<0.0001**		
Tmin(Jan) × PPT(Dec)	1	33287	165.71	8.51	**<0.0001**		
Tmin(Dec) × Tmin(Jan) × PPT(Dec)	1	12630	62.88	0.68	**<0.0001**		
Model	8	122336	76.13		**<0.0001**		
Error	14	2812					
Total	22	125148				0.98	0.96
Recent fruit drop							
Tmin(December)	1	5239	24.68	120.05	**0.0002**		
Tmin(March)	1	1164	5.48	−91.71	**0.0345**		
PPT(March)	1	1065	5.02	−3.00	**0.0418**		
Tmin(Dec) × Tmin(Mar)	1	9201	43.34	16.69	**<0.0001**		
Tmin(Dec) × PPT(Mar)	1	3755	17.69	1.89	**0.0009**		
Tmin(March) × PPT(Mar)	1	200	0.94	−0.69	0.3480		
Tmin(Dec) × Tmin(Mar) × PPT(Mar)	1	6807	32.06	0.68	**<0.0001**		
Model	7	76520	51.49		**<0.0001**		
Error	14	2972					
Total	21	79493				0.96	0.94

all phenophases appeared to be influenced by interactions between Tmin and precipitation.

DISCUSSION

The repeated monitoring of multiple individuals per species across several years and sites allowed us to detect variation in the timing of the onset of different phenophases that was due to phenotypic plasticity in response to environmental variation (including climate), age-based variation, and/or genetic variation among sites. The relationships between local environmental conditions and the DOY of phenophase onset presented here provide a baseline for the phenological behavior of four widespread, local-

Table 6. Summary of stepwise regressions to detect significant associations between the date of onset of vegetative and reproductive phenophases and winter monthly climatic parameters among monitored sites and years in *Eriogonum fasciculatum*. The Adj R^2 value is the proportion of variance in the DOY of the onset of a phenophase explained by the model, adjusted for the degrees of freedom; it provides an R^2 that is comparable across models that differ in the number of parameters. PPT refers to monthly precipitation; Tmin refers to mean monthly minimum daily temperature. Significant p-values ($\alpha < 0.05$) are shown in boldface; marginally non-significant p-values ($0.05 < p < 0.1$) are shown in italics.

Source	df	Sums of squares	F ratio	Regression coefficient	p-value	R^2	Adj R^2
Young leaves							
PPT(December)	1	64051	13.90	0.67	**0.0005**		
PPT(January)	1	13164	2.86	0.99	0.0975		
PPT(March)	1	308369	66.91	2.03	**<0.0001**		
PPT(Jan) × PPT(Mar)	1	198042	42.97	0.11	**<0.0001**		
Model	4	520518	28.23		**<0.0001**		
Error	48	221234					
Total	52	741752				0.70	0.68
Flowers or flower buds							
Tmin(March)	1	3301	10.88	11.44	**0.0026**		
PPT(January)	1	3000	9.89	−2.95	**0.0038**		
PPT(February)	1	3059	10.09	7.31	**0.0035**		
Tmin(Mar) × PPT(Jan)	1	261	0.86	−0.27	0.3608		
Tmin(Mar) × PPT(Feb)	1	4273	14.09	5.49	**0.0008**		
PPT(Jan) × PPT(Feb)	1	1149	3.79	0.22	*0.0613*		
Tmin(Mar) × PPT(Jan) × PPT(Feb)	1	3744	12.34	0.29	**0.0015**		
Model	7	32565	15.34		**<0.0001**		
Error	29	8797					
Total	36	41362				0.79	0.74
Fruits							
Tmin(March)	1	3776	3.62	5.10	*0.0657*		
PPT(January)	1	412	0.40	0.30	0.5338		
PPT(February)	1	5886	5.65	−1.28	**0.0234**		
Tmin(Mar) × PPT(Jan)	1	23008	22.08	0.83	**<0.0001**		
Model	4	97192	23.31		**<0.0001**		
Error	33	34394					
Total	37	131586				0.74	0.71
Ripe fruits							
Tmin(March)	1	8370	8.20	48.11	**0.0076**		
PPT(January)	1	1773	1.74	1.47	0.1974		
PPT(February)	1	650	0.64	2.60	0.4310		
Tmin(Mar) × PPT(Jan)	1	17971	17.62	2.00	**0.0002**		
Tmin(Mar) × PPT(Feb)	1	6027	5.91	5.97	**0.0213**		
PPT(Jan) × PPT(Feb)	1	1814	1.78	0.21	0.1924		
Tmin(Mar) × PPT(Jan) × PPT(Feb)	1	5411	5.30	0.26	**0.0284**		
Model	7	140773	19.71		**<0.0001**		
Error	30	30605					
Total	37	171377				0.82	0.78

ly and ecologically important plant species in California and demonstrate that frequent monitoring can detect associations between the DOY of phenophase onset and monthly temperatures and precipitation. For these species, the statistical effects of the most recent winter's monthly Tmin or precipitation on the phenophase onset dates reported here may be used with caution to predict their phenological responses to future changes in climatic conditions. However, the strong interactions among monthly conditions that contributed to the variation in onset dates were complex, making it difficult to predict phenological changes on the basis of individual monthly parameters alone. The reliability of the relationships reported here may be more fully realized (or challenged) by future monitoring of the same plants or sites following a longer period of climate variability. Moreover, phenological observations from the present may be compared to those recorded in the future in order to detect the longer-term effects of ongoing climate change and variability on the timing and abundance of seasonal resources on which many animals depend for food, shade, or shelter.

Within the timeframe of this study, we

detected phenological variation among sites and years that was strongly associated with site-specific monthly winter minimum temperatures or precipitation. While the use of monthly parameters (vs. a moving window of climatic conditions prior to each onset date, or the selection of a duration other than one month) as independent variables is somewhat arbitrary (Cook et al. 2012b), it allows consistent comparisons between species and phenophases. Among the four California woody taxa studied here, for which the growing season was likely to have been more water- than temperature-limited at most sites (except, perhaps, at Redwood National and State Parks), phenological onset dates of vegetative traits (bud break or young leaves) tended to be more sensitive to variation in precipitation than in temperature (except for *Sambucus nigra*). In all four species, phenophases differed with respect to their sensitivity to individual monthly conditions (Tables 3–6). Moreover, within species, the associations between monthly Tmin or precipitation and phenological onset dates often differed qualitatively among months. These patterns could not have been detected by an analysis of mean annual (or winter) temperatures or of cumulative annual rainfall. A better understanding of how phenology responds to the *timing* of winter precipitation and temperature may allow more sophisticated predictions of how these species will respond to future climate change, which is unlikely to affect all winter months equally.

Overall, winter conditions accounted for greater variation in the onset of vegetative and reproductive phenophases in *Q. lobata, S. nigra, and E. fasciculatum* than in *B. pilularis*; see R^2 values for the regressions (Tables 3–6). Winter conditions may have a weaker biological effect on the relatively late-flowering *B. pilularis*, but the variation among taxa in the R^2 values of the regression models may also reflect variation in the ability of observers to unambiguously detect phenophase transitions in these species.

Variation among phenophases and species in their sensitivity to mean winter monthly Tmin

Although *B. pilularis* flowers in late summer, the onset of its reproductive and vegetative phenophases was associated with conditions during the previous winter months. Pollen release appeared to respond to warm winter conditions differently than fruit ripening, suggesting that there may be gender-specific responses to variation in climate in this dioecious species. If the accelerating effects on pollen release of high March Tmin are not mirrored by similar effects on female flower development, then pollen dispersal may occur too early to ensure successful pollination. Given that the genders of many dioecious species differ physiologically (Dudley and Galen 2007, Isogimi et al. 2011, Alvarez-Cansino et al. 2012, Montesinos et al. 2012, Chen et al. 2014, Cruz Diaz-Barradas et al. 2014, Zhang et al. 2014), gender-specific phenological responses to climate change may be common and represent a type of phenological disruption that merits further investigation.

In all four species, one or more phenophases appeared to respond to higher winter Tmin with a delayed onset date. In *B. pilularis*, high January Tmin was associated with delayed flowering, pollen release, and fruit ripening (Table 3). In *Q. lobata*, high March Tmin was associated with delayed breaking leaf buds; high January Tmin was associated with delayed pollen release; and high December Tmin was associated with delayed fruit drop (Table 4). In *S. nigra*, high December Tmin was associated with delayed vegetative budbreak and fruit drop, while high January Tmin was associated with delayed fruit ripening (Table 5). In *E. fasciculatum*, high March Tmin was associated with delayed leaf production, flowering, fruiting ($P > 0.0657$), and fruit ripening (Table 6).

Associations between warmer autumn or winter conditions and subsequent phenological delays might be due to a vernalization requirement (Menzel et al. 2006); in the absence of a sufficient winter chill, some species may not receive the cue necessary to promote early spring growth and reproduction. The associations between winter warmth and delayed phenology observed here contrasts with the patterns reported in a comprehensive meta-analysis of 542 species in Europe (Menzel et al. 2006), in which 30% of the spring onset dates significantly advanced from 1971 to 2000 (corresponding to temporal increases in winter/spring temperature), while only 3% of the records reflect significant phenological delays. Whether the

influence on phenology of warming winters differs qualitatively between water-limited and temperature-driven ecosystems remains an open question.

In two of the four species analyzed here, warm winter conditions were—for some phenophases—associated with earlier onset dates, as is commonly found in temperate zone ecosystems (Menzel et al. 2006, Cook et al. 2012b, Mazer et al. 2013). In *B. pilularis*, sites with higher December Tmin started to flower, to release pollen, and to ripen fruits earlier than sites with low December Tmin (Table 3). In *S. nigra*, sites with higher February Tmin exhibited relatively early vegetative bud break, and sites with higher March Tmin produced fruits relatively early. In addition, in *S. nigra*, sites with relatively high December and February Tmin ripened their fruits relatively early, and sites with warm March conditions exhibited earlier fruit drop than sites with low March Tmin. In neither *Q. lobata* nor *E. fasciculatum* did we detect a phenophase that appeared to respond to warmer winter Tmin with an earlier onset date.

The two deciduous species examined here—*Q. lobata and S. nigra*—exhibited strong associations between Tmin and vegetative bud break, although the sign of the relationship changed from month to month in *S. nigra*. By contrast, the evergreen species (*B. pilularis* and *E. fasciculatum*) exhibited no sensitivity of leaf production to winter month Tmin; the production of new leaves in these evergreen taxa was strongly associated with winter precipitation. This difference between deciduous and evergreen taxa contrasts with the pattern detected by de Oliveira et al. (2015), who examined vegetative phenological responses to seasonal rainfall in a semi-arid environment (Pentecoste, Céara, in northeast Brazil) among 22 species representing four functional groups (evergreen/high density wood; evergreen/low density wood; deciduous/high density; deciduous/low density). In the Brazilian sample, the vegetative phenology of the evergreen species was independent of rainfall, while the responses of the deciduous species depended strongly on their wood density (de Oliveira et al. 2015). Clearly, understanding the mechanistic basis for the interspecific variation in phenological responses observed among the California taxa reported here will require a larger sample size and the simultaneous examination of other functional traits.

Variation among phenophases and species in their sensitivity to monthly precipitation

Similar to Tmin, the effects of winter precipitation differed among species and phenophases. In *B. pilularis*, high February precipitation was associated with the delayed appearance of young leaves and pollen release; and high December or January precipitation was associated with late flowering or fruit ripening. By contrast, high December precipitation was associated with early pollen release, and high March precipitation with early pollen release and early fruit ripening.

In *Q. lobata*, winter rainfall influenced the timing of vegetative bud break, but the direction of its effect differed among months. High rainfall in December and March was associated with delayed bud break while high rainfall in February advanced bud break. The onset of flowering in *Q. lobata* was also associated with winter precipitation; high precipitation in either January or March was coupled with earlier flowering, while high precipitation in March was associated with earlier pollen release.

In *S. nigra*, the onset of leaf production was apparently insensitive to winter precipitation. This species also has a much wider geographic distribution (partly due to its widespread introduction and cultivation throughout the world; Kabuce and Priede 2006) than the other three taxa, and may not have evolved in a highly water-limited ecosystem. Nevertheless, high precipitation was associated with delayed fruiting and ripening in this species (Table 5).

The effects of precipitation on *E. fasciculatum* similarly differed among phenophases. The appearance of young leaves in California buckwheat appeared to be delayed by high December and March precipitation. Early flowering was associated with high January precipitation but low February precipitation, and early fruiting was associated with high February precipitation.

Other studies conducted in water-limited ecosystems of the North American southwest have found a strong link between winter precipitation and plant phenology (Beatley 1974, Bowers and Dimmit 1994, Crimmins et al. 2010), and Crimmins et al. (2010) found that

increases in autumn precipitation were associated with earlier onset dates. However, the role of interactions between temperature and precipitation or between the conditions in successive months, as documented here, have not been well characterized. Future work on the mechanistic nature of these interactions will greatly improve the ability of models to predict plant and ecosystem responses to future climate change.

Collectively, these results have implications for climate scenario planning in water-limited regions. Predicted changes in the timing and magnitude of precipitation (i.e., larger but more infrequent events) are likely to have a strong effect on phenological patterns, which will ultimately affect population dynamics, species interactions, and ecosystem processes (e.g., carbon cycling). Currently, many phenological forecast models are based primarily on predicted changes in temperature, often using phenological data from temperate ecosystems (e.g., Jeong et al. 2013, Euskirchen et al. 2014, Jeong and Medvigy 2014). Thus, we see an opportunity for increased research on the consequences of phenological change driven by multiple climatic drivers—and their interactions—in a greater diversity of ecosystems (Diez et al. 2014).

Strengths and limitations of the current study

The detection of the statistical associations shown here depended on the proficiency of the California Phenology Project to engage and to train park staff and members of the public to contribute standardized phenological data to the nationwide database managed by the USA-NPN. Phenological monitoring at a frequency of two times per week was sufficient to detect phenological differences associated with climate among species, sites, and years. Moreover, the wide geographic (and climatic) sampling achieved here was sufficient to distinguish statistically independent effects of minimum monthly temperatures and cumulative precipitation on the mean onset dates of targeted phenophases among sites.

Most long-term studies conducted to date in the U.S. did not comprise frequent monitoring of the same individuals, but instead detected onset dates by surveying at the community or population level (e.g., Fitter et al. 1995, Bradley et al. 1999, Menzel 2000, Abu-Asab et al. 2001, Fitter

and Fitter 2002, Ahas and Aasa 2006, Menzel et al. 2006, Zhang et al. 2007, Cook et al. 2008, 2012a, 2012b, Gordo and Sanz 2009, 2010, Travers et al. 2009, Amano et al. 2010, Beaubien and Hamann 2011, Wolkovich et al. 2012; see Bertin 2008 for other examples). The onset dates reported in these studies may be biased towards early values because it is the first onset date exhibited by *any* plant that is reported, not the first onset date for the "average" plant.

Implications for nationwide monitoring in public lands

The California Phenology Project and similar efforts, such as those led by the NPS Northeast Temperate Network (Tierney et al. 2013) and the Appalachian Trail Seasons project (https://www. usanpn.org/appalachian), can serve as models for protected areas across the U.S. to engage in coordinated phenological monitoring at large geographic scales, using standardized protocols and targeted "indicator" species. The frequent monitoring of hundreds of plants across a wide geographic area can capture more variation in a short period in monthly temperature and precipitation than monitoring conducted at single locations. This broad sampling can, in turn, lead to the rapid detection of associations between climatic conditions and the onset of vegetative and reproductive phenophases, facilitating predictions of the effects of longer-term *temporal* variation in climate on phenology.

Standardized phenological data can be useful to natural resource managers for a variety of applications, including planning for the timing of critical activities (such as fire management and invasive species control) as well as climate response planning (e.g., generating predictive models and vulnerability assessments) (Enquist et al. 2014). The results presented here demonstrate the complexity of plant phenological responses to climate, providing fundamental information that may be of use to resource managers. Engaging park staff and visitors in phenological monitoring, however, may also help to fulfill a major goal of the national parks: to address the effects of climate change on each park's natural resources (Jarvis 2011). Phenological monitoring in national parks offers a way for staff to share with visitors the sensitivity of their park's flora and fauna to local environmental

conditions, and provides a shared research and education focus for interpreters, resource managers, and outdoor educators.

LITERATURE CITED

Abu-Asab, M. S., P. M. Peterson, S. G. Shetler, and S. S. Orli. 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodiversity and Conservation 10:597–612.

Ahas, R., and A. Aasa. 2006. The effects of climate change on the phenology of selected Estonian plant, bird and fish populations. International Journal of Biometeorology 51:17–26.

Alvarez-Cansino, L., M. C. D. Barradas, M. Zunzunegui, M. P. Esquivias, and T. E. Dawson. 2012. Gender-specific variation in physiology in the dioecious shrub *Corema album* throughout its distributional range. Functional Plant Biology 39:968–978.

Amano, T., R. J. Smithers, T. H. Sparks, and W. J. Sutherland. 2010. A 250-year index of first flowering dates and its response to temperature changes. Proceedings of the Royal Society B 277:2451–2457.

Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave desert ecosystems. Ecology 55:856–863.

Beaubien, E., and A. Hamann. 2011. Spring flowering response to climate change between 1936 and 2006 in Alberta, Canada. BioScience 61:514–524.

Bertin, R. I. 2008. Plant phenology and distribution in relation to recent climate change. Journal of the Torrey Botanical Society 135:126–146.

Bowers, J. E., and M. A. Dimmitt. 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. Bulletin of the Torrey Botanical Club 121:215–229.

Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in Wisconsin. Proceedings of the National Academy of Sciences 96:9701–9704.

Chen, J., B. L. Duan, M. L. Wang, H. Korpelainen, and C. Y. Li. 2014. Intra- and inter-sexual competition of *Populus cathayana* under different watering regimes. Functional Ecology 28:124–136.

Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. Ecology 93:1765–1771.

Cook, B. I., E. R. Cook, P. C. Huth, J. E. Thompson, A. Forster, and D. Smiley. 2008. A cross-taxa phenological dataset from Mohonk Lake, NY and its relationship to climate. International Journal of Climatology 28:1369–1383.

Cook, B. I., E. M. Wolkovich, and C. Parmesan. 2012*a*. Divergent responses to spring and winter warming drive community level flowering trends. Proceedings of the National Academy of Sciences 109:9000–9005.

Cook, B. I., et al. 2012*b*. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. Ecosystems 15:1283–1294.

Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2010. Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. Journal of Ecology 98:1042–1051.

Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2011. Onset of summer flowering in a 'Sky Island'

is driven by monsoon moisture. New Phytologist 191:468–479.

Cruz Diaz-Barradas, M., M. Zunzunegui, M. Collantes, L. Alvarez-Cansino, and F. G. Novo. 2014. Gender-related traits in the dioecious shrub *Empetrum rubrum* in two plant communities, in the Magellanic steppe. Acta Oecologica 60:40–48.

Davies, T. J., et al. 2013. Phylogenetic conservatism in plant phenology. Journal of Ecology 101:1520–1530.

Davis, C. C., C. G. Willis, R. B. Primack, and A. J. Miller-Rushing. 2010. The importance of phylogeny to the study of phenological response to global climate change. Philosophical Transactions of the Royal Society B. 365:3201–3213.

Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. F. Enquist, P. Guertin, A. H. Rosemartin, M. D. Schwartz, K. A. Thomas, and J. F. Weltzin. 2014. Standardized phenology monitoring methods to track plants and animal activity for science and resource management applications. International Journal of Biometeorology 58:591–601.

de Oliveira, C. C., R. B. Zandavalli, A. L. Alves de Lima, and M. J. Nogueira Rodal. 2015. Functional groups of woody species in semi-arid regions at low latitudes. Austral Ecology 40:40–49.

Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen, and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. Ecology Letters 15:545–553.

Diez, J. M., I. Ibanez, J. A. Silander, R. B. Primack, H. Higuchi, H. Kobori, A. Sen, and T. Y. James. 2014. Beyond seasonal climate: statistical estimation of phenological responses to weather, 1793–1802. Ecological Applications 24:7.

Dudley, L. S. and C. Galen. 2007. Stage-dependent patterns of drought tolerance and gas exchange vary between sexes in the alpine willow, *Salix glauca*. Oecologia 143:1–9.

Dunnell, K. L., and S. E. Travers. 2011. Shifts in the flowering phenology of the Northern Great Plains: patterns over 100 years. American Journal of Botany 98:935–945.

Easterling, D. R., B. Horton, P. D. Jones, T. C. Peterson, T. R. Karl, D. E. Parker, M. J. Salinger, V. Razuvayev, N. Plummer, P. Jamason, and C. K. Folland. 1997. Maximum and minimum temperature trends for the globe. Science 277:364–367.

Enquist, C. A. F., J. L. Kellermann, K. L. Gerst, and A. J. Miller-Rushing. 2014. Phenology research for natural resource management in the United States. International Journal of Biometeorology 58:579–589.

Euskirchen, E. S., T. B. Carman, and A. D. McGuire. 2014. Changes in the structure and function of northern Alaskan ecosystems when considering variable leaf-out times across groupings of species in a dynamic vegetation model. Global Change Biology, 20:963–978.

Fitter, A. H., and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. Science 296:1689–1691.

Fitter, A. H., R. S. R. Fitter, I. T. B. Harris, and M. H. Williamson. 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. Functional Ecology 9:55–60.

Gordo, O., and J. J. Sanz. 2009. Long-term temporal changes of plant phenology in the Western Mediterranean. Global Change Biology 15:1930–1948.

Gordo, O., and J. J. Sanz. 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. Global Change Biology 16:1082–1106.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Isogimi, T., M. Matsushita, Y. Watanabe, and M. Nakagawa. 2011. Sexual differences in physiological integration in the dioecious shrub *Lindera triloba*: a field experiment using girdling manipulation. Annals of Botany 107:1029–1037.

Jarvis, J. 2011. A call to action: preparing for a second century of stewardship and engagement. National Park Service, U.S. Department of the Interior, Washington, D.C., USA.

Jeong, S.-J., D. Medvigy, E. Shevliakova, and S. Malyshev. 2013. Predicting changes in temperate forest budburst using continental-scale observations and models. Geophysical Research Letters 40:359–364.

Jeong, S.-J., and D. Medvigy. 2014. Macroscale prediction of autumn leaf coloration throughout the continental United States. Global Ecology and Biogeography 23:1245–1254.

Kabuce, N., and N. Priede. 2006. NOBANIS—Invasive alien species fact sheet—*Sambucus nigra*. www.nobanis.org

Karl, T. R., P. D. Jones, R. W. Knight, G. Kukla, N. Plummer, V. Razuvayev, K. P. Gallo, J. Lindseay, R. J. Charlson, and T. C. Peterson. 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. Bulletin of the American Meteorological Society 74:1007–1023.

Lu, P., Q. Yu, J. Liu, and X. Le. 2006. Advance of tree-flowering dates in response to urban climate change. Agricultural and Forest Meteorology 138:120–131.

Matthews, E. R., K. L. Gerst, S. J. Mazer, C. Brigham, A. Evenden, A. Forrestel, B. Haggerty, S. Haultain, J. Hoines, S. Samuels, and F. Villalba. 2013. California Phenology Project: Report on pilot phase activities,

2010-2013. Natural Resource Report NPS/PWRO/NRR—2013/743. National Park Service, Fort Collins, Colorado, USA.

Matthews, E. R., K. L. Gerst, S. J. Mazer, C. Brigham, A. Evenden, A. Forrestel, B. Haggerty, S. Haultain, J. Hoines, S. F. Samuels, and F. Villalba. 2014. California Phenology Project (CPP) plant phenological monitoring protocol: Version 1. Natural Resource Report. NPS/PWR/NRR—2014/763. National Park Service, Fort Collins, Colorado, USA.

Mazer, S. J., S. E. Travers, B. I. Cook, T. J. Davies, K. Bolmgren, N. J. B. Kraft, N. Salamin, and D. W. Inouye. 2013. Flowering date of taxonomic families predicts phenological sensitivity to temperature: implications for forecasting the effects of climate change on unstudied taxa. American Journal of Botany 100:1–17.

McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. Ecology 93:1987–1993.

Menzel, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. International Journal of Biometeorology 44:76–81.

Menzel, A., et al. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969–1976.

Miller-Rushing, A. J., D. W. Inouye, and R. B. Primack. 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. Journal of Ecology 96:1289–1296.

Montesinos, D., P. Villar-Salvador, P. Garcia-Fayos, and M. Verdu. 2012. Genders in *Juniperus thurifera* have different functional responses to variations in nutrient availability. New Phytologist 193:705–712.

Munguía-Rosas, M. A., J. Ollerton, V. Parra-Tabla, and J. Arturo De-Nova. 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favored. Ecology Letters 14:511–521.

Polgar, C., et al. 2013. Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau's Concord. New Phytologist 202:106–115.

Richardson, A. D., et al. 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. Philosophical Transactions of the Royal Society B 365:3227–3246.

Schwartz, M. D., J. L. Betancourt, and J. F. Weltzin. 2012. From Caprio's lilacs to the USA National Phenology Network. Frontiers in Ecology and the Environment 10:324–327.

Tierney, G., et al. 2013. Phenology monitoring protocol: Northeast Temperate Network. Natural Resource Report. NPS/NETN/NRR—2013/681. National Phenology Network, Fort Collins, Colorado, USA.

Travers, S. E., K. L. Dunnell, and W. K. Michener. 2009. First-flowering dates of plants in the Northern Great Plains. Ecology 90:2332.

USA National Phenology Network. 2014. Plant phenology data for the United States, 2009-2013. USA-NPN, Tucson, Arizona, USA.

Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species' success in Thoreau's woods. PLoS ONE 5:e8878.

Wolkovich, E. M., et al. 2012. Experimental warming underestimates plant responses to climate warming. Nature 485:494–497.

Zhang, S., H. Jiang, H. X. Zhao, H. Korpelainen, and C. Y. Li. 2014. Sexually different physiological responses of *Populus cathayana* to nitrogen and phosphorus deficiencies. Tree Physiology 34:343–354.

Zhang, X., D. Tarpley, and J. T. Sullivan. 2007. Diverse responses of vegetation phenology to a warming climate. Geophysical Research Letters 34:L19405.

SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Summary of monthly and annual precipitation (PPT, mm), mean monthly and annual minimum temperature (Tmin, °C), and departures from 30-year normals (1971–2000) for the years of phenological monitoring conducted by the CPP included in this study. At each park or reserve included in this study, one or two locations were selected for comparison to 30-year normals, using data downloaded from the PRISM database.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
Redwood National and State Parks–Kuchel Visitor Center (124.092 W, 41.287 N)					
PPT (monthly totals, mm)					
January	81.41	256.16	103.18	65.70	221.82
February	134.47	102.23	48.38	232.97	204.00
March	375.80	409.42	94.01	239.11	207.67
April	158.61	175.64	77.16	63.97	109.07
May	51.41	37.88	57.88	49.02	71.20
June	42.56	83.51	27.95	17.54	27.42
July	6.15	23.47	0.00	0.11	6.59
August	1.50	1.27	0.72	0.00	12.86
September	6.44	0.03	123.47	81.00	31.30
October	111.66	109.97	1.70		93.33
November	143.61	287.47	59.83		217.30
December	93.37	344.33	32.15		227.08
Annual total PPT	**1206.99**	**1831.38**	**626.43**	**749.42**	**1429.64**
Tmin (monthly means, °C)					
January	5.11	6.17	3.02	5.26	**3.89**
February	3.60	5.59	3.06	6.67	4.78
March	6.53	4.84	5.34	7.42	5.25
April	5.73	7.11	6.59	7.00	5.87
May	7.09	6.92	8.02	9.53	7.46
June	9.85	8.71	9.85	9.55	9.42
July	10.48	10.78	10.78	11.65	10.88
August	11.15	10.75	11.25	11.89	10.91
September	11.07	8.27	11.07	11.31	9.61
October	10.96	8.85	6.44		7.67
November	2.71	8.35	5.69		5.75
December	6.07	5.44	2.59		3.74
Mean monthly Tmin	**7.53**	**7.65**	**6.98**	**8.92**	**7.10**
Departures from PPT normals (mm)					
January	−140.41	34.34	−118.64	−156.12	
February	−69.53	−101.77	−155.62	28.97	
March	168.13	201.75	−113.66	31.44	
April	49.54	66.57	−31.91	−45.10	
May	−19.79	−33.32	−13.32	−22.18	
June	15.14	56.09	0.53	−9.88	
July	−0.44	16.88	−6.59	−6.48	
August	−11.36	−11.59	−12.14	−12.86	
September	−24.86	−31.27	92.17	49.70	
October	18.33	16.64	−91.63		
November	−73.69	70.17	−157.47		
December	−133.71	117.25	−194.93		
Annual PPT	**−222.65**	**401.74**	**−803.21**	**−142.51**	
Summary of difference†	2011 drier than normal	2012 wetter than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	1.22	2.28	−0.87	1.37	
February	−1.18	0.81	−1.72	1.89	
March	1.28	−0.41	0.09	2.17	
April	−0.14	1.24	0.72	1.13	
May	−0.37	−0.54	0.56	2.07	
June	0.43	−0.71	0.43	0.13	
July	−0.40	−0.10	−0.10	0.77	

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
August	0.24	−0.16	0.34	0.98	
September	1.46	−1.34	1.46	1.70	
October	3.29	1.18	−1.23		
November	−3.04	2.60	−0.06		
December	2.33	1.70	−1.15		
Annual mean monthly Tmin	**0.43**	**0.55**	**−0.13**	**1.36**	
Summary of difference†	2011 warmer than normal	2012 warmer than normal	2013 cooler than normal	2014 warmer than normal	
Golden Gate NRA–Old Bunker Road (122.534 W, 37.833 N)					
PPT (monthly totals, mm)					
January	39.79	90.01	14.57	3.09	143.59
February	129.55	27.75	15.77	187.44	136.46
March	208.80	187.80	22.39	78.31	111.30
April	17.34	76.88	33.54	63.54	40.54
May	34.04	2.66	2.81	2.06	20.21
June	62.49	3.72	12.39	0.00	4.89
July	1.00	0.50	0.00	2.31	1.64
August	0.18	0.00	2.42	0.41	3.42
September	1.15	0.00	19.72	14.18	10.57
October	43.58	36.84	0.00		38.81
November	50.56	151.17	33.65		112.44
December	5.36	259.20	12.89		101.96
Annual total PPT	**593.84**	**836.53**	**170.15**	**351.34**	**725.83**
Tmin (monthly means, °C)					
January	6.88	6.71	5.96	7.86	6.20
February	6.23	7.32	6.57	8.93	7.48
March	8.11	7.44	7.63	9.90	8.07
April	8.75	9.17	8.98	9.14	8.73
May	9.03	9.63	10.05	11.47	9.99
June	9.93	9.81	11.72	11.10	11.37
July	11.60	11.35	12.03	13.39	12.25
August	11.53	11.51	13.09	13.78	12.70
September	12.18	10.81	13.21	14.69	12.64
October	12.39	12.14	10.47		11.11
November	8.48	10.61	9.72		8.56
December	6.11	8.22	5.51		6.20
Mean monthly Tmin	**9.27**	**9.56**	**9.58**	**11.14**	**9.61**
Departures from PPT normals (mm)					
January	−103.80	−53.58	−129.02	−140.50	
February	−6.91	−108.71	−120.69	50.98	
March	97.50	76.50	−88.91	−32.99	
April	−23.20	36.34	−7.00	23.00	
May	13.83	−17.55	−17.40	−18.15	
June	57.60	−1.17	7.50	−4.89	
July	−0.64	−1.14	−1.64	0.67	
August	−3.24	−3.42	−1.00	−3.01	
September	−9.42	−10.57	9.15	3.61	
October	4.77	−1.97	−38.81		
November	−61.88	38.73	−78.79		
December	−96.60	157.24	−89.07		
Annual PPT	**−131.99**	**110.70**	**−555.68**	**−121.28**	
Summary of difference†	2011 drier than normal	2012 wetter than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	0.68	0.51	−0.24	1.66	
February	−1.25	−0.16	−0.91	1.45	
March	0.04	−0.63	−0.44	1.83	
April	0.02	0.44	0.25	0.41	
May	−0.96	−0.36	0.06	1.48	
June	−1.44	−1.56	0.35	−0.27	
July	−0.65	−0.90	−0.22	1.14	
August	−1.17	−1.19	0.39	1.08	
September	−0.46	−1.83	0.57	2.05	
October	1.28	1.03	−0.64		
November	−0.08	2.05	1.16		
December	−0.09	2.02	−0.69		

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
Annual mean monthly Tmin	**−0.34**	**−0.05**	**−0.03**	**1.20**	
Summary of difference†	2011 cooler than normal	2012 cooler than normal	2013 cooler than normal	2014 warmer than normal	
Lassen Volcanic National Park–Manzanita Lake (121.577 W, 40.544 N)					
PPT (monthly totals, mm)					
January	34.06	107.11	26.43	16.12	148.64
February	58.15	24.75	17.31	175.16	147.53
March	254.88	270.10	67.61	282.66	151.13
April	130.67	129.64	53.43	55.86	84.60
May	187.25	54.90	83.97	41.09	73.26
June	69.66	38.65	41.09	30.40	41.01
July	0.00	0.00	7.69	3.51	10.99
August	0.00	0.79	9.81	21.14	16.90
September	5.69	0.00	29.00	49.84	40.15
October	70.01	51.95	28.47		78.35
November	79.97	221.74	51.88		136.55
December	12.93	253.78	15.32		129.48
Annual total PPT	**903.27**	**1153.41**	**432.01**	**675.78**	**1058.59**
Tmin (monthly means, °C)					
January	−4.26	−4.78	−6.63	−2.57	−6.05
February	−6.44	−4.98	−5.53	−3.61	−5.36
March	−3.91	−4.34	−3.10	−2.15	−4.58
April	−3.20	−2.00	−0.34	−1.47	−2.74
May	−0.82	1.32	2.03	1.97	0.65
June	3.30	3.67	5.82	5.01	4.57
July	5.67	5.73	8.97	9.48	7.04
August	5.82	7.92	6.53	8.10	6.57
September	5.94	5.55	4.46	6.71	4.86
October	0.91	1.25	−0.61		0.65
November	−3.95	−1.70	−2.38		−3.75
December	−4.53	−6.57	−5.96		−5.65
Mean monthly Tmin	**−0.46**	**0.09**	**0.27**		**−0.32**
Departures from PPT normals (mm)					
January	−114.58	−41.53	−122.21	−132.52	
February	−89.38	−122.78	−130.22	27.63	
March	103.75	118.97	−83.52	131.53	
April	46.07	45.04	−31.17	−28.74	
May	113.99	−18.36	10.71	−32.17	
June	28.65	−2.36	0.08	−10.61	
July	−10.99	−10.99	−3.30	−7.48	
August	−16.90	−16.11	−7.09	4.24	
September	−34.46	−40.15	−11.15	9.69	
October	−8.34	−26.40	−49.88		
November	−56.58	85.19	−84.67		
December	−116.55	124.30	−114.16		
Annual PPT	**−155.32**	**94.82**	**−626.58**	**−38.43**	
Summary of difference†	2011 drier than normal	2012 wetter than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	1.79	1.27	−0.58	3.48	
February	−1.08	0.38	−0.17	1.75	
March	0.67	0.24	1.48	2.43	
April	−0.46	0.74	2.40	1.27	
May	−1.47	0.67	1.38	1.32	
June	−1.27	−0.90	1.25	0.44	
July	−1.37	−1.31	1.93	2.44	
August	−0.75	1.35	−0.04	1.53	
September	1.08	0.69	−0.40	1.85	
October	0.26	0.60	−1.26		
November	−0.20	2.05	1.37		
December	1.12	−0.92	−0.31		
Annual mean monthly Tmin	**−0.14**	**0.41**	**0.59**	**1.83**	
Summary of difference†	2011 cooler than normal	2012 warmer than normal	2013 warmer than normal	2014 warmer than normal	

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
Sequoia and Kings Canyon National Parks–Lower Kaweah Air Quality Station (118.778 W, 36.566 N)					
PPT (monthly totals, mm)					
January	88.90	187.30	55.79	32.25	213.74
February	156.03	53.09	27.07	101.94	196.60
March	339.13	148.72	31.52	114.23	202.21
April	60.04	165.41	27.89	103.26	83.09
May	110.59	3.27	31.18	35.00	41.38
June	46.77	3.25	0.00	0.00	20.44
July	39.95	0.00	6.61	2.86	5.82
August	12.32	0.03	3.90	2.23	7.23
September	30.56	0.00	4.92	17.27	29.11
October	106.94	27.67	35.54		51.26
November	57.88	82.48	15.78		110.63
December	0.00	261.73	28.09		143.84
Annual total PPT	**1049.11**	**932.95**	**268.29**	**409.04**	**1105.35**
Tmin (monthly means, °C)					
January	−2.85	−1.36	−6.17	−0.01	−1.73
February	−5.82	−3.50	−4.98	−1.74	−2.02
March	−3.33	−2.64	−0.05	−0.40	−1.30
April	−0.68	0.47	1.67	1.21	0.38
May	1.00	5.63	5.01	4.61	4.07
June	6.32	7.67	9.46	10.72	8.76
July	11.72	11.60	13.78	13.23	11.67
August	13.27	14.97	11.10	12.14	11.47
September	12.13	12.38	8.92	10.52	9.40
October	7.05	6.67	3.08		5.35
November	−0.38	2.05	1.08		0.69
December	−1.59	−4.34	−1.07		−1.71
Mean monthly Tmin	**3.07**	**4.13**	**3.49**		**3.75**
Departures from PPT normals (mm)					
January	−124.84	−26.44	−157.95	−181.49	
February	−40.57	−143.51	−169.53	−94.66	
March	136.92	−53.49	−170.69	−87.98	
April	−23.05	82.32	−55.20	20.17	
May	69.21	−38.11	−10.20	−6.38	
June	26.33	−17.19	−20.44	−20.44	
July	34.13	−5.82	0.79	−2.96	
August	5.09	−7.20	−3.33	−5.00	
September	1.45	−29.11	−24.19	−11.84	
October	55.68	−23.59	−15.72		
November	−52.75	−28.15	−94.85		
December	−143.84	117.89	−115.75		
Annual PPT	**−56.24**	**−172.40**	**−837.06**	**−390.58**	
Summary of difference†	2011 drier than normal	2012 drier than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	−1.12	0.37	−4.44	1.72	
February	−3.80	−1.48	−2.96	0.28	
March	−2.03	−1.34	1.25	0.90	
April	−1.06	0.09	1.29	0.83	
May	−3.07	1.56	0.94	0.54	
June	−2.44	−1.09	0.70	1.96	
July	0.05	−0.07	2.11	1.56	
August	1.80	3.50	−0.37	0.67	
September	2.73	2.98	−0.48	1.12	
October	1.70	1.32	−2.27		
November	−1.07	1.36	0.39		
December	0.12	−2.63	0.64		
Annual mean monthly Tmin	**−0.68**	**0.38**	**−0.27**	**1.06**	
Summary of difference†	2011 cooler than normal	2012 warmer than normal	2013 cooler than normal	2014 warmer than normal	
Sequoia and Kings Canyon National Parks–Foothill Visitor Center (118.825 W, 36.491)					
PPT (monthly totals, mm)					
January	52.88	115.97	42.00	17.03	125.70
February	112.02	40.34	31.53	73.23	119.60
March	203.80	123.15	25.32	62.50	125.76

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
April	21.39	125.01	14.69	60.20	53.70
May	52.24	1.57	10.36	16.27	26.83
June	24.80	1.67	0.00	0.00	10.96
July	1.59	0.00	3.96	0.83	2.92
August	6.38	0.00	4.28	0.00	2.96
September	4.57	0.00	1.70	13.07	16.91
October	72.66	38.93	17.45		35.71
November	40.25	41.70	17.80		70.80
December	0.00	176.49	16.87		79.78
Annual total PPT	**592.58**	**664.83**	**185.96**		**671.63**
Tmin (monthly means, °C)					
January	3.60	5.15	2.41	6.21	2.31
February	1.04	3.45	3.24	5.75	3.90
March	3.36	4.42	6.73	6.40	5.32
April	5.86	6.32	8.52	8.10	7.29
May	7.38	11.52	12.09	11.84	11.08
June	12.34	14.77	16.53	16.65	15.50
July	17.44	18.48	21.29	20.80	19.06
August	18.65	21.38	19.12	19.17	18.69
September	18.09	18.95	16.22	17.48	15.35
October	13.22	12.89	11.06		10.62
November	6.32	8.14	7.80		5.26
December	3.11	3.68	3.97		2.33
Mean monthly Tmin	**9.20**	**10.76**	**10.75**		**9.73**
Departures from PPT normals (mm)					
January	−72.82	−9.73	−83.70	−108.67	
February	−7.58	−79.26	−88.07	−46.37	
March	78.04	−2.61	−100.44	−63.26	
April	−32.31	71.31	−39.01	6.50	
May	25.41	−25.26	−16.47	−10.56	
June	13.84	−9.29	−10.96	−10.96	
July	−1.33	−2.92	1.04	−2.09	
August	3.42	−2.96	1.32	−2.96	
September	−12.34	−16.91	−15.21	−3.84	
October	36.95	3.22	−18.26		
November	−30.55	−29.10	−53.00		
December	−79.78	96.71	−62.91		
Annual PPT	**−79.05**	**−6.80**	**−485.67**	**−242.21**	
Summary of difference†	2011 drier than normal	2012 drier than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	1.29	2.84	0.10	3.90	
February	−2.86	−0.45	−0.66	1.85	
March	−1.96	−0.90	1.41	1.08	
April	−1.43	−0.97	1.23	0.81	
May	−3.70	0.44	1.01	0.76	
June	−3.16	−0.73	1.03	1.15	
July	−1.62	−0.58	2.23	1.74	
August	−0.04	2.69	0.43	0.48	
September	2.74	3.60	0.87	2.13	
October	2.60	2.27	0.44		
November	1.06	2.88	2.54		
December	0.78	1.35	1.64		
Annual mean monthly Tmin	**−0.53**	**1.04**	**1.02**	**1.54**	
Summary of difference†	2011 cooler than normal	2012 warmer than normal	2013 warmer than normal	2014 warmer than normal	
Santa Monica Mountains NRA–Rancho Sierra Vista/Satwiwa Cultural Center (118.961 W, 34.146 N)					
PPT (monthly totals, mm)					
January	19.01	44.18	40.33	0.70	101.17
February	86.09	2.55	6.05	60.00	87.91
March	153.97	86.23	20.70	69.40	86.03
April	0.03	53.31	3.58	7.21	17.35
May	15.47	1.02	9.02	0.00	5.39
June	4.13	0.00	0.00	0.00	1.10
July	0.00	0.00	0.37	0.05	0.01

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
August	0.00	0.46	0.00	0.49	0.06
September	0.38	0.00	0.00	0.00	10.61
October	37.06	6.11	9.09		10.38
November	52.59	45.13	18.28		42.15
December	14.85	87.51	6.84		73.02
Annual total PPT	**383.58**	**326.50**	**114.26**		**435.18**
Tmin (monthly means, °C)					
January	8.72	9.69	5.67	11.01	8.27
February	5.11	6.92	5.76	7.98	8.75
March	6.69	6.38	6.98	8.60	9.16
April	8.85	8.27	8.68	9.14	9.93
May	9.14	10.31	10.73	12.22	12.02
June	10.63	11.52	12.60	12.22	13.58
July	14.25	13.18	14.67	14.93	15.64
August	14.80	17.45	15.01	14.85	16.75
September	13.85	16.77	15.17	16.06	15.22
October	12.30	13.43	10.59		12.99
November	8.35	9.43	10.10		10.01
December	6.38	6.15	8.15		8.25
Mean monthly Tmin	**9.92**	**10.79**	**10.34**		**11.71**
Departures from PPT normals (mm)					
January	−82.16	−56.99	−60.84	−100.47	
February	−1.82	−85.36	−81.86	−27.91	
March	67.94	0.20	−65.33	−16.63	
April	−17.32	35.96	−13.77	−10.14	
May	10.08	−4.37	3.63	−5.39	
June	3.03	−1.10	−1.10	−1.10	
July	−0.01	−0.01	0.36	0.04	
August	−0.06	0.40	−0.06	0.43	
September	−10.23	−10.61	−10.61	−10.61	
October	26.68	−4.27	−1.29		
November	10.44	2.98	−23.87		
December	−58.17	14.49	−66.18		
Annual PPT	**−51.60**	**−108.68**	**−320.92**	**−171.78**	
Summary of difference†	2011 drier than normal	2012 drier than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	0.45	1.42	−2.60	2.74	
February	−3.64	−1.83	−2.99	−0.77	
March	−2.47	−2.78	−2.18	−0.56	
April	−1.08	−1.66	−1.25	−0.79	
May	−2.88	−1.71	−1.29	0.20	
June	−2.95	−2.06	−0.98	−1.36	
July	−1.39	−2.46	−0.97	−0.71	
August	−1.95	0.70	−1.74	−1.90	
September	−1.37	1.55	−0.05	0.84	
October	−0.69	0.44	−2.40		
November	−1.66	−0.58	0.09		
December	−1.87	−2.10	−0.10		
Annual mean monthly Tmin	**−1.79**	**−0.92**	**−1.37**	**−0.26**	
Summary of difference†	2011 cooler than normal	2012 cooler than normal	2013 cooler than normal	2014 cooler than normal	
University of California Natural Reserve System–Sedgwick Ranch Reserve (120.041 W, 34.675 N)					
PPT (monthly totals, mm)					
January	37.95	47.66	45.68	0.23	119.57
February	98.30	11.06	12.30	77.84	140.36
March	237.27	103.83	24.84	103.86	130.10
April	4.48	78.16	5.11	23.29	31.90
May	20.93	0.00	3.34	0.66	11.28
June	17.27	0.00	0.00	0.00	1.54
July	0.00	0.00	0.37	0.00	0.05
August	0.00	0.00	0.00	0.00	1.15
September	1.29	1.42	0.00	0.00	9.67
October	24.96	9.68	7.40		19.89
November	60.93	45.22	20.32		40.53
December	9.23	116.69	8.60		79.82

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971–2000)
Annual total PPT	**512.61**	**413.72**	**127.96**		**585.86**
Tmin (monthly means, °C)					
January	3.54	2.57	1.52	3.50	4.29
February	2.03	3.29	2.03	4.07	5.10
March	4.92	3.92	5.11	6.01	5.79
April	6.44	6.28	6.75	6.34	6.59
May	7.15	7.96	8.40	9.22	8.91
June	9.72	9.55	10.81	10.43	10.98
July	12.22	11.64	12.22	12.63	13.02
August	11.50	12.35	11.64	12.26	13.50
September	11.31	11.21	10.86	12.19	12.09
October	9.10	9.05	5.94		9.53
November	4.07	6.17	4.48		5.90
December	0.91	3.23	0.72		3.94
Mean monthly Tmin	**6.91**	**7.27**	**6.71**		**8.30**
Departures from PPT normals (mm)					
January	−81.62	−71.91	−73.89	−119.34	
February	−42.06	−129.30	−128.06	−62.52	
March	107.17	−26.27	−105.26	−26.24	
April	−27.42	46.26	−26.79	−8.61	
May	9.65	−11.28	−7.94	−10.62	
June	15.73	−1.54	−1.54	−1.54	
July	−0.05	−0.05	0.32	−0.05	
August	−1.15	−1.15	−1.15	−1.15	
September	−8.38	−8.25	−9.67	−9.67	
October	5.07	−10.21	−12.49		
November	20.40	4.69	−20.21		
December	−70.59	36.87	−71.22		
Annual PPT	**−73.25**	**−172.14**	**−457.90**	**−239.74**	
Summary of difference†	2011 drier than normal	2012 drier than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	−0.75	−1.72	−2.77	−0.79	
February	−3.07	−1.81	−3.07	−1.03	
March	−0.87	−1.87	−0.68	0.22	
April	−0.15	−0.31	0.16	−0.25	
May	−1.76	−0.95	−0.51	0.31	
June	−1.26	−1.43	−0.17	−0.55	
July	−0.80	−1.38	−0.80	−0.39	
August	−2.00	−1.15	−1.86	−1.24	
September	−0.78	−0.88	−1.23	0.10	
October	−0.43	−0.48	−3.59		
November	−1.83	0.27	−1.42		
December	−3.03	−0.71	−3.22		
Annual mean monthly Tmin	**−1.39**	**−1.04**	**−1.60**	**−0.40**	
Summary of difference†	2011 cooler than normal	2012 cooler than normal	2013 cooler than normal	2014 cooler than normal	
Joshua Tree National Park–Oasis Visitor Center (116.040 W, 34.128 N)					
PPT (monthly totals, mm)					
January	0.00	0.00	4.32	0.00	15.28
February	2.05	0.00	0.00	4.76	15.94
March	0.00	1.67	0.00	1.71	13.25
April	0.00	0.00	0.00	1.54	4.06
May	0.00	0.00	0.00	0.00	3.03
June	0.00	0.00	0.00	0.00	0.03
July	6.28	10.89	7.40	58.95	14.25
August	46.81	22.25	13.77	7.01	15.14
September	4.25	6.44	15.60	7.42	12.95
October	0.00	0.60	0.10		4.10
November	2.23	0.00	18.79		5.09
December	31.77	3.85	1.34		10.17
Annual total PPT	**93.39**	**45.70**	**61.32**	**81.39**	**113.29**
Tmin (monthly means, °C)					
January	4.73	5.07	2.65	6.55	2.74
February	3.89	5.42	4.38	8.27	4.49
March	8.28	7.98	10.98	10.47	6.60

Table A1. Continued.

Month	2011	2012	2013	2014	30-year normals (1971-2000)
April	11.18	12.19	13.31	13.18	9.44
May	13.52	17.88	17.00	16.81	13.30
June	19.12	20.62	21.96	21.65	17.70
July	23.65	23.79	26.55	25.98	21.15
August	24.07	25.42	22.31	23.17	21.00
September	20.90	21.18	19.03	20.88	17.44
October	14.18	13.61	10.48		11.53
November	6.17	8.18	6.65		5.49
December	2.58	3.96	4.13		2.29
Mean monthly Tmin	**12.69**	**13.78**	**13.29**	**16.33**	**11.10**
Departures from PPT normals (mm)					
January	−15.28	−15.28	−10.96	−15.28	
February	−13.89	−15.94	−15.94	−11.18	
March	−13.25	−11.58	−13.25	−11.54	
April	−4.06	−4.06	−4.06	−2.52	
May	−3.03	−3.03	−3.03	−3.03	
June	−0.03	−0.03	−0.03	−0.03	
July	−7.97	−3.36	−6.85	44.70	
August	31.67	7.11	−1.37	−8.13	
September	−8.70	−6.51	2.65	−5.53	
October	−4.10	−3.50	−4.00		
November	−2.86	−5.09	13.70		
December	21.60	−6.32	−8.83		
Annual PPT	**−19.90**	**−67.59**	**−51.97**	**−12.54**	
Summary of difference†	2011 drier than normal	2012 drier than normal	2013 drier than normal	2014 drier than normal	
Departures from Tmin normals (°C)					
January	1.99	2.33	−0.09	3.81	
February	−0.60	0.93	−0.11	3.78	
March	1.68	1.38	4.38	3.87	
April	1.74	2.75	3.87	3.74	
May	0.22	4.58	3.70	3.51	
June	1.42	2.92	4.26	3.95	
July	2.50	2.64	5.40	4.83	
August	3.07	4.42	1.31	2.17	
September	3.46	3.74	1.59	3.44	
October	2.65	2.08	−1.05		
November	0.68	2.69	1.16		
December	0.29	1.67	1.84		
Annual mean monthly Tmin	**1.59**	**2.68**	**2.19**	**3.68**	
Summary of difference†	2011 warmer than normal	2012 warmer than normal	2013 warmer than normal	2014 warmer than normal	

† The summary of difference is that between recent conditions and 30-year normals.