

Detecting nonlinear response of spring phenology to climate change by Bayesian analysis

KATHERINE S. POPE*, VOLKER DOSE†, DAVID DA SILVA*, PATRICK H. BROWN*, CHARLES A. LESLIE* and THEODORE M. DEJONG*

*Department of Plant Sciences, University of California, Davis, CA 95616, USA, †Max-Planck-Institut für Plasmaphysik, EURATOM Association, Boltzmannstrasse 2, D-85748, Garching bei München, Germany

Abstract

The impact of climate change on the advancement of plant phenological events has been heavily studied in the last decade. Although the majority of spring plant phenological events have been trending earlier, this is not universally true. Recent work has suggested that species that are not advancing in their spring phenological behavior are responding more to lack of winter chill than increased spring heat. One way to test this hypothesis is by evaluating the behavior of a species known to have a moderate to high chilling requirement and examining how it is responding to increased warming. This study used a 60-year data set for timing of leaf-out and male flowering of walnut (*Juglans regia*) cultivar 'Payne' to examine this issue. The spring phenological behavior of 'Payne' walnut differed depending on bud type. The vegetative buds, which have a higher chilling requirement, trended toward earlier leaf-out until about 1994, when they shifted to later leaf-out. The date of male bud pollen shedding advanced over the course of the whole record. Our findings suggest that many species which have exhibited earlier bud break are responding to warmer spring temperatures, but may shift into responding more to winter temperatures (lack of adequate chilling) as warming continues.

Keywords: Bayesian, change point, chilling, climate change, *Juglans regia*, phenology, temperature, walnut

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Introduction

Phenology, the study of the timing of biological events in a plant's life cycle and the causes of that timing (Lieth, 1974), has in recent times been examined as both a signal of climate change and a gauge of how plants (and animals) will respond to warmer conditions (Parmesan & Yohe, 2003; Root *et al.*, 2003; Rosenzweig *et al.*, 2008). The majority of spring plant phenological events studied are trending toward coming earlier than in previous decades across Europe (Menzel *et al.*, 2006; Gordo & Sanz, 2009), North America (Abu-Asab *et al.*, 2001; Schwartz *et al.*, 2006), and Asia (Primack *et al.*, 2009; Ma & Zhou, 2012). Researchers have extrapolated from these studies that bloom and leaf-out will continue to march forward, resulting in spring phenological events occurring weeks or months earlier than before industrial era global warming (e.g., Crepinsek *et al.* (2009)).

However, the forward march of spring has not been consistent or universal, with some phenological events coming later or remaining unchanged, depending on species or location (Ahas *et al.*, 2002; Zhang *et al.*, 2007; Doi & Katano, 2008; Schleip *et al.*, 2009b). Furthermore, the advancing response of phenology to increased

temperatures is not linear. In many experiments and observations, spring phenology advances more days per degree with an initial temperature increase than with a second temperature increase in equal magnitude (Morin *et al.*, 2010; Schwartz & Hanes, 2010; Gunderson *et al.*, 2012). Satellite data from North America and Asia have shown, *en masse*, ecosystems greening earlier or later, depending on temperature thresholds, over the course of the last thirty warming years (Zhang *et al.*, 2007; Haiying *et al.*, 2010).

The flower and vegetative buds of temperate trees become dormant in the fall and require exposure to winter chill, of an amount specific to species and cultivar, to exit this state (Westwood, 1993). The response of a given temperate perennial species to warmth in spring differs depending on how close that species is to meeting its chilling requirement (Landsberg, 1974; Murray *et al.*, 1989). Cook *et al.* (2012) have recently provided a framework for viewing the varying behaviors of different species in response to global warming. They categorized species into four groups; 'spring-only responders' – advancing phenological events in reaction to increased spring temperatures with no sensitivity to temperatures during other season, 'vernalization-only responders' – delaying phenological events in reaction to decreased winter chilling, 'divergent responders' – advancing of some processes due to

Correspondence: Katherine S. Pope, tel. +001 530 574 3794, fax 530 752 8502, e-mail: kspope@ucdavis.edu

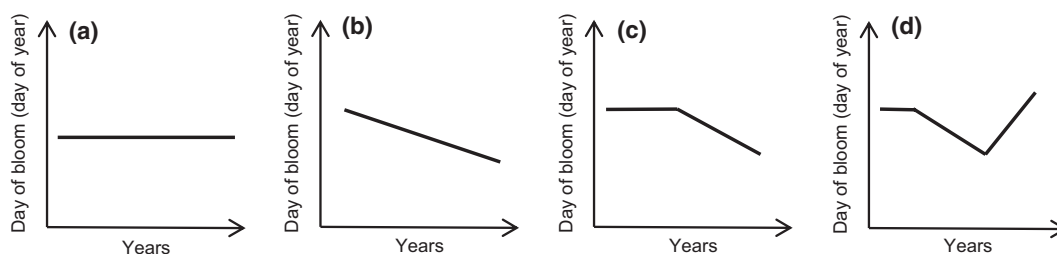


Fig. 1 Theoretical framework of detecting changing spring phenology based on spring heat and winter chill accumulation using Bayesian change point analysis. (a) Constant Model – no response to temperature change, (b) Linear Model – response to warmer spring temperature given data set that does not include prewarming years, (c) One-Change Point Model – stable conditions, then response to warmer spring temperatures, (d) Two-Change Point Model – stable conditions, then response to warmer spring temperatures, then response to decreased winter chill. Models with three and four change points are not shown, but similar to the two-change points model, would reflect four and five distinct trends, respectively.

increased spring heat but delaying of other processes due to decreased fall and winter chilling, and ‘non-responders’ – no phenological response to changing temperature trends in any season. Whereas 72% of the 490 species they analyzed were spring-only responders, 17% were divergent responders, 4% vernalization-only, and 8% nonresponders.

However, spring-only responders may simply be potential divergent responders with chill accumulation well above what the genotype requires. Across a number of temperate perennial species, there is an inverse, compensatory relationship between the amounts of chill the buds of a tree experience and the amount of heat necessary to flower or leaf-out (Chandler *et al.*, 1937; Cannell, 1989; Sparks, 1993; Harrington *et al.*, 2010), with high chill accumulation (henceforth ‘optimal chill’) necessitating minimal spring heat for bloom or leaf-out and chill below a certain threshold (henceforth ‘sub-optimal chill’) necessitating a higher accumulation of heat in spring. One way to examine whether spring-only responders, as a category, could be sensitive to temperatures outside the spring season is by examining the historic phenological response of vernalization-only or divergent responders. A vernalization-only or divergent responder would behave like a spring-only responder during years with warmer springs and optimal chill, but behave differently as winter chill became suboptimal and spring temperatures continued to increase.

Bayesian change point analysis provides an ideal way to detect this manner of response. Bayesian change point analysis has been used to detect whether plant phenology has responded to increased temperatures over several decades by comparing the probability of three models: no change in phenological event timing, a linear response over the entirety of the record, or a period of stability followed by a period of changed event timing (Dose & Menzel, 2004). By adding the possibility of a multiple change point model, and comparing the

probability of six different models, with between zero and five distinct trends over the course of the record (Fig. 1a–d), spring phenological responses to warming of both winter and spring can be evaluated. Furthermore, responses to warmer winters and the influence of warmer springs can be separately detected. The constant model (the first model) should describe a species that does not respond to warming conditions, a ‘non-responder’. Given adequate chill, spring warming should advance spring phenology. A linear model (the second model) should provide a good fit if the record were not long enough to show stable prewarming phenological timing. A one-change point model (the third model) would be most probable if the data included stable, prewarming years. High probability for either the linear or one-change point model would indicate a ‘spring-only’ responder species. If, over the course of the record, chill becomes suboptimal, a ‘divergent responder’ would first exhibit earlier phenological timing, then shift toward events occurring later. Provided the inclusion of stable, prewarming years in the data set, a two-change point model (the fourth model) should be most probable in this situation. A high probability of a model with three or four change points (the fifth and sixth model, not shown) would indicate the strong influence of factors beyond winter chill and spring heat.

The ideal data set for testing this framework would be the spring phenology record of a mid-to-high chill requirement perennial, in a location where spring and winter has been warming. Annual spring temperatures in the Sacramento Delta have increased significantly, both over the last century and more recently (Table 1), with similar trends across the whole of Northern California (data not shown). Since 1918 there has been a significant increase in daily minimum and maximum temperatures in all seasons, including the winter and summer. This trend has been increasing since 1970.

A 60-year-long data set (1953–2012) from the California Walnut Improvement Program was used for this

Table 1 Increasing trends of maximum and minimum temperature, both annually and seasonally, (change in Celsius per decade relative to 1918 and 1970), in the Delta region of California's Central Valley. Adapted from Cordero *et al.* (2011)

| Location | Season | 1918–2006 | | 1970–2006 | |
|-------------------------|--------|-----------|---------|-----------|---------|
| | | Maximum | Minimum | Maximum | Minimum |
| Sacramento-Delta region | Annual | 0.17* | 0.26* | 0.34* | 0.37* |
| | DJF | 0.14* | 0.19* | 0.25 | 0.33 |
| | MAM | 0.21* | 0.23* | 0.34 | 0.41* |
| | JJA | 0.16* | 0.32* | 0.32* | 0.38* |
| | SON | 0.17* | 0.29* | 0.40* | 0.34* |

DJF, December, January, and February; MAM, March, April, and May; JJA, June, July, and August; SON: September, October, and November.

*95% confidence interval.

study. This data set contained the dates of spring leaf-out and male flowering for the *Juglans regia* cv. 'Payne' in Davis, California. Minimum temperature records from the Davis Experimental Farm show temperatures increased significantly (95% confidence) from 1957 to 1975, with increases becoming highly significant (99%) from 1978 to 2006. Maximum temperature records show a highly significant trend starting in 1986 (Cordero *et al.*, 2011). Thus, this data set is appropriate for the two-change point framework because it includes years before temperature trends were significantly warmer.

The objective of this study was to determine if chill accumulation in California's Central Valley has decreased to a level that is suboptimal for walnuts, such that increased temperatures initially caused earlier spring phenological behavior while chilling was optimal and later spring phenological behaviors in more recent years when chilling accumulation was substantially reduced. The high chilling requirement of walnut cultivars grown in California makes these cultivars an ideal test case for this phenomenon. Given the high chilling requirement of California walnuts, we expect to find that walnut leaf-out and male flowering was stable before the 1970s, but advanced after the late 1970s and early 1980s, responding to warmer springs, and then changed again, receding as warmer winters and the lack of chilling began to outweigh the advancing force of warm spring conditions.

Materials and methods

Phenological data

The data set we used for our analysis came from records kept by researchers in charge of the California Walnut Improvement Program, a cooperative effort of the University of California at Davis, the United States Department of Agriculture and the California Walnut Marketing Board, in operation since 1948. Beginning in 1953, the phenological timing of events of existing cultivars and experimental crosses were recorded.

Walnut have two bud types – male buds or 'catkins' are borne laterally, whereas mixed vegetative-female flower buds can be borne terminally or laterally, depending on the cultivar. Phenological events recorded included 5% bloom, 50% bloom, and 95% bloom for both male and female flowers, as well as 50% leaf-out date. For male buds, 50% bloom was when the maximum number of catkins was shedding pollen, equivalent to Stage 6, Code 65 on the BBHC scale (Meier, 2001). For vegetative buds, 50% leaf-out was judged when 50% of terminal buds showed a leaflet reflexed from the bud, equivalent to Stage 1, Code 10 on the BBCH scale. We have chosen to exclude analysis of the female bloom record because the female flowers are borne at the end of vegetative growth and thus their timing is reliant on the timing of vegetative bud break and weather conditions thereafter.

The longest record from this program was that of *J. regia* cv. 'Payne' for the observational site on the University of California at Davis campus, Davis, CA. The data were continuous aside from missing data for both bud types in 1996, and for the male buds in 1973. Only 5% and 95% bloom was recorded for male buds until 1989. Because the rate of progress from 5% to 95% bloom varies slightly every year depending on chill accumulation and temperature during bloom (NeSmith & Bridges, 1992), rather than applying a model fitted from the 1990–2012 data to the 1953–1989 data, 50% bloom was interpolated by simple linear regression. The consistency of the data was assured by the fact that only five individuals collected these data with each person trained by the preceding one. Trees were visited twice weekly. New trees were integrated periodically, as trees aged. Phenological event data were not recorded until trees were at least 2–3 years of age. Observation plots were within a mile of one another for the entirety of the record. Trees were on 'Paradox' (*Juglans hindsii* x *J. regia*) and Northern California Black (*J. hindsii*) walnut rootstock. Each record is the average date of the event for two to four trees.

Bayesian analysis

The analysis of our data is based on an article by Dose & Menzel (2004). These authors analyzed phenology time series in terms of three models: a constant model, a linear model and a change point model. The latter employs a function consisting of two linear sections which match at the change point t_c

where t_c can be any time from the second to the $N-1$ th entry in the time series where N is the number of observation years. A specific element of these $N-2$ possible functions is a simple triangle with peak at the change point time t_c . The generalization of this model consists of allowing for polygons with an arbitrary number of change points. The data model at year t_i for $t_k \leq t_i \leq t_{k+1}$ is then

$$d_i - f_k * \frac{(t_{k+1} - t_i)}{(t_{k+1} - t_k)} + f_{k+1} * \frac{(t_i - t_k)}{(t_{k+1} - t_k)} = \varepsilon_i \quad (1)$$

where f_k and f_{k+1} are the functional values at change points t_k and t_{k+1} , d_i the observation in year t_i , and ε_i the uncertainty of d_i . In the notation of Dose & Menzel (2004) the coefficient of f_k is the (i, k) element of a matrix \mathbf{A} and correspondingly f_{k+1} the $(i, k + 1)$ element where i is the row index and k the column index of matrix \mathbf{A} (capital bold face letters denote matrices, lower case bold face letters vectors).

Application of Bayesian methods to this model is very different from conventional least squares fitting. While the least squares result for a one-change point model would be a triangle with peak at the change point t_{ML} and in the generalized case a polygon with change points t_{ML} , the Bayesian treatment considers not only the most likely change points but also neighboring, hence less optimal configurations. The probability of a particular configuration can be calculated within the Bayesian theory.

The calculation of this quantity needs the specification of a prior probability for the support functional values \mathbf{f} . Our experience with multiple change point problems has shown that the choice in Dose & Menzel (2004) was much too simplified to provide a reasonable probability assignment as a function of model complexity. We have therefore used in this study a prior distribution successfully employed by Bretthorst (1990) in his work on nuclear magnetic resonance signal detection and model comparison. In the notation of Dose & Menzel (2004) this reads

$$p(\mathbf{f}|\mathbf{A}, n_p, \lambda) = \left(\frac{\lambda}{\pi}\right)^{\frac{n_p}{2}} (\det \mathbf{A}^T \mathbf{A})^{\frac{1}{2}} \exp(-\lambda \mathbf{f}^T \mathbf{A}^T \mathbf{A} \mathbf{f}) \quad (2)$$

where n_p is the number of pivots, i.e., the number of change points plus two (end points), and λ an unknown hyperparameter. λ may be removed from the calculation by marginalizing with Jeffreys' prior $\frac{d\lambda}{\lambda}$ to yield

$$p(\mathbf{f}|\mathbf{A}, n_p) = \frac{1}{2} \frac{\Gamma(\frac{n_p}{2})}{(\pi)^{\frac{n_p}{2}}} * \frac{(\det \mathbf{A}^T \mathbf{A})^{\frac{1}{2}}}{(\mathbf{f}^T \mathbf{A}^T \mathbf{A} \mathbf{f})^{\frac{n_p}{2}}} \quad (3)$$

Note that this function is varying very slowly with \mathbf{f} compared with the variations exhibited by the likelihood. Following Bretthorst (1990), in integrals involving likelihood and prior, the prior may be taken constant with \mathbf{f} set to maximum likelihood value \mathbf{f}_{ML} . With these specifications the calculation of a change point configuration E (n_p), the corresponding unnormalized probability of a model given the change point configuration E (n_p), the estimate of the functional behavior and its derivative including uncertainties follows exactly the path of Dose & Menzel (2004) with two exceptions. The first exception concerns the average over change point configurations. In the one-change point case the number of choices is

exactly n_p-2 and the average can easily be calculated in a deterministic way. For more than one-change point the number of configurations scales approximately as N^{n_p-2} . With $N \approx 60$ and $n_p = 10$ this would mean the order of 10^{14} ! As this is not easily tractable, we have employed for all $n_p \geq 3$ Monte Carlo evaluations of averages. For these calculations, we need random numbers in $[0,1]$ which add up to one. The appropriate generator is

$$j = 1 \dots (n_p - 1) \quad (4)$$

$$z(j) = -\ln(1 - \mu(0,1))$$

where $\mu(0,1)$ are uniform random numbers with $0 < \mu(0,1) < 1$. $z(j)$ is then normalized to one and used to calculate the partial sums

$$t_k = \sum z(j), j = 1 \dots k \quad (5)$$

t_k are then shifted $t_i \rightarrow t_{i+1}$ and provide then with $t_1 = 0$, an ordered set of random numbers in $[0,1]$ which lastly needs translation and dilation to match the support of the actual time series. The sought-after averages are then calculated by summing up the results of N_{MC} change point configurations weighted by their respective probabilities and divided by N_{MC} . This is the second difference from Dose & Menzel (2004) for estimation of function (trend) and derivative (rate of change) for the time series but not for their uncertainties. For uncertainties, we need to go back to the moments m_1 and m_2 by $function(j) = m_1(j)$ and $variance(j) = m_2(j) - (m_1(j))^2$. We then take the averages over moments weighted by the probabilities of the corresponding change point configuration to yield M_1 and M_2 and obtain finally

$$function(j)_{av} = M_1(j), variance(j)_{av} = M_2(j) - (M_1(j))^2 \quad (6)$$

The same scheme applies to the derivative.

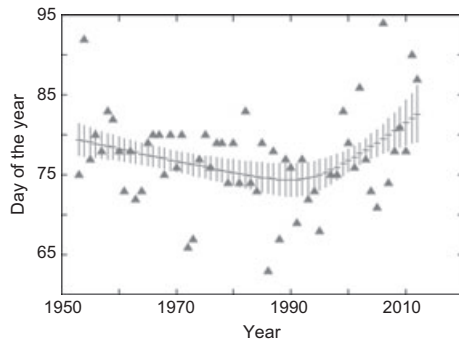
Results

Analysis of the 60 years of leaf-out and male flowering data from 1953 to 2012 revealed a distinct one-change point trend for the leaf-out data and a linear trend for the male data. There was a trend toward earlier leaf-out until approximately 1994, and subsequently leaf-out started coming later, with a much steeper slope than the initial earliness. Thus, by the middle of the first decade of the 21st century, the leaf-out trend was later than ever previously recorded. This corresponds to theoretical framework of Fig. 1d, except without the initial period of stability. A linear model (Fig. 1b) fits the male data better than a constant model, both of which are more likely than either change point models.

The six model options fit the leaf-out data with varying amounts of probability (Table 2). The constant model specified by a single scalar f had a probability of 0.134 and a residual sum of squares (RSS) of 1980.6. The linear model specified by the two values of f at the beginning and end of the time series had a probability of 0.033, with an RSS of 1976.6. The change point

Table 2 Model residuals and probability for leaf-out

| Number of pivots n_p | RSS | Probability |
|------------------------|--------|-------------|
| 1 | 1980.6 | 0.134 |
| 2 | 1976.6 | 0.033 |
| 3 | 1564.7 | 0.804 |
| 4 | 1542 | 0.027 |
| 5 | 1510.1 | 0.001 |
| 6 | 1485.2 | 0 |

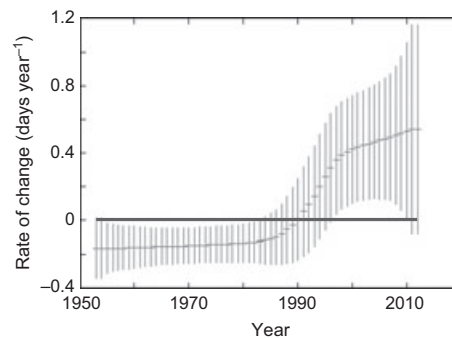
**Fig. 2** Model averaged function fit of leaf-out data. This and all remaining figures prepared with gnuplot (Williams & Kelley, 2012).

models have $n_p - 2$ change points with $n_p \geq 3$. Note that the residuals diminish with rising n_p , whereas the model probability passes through a maximum for $n_p = 3$ (i.e., the one-change point model). This is a demonstration of Ockham's razor contained in Bayesian theory (Garrett, 1991), which penalizes an increase in model complexity unless it is accompanied by a sufficiently substantial decrease in the residuals.

Rather than selecting the model with the highest probability and drawing conclusions from that model, disregarding the nonnegligible probability of other models, the Bayesian approach instead draws conclusions from a model averaged function, averaging function and derivative of the respective models with model probabilities as weights. The relative probability of the one-change point model is so much higher than the other models the average model (Fig. 2) is virtually indistinguishable from the one-change point model.

While the change point trend is clear, there is a large degree of uncertainty in the magnitude of the rate of change in the last 20 years (Fig. 3). Interestingly, the derivative changes sign and magnitude from -0.16 ± 0.17 in 1953 to $+0.55 \pm 0.63$ in 2012.

The probability distribution of the potential change points for the leaf-out data has a maximum likelihood at 1994. The residuals had no pattern to their scatter. The distribution of the residuals followed a Gaussian distribution, satisfying an assumption of the analysis. The data were also analyzed for autocorrelation. The

**Fig. 3** Derivative of model averaged function fit of leaf-out data.**Table 3** Model residuals and probability for male flowering

| Number of pivots n_p | RSS | Probability |
|------------------------|--------|-------------|
| 1 | 2659.1 | 0.367 |
| 2 | 2485.4 | 0.542 |
| 3 | 2449.1 | 0.09 |
| 4 | 2413.6 | 0.002 |
| 5 | 2359 | 0 |
| 6 | 2303.6 | 0 |

autocorrelation function was different from zero only for delay 0, meaning the data were independent.

The six model options fit the male flowering data differently (Table 3). The constant model had a probability of 0.367 and an RSS of 2659.1. The linear model had a probability of 0.542 and an RSS of 2485.4. The one-change point model had a probability of 0.090, an RSS of 2449.1. The change point models share the remaining 0.091 probability and are therefore relatively unimportant for the overall explanation of the data.

Because the probabilities of the constant and linear models do not differ as much as with the leaf-out data, it is worth noting that in Bayesian model comparison, if the natural logarithm of the probabilities differs by less than 1.0, they are considered not significantly different (Kass & Raftery, 1995). The difference between the natural logarithm of the constant and linear model was 0.4, thus they were not significantly different. As the probability of both the constant and linear models is high (Fig. 4), the model averaged function is primarily a composite of the constant and linear models, hence again a linear function with a distinct linear slope, but a slope that is of lesser magnitude than the linear model alone (Fig. 5). As the derivative of a linear function is simply a constant, it is not displayed here. The slopes at the beginning and the end of the time series are -0.06 ± 0.30 in 1953 and $+0.01 \pm 0.65$ in 2012, respectively. For strict linearity the two numbers are expected to be equal. The difference between the two numbers signals a contribution of the one-change point results to

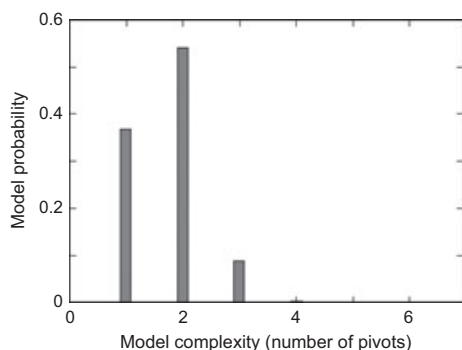


Fig. 4 Comparison of model probabilities for male bud data.

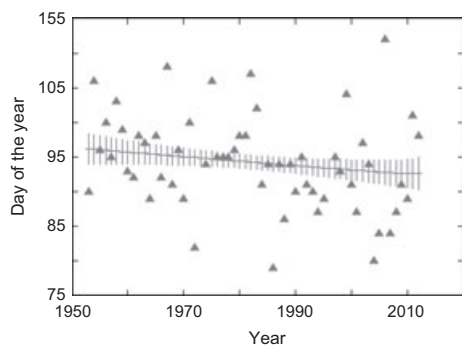


Fig. 5 Model averaged function fit of male bud data.

the average near 2012. It is from this model averaged function that we draw the conclusion of linearity of the male flowering trend.

Discussion

The walnut cultivar presently studied appears to have responded to recent global warming with two very different phenological behaviors. The date of leaf-out was first advanced and then delayed while the date of male flowering only advanced. These results were somewhat unexpected. Although it is generally accepted that walnuts grown commercially in California have a higher chilling requirement than most cultivated temperate tree crops in this region (Hasey *et al.*, 1994; Charrier *et al.*, 2011), recent works (Aslamarz *et al.*, 2009; Luedeling & Gassner, 2012) have indicated that 'Payne' and the closely related 'Serr' cultivar have a moderate chill requirement, generally satisfied in early to mid-January. In view of these recent works, we would have expected this species and specific cultivar to advance in the timing of male flowering and leaf-out in response to warmer temperature patterns, indicative of a 'spring only' responder. Instead it appears that captured in the record of one cultivar is one bud type (male) that is more representative of a spring-only responder, with a satisfied chilling requirement, and another bud

type (vegetative) with a divergent response, behaving like a spring-only responder until about 1994, when chilling apparently became suboptimal.

The duality of our data set is in keeping with the global literature regarding phenology and climate change. While the forward march of spring has often been cited as ecological evidence that climates are warming (Rosenzweig *et al.*, 2007), numerous species have not been found to have advanced spring phenological stages (Menzel, 2000; Abu-Asab *et al.*, 2001; Primack *et al.*, 2009; Rumpff *et al.*, 2010). Nor is the change point nature of the phenological stage trends unusual. In a Bayesian analysis of 2600 time series from 181 stations in Central and Eastern Europe, 62% of the time series were best represented by a one-change point model, 24% by a linear model, and 14% by a constant model (Schleip *et al.*, 2009b).

Although many species have been shown to have a change point in their phenological record, and many have had increasingly delayed phenological events, this study is the first reported case of a spring phenology record for a species getting earlier, and then later. These ground-based data support conclusions drawn from Normalized Difference Vegetation Index ratios derived from satellite images that spring phenological event timing has, *en masse*, been advancing and then delaying (Zhang *et al.*, 2007; Haiying *et al.*, 2010). This also supports experimental evidence that the temperature response of spring phenological timing is not linear (Morin *et al.*, 2010; Schwartz & Hanes, 2010; Gunderson *et al.*, 2012). A lack of winter chilling was often speculated to be at least a partial determinant of this phenomenon.

Here, too, the likely mechanisms responsible for this behavior are the chilling requirements of the species involved. While photoperiod has been shown to impact the phenology of some species, opportunistic species such as walnut have generally not been found to be sensitive to photoperiod (Caffarra & Donnelly, 2011; Taugourdeau *et al.*, 2011; Basler & Korner, 2012), thus implicating temperature. The flower and vegetative buds of temperate trees enter endodormancy in the fall and require exposure to winter chill, of an amount specific to species and cultivar, to exit this state (Westwood, 1993). Higher heat requirements under suboptimal chill (Sparks, 1993; Harrington *et al.*, 2010), along with possibly an increased chilling requirement due to warmer autumn temperatures (Walser *et al.*, 1981; Heide, 2003), and a longer amount of time necessary to accumulate chill with warmer winters, can all contribute to a longer amount of time necessary to achieve leaf-out or flowering, depending on the chilling requirement of the species and cultivar.

Our findings differ significantly from those of similar studies that have been conducted on walnut. Crepinsek

et al. (2009) found that leaf bud break came 3 and 7 days earlier between 1984 and 2006, respectively, in 'Franquette', a late cultivar, and 'G-139', a cultivar with midseason leaf-out. Gordo & Sanz (2009) also reported that leaf-out advanced linearly by 0.262 days per year since 1943, and flowering became progressively later from 1943 until 1974, when it began to occur earlier. These disparate results could be attributed to differences in climate and differences among cultivars. 'Payne' is an earlier variety than 'Franquette' (Hendricks *et al.*, 1998) and winters in Slovenia, where the Crepinsek *et al.* (2009) was conducted, are generally not as mild as in Davis, California. It is difficult to account for the disparity with the results of Gordo & Sanz (2009) because the cultivar was not cited.

The divergent behavior of the two bud types of walnut, within one cultivar, provided a serendipitous comparison. The chilling requirement of protandrous male buds, are lower than the chilling requirement of leaf buds in walnut (Aslamarz *et al.*, 2009; Luedeling & Gassner, 2012). Thus, it would appear that chilling is still optimal for the male buds, and for this reason male buds behaved as a 'spring-only' responder. The results presented here suggest that chill was also adequate for the leaf buds until about 1994, causing leaf-out timing to advance with warmer spring temperatures, consistent with a 'spring-only' responder. However, around 1994 chilling apparently became suboptimal, and spring phenological timing of the leaf buds became a balance of both fulfilling chill requirements and heat requirements, behaving as a 'divergent' responder. Thus, for the 'Payne' leaf buds, whether they were classified as divergent responders or spring-only responders depended on how much of the record was examined.

The implications of these findings are numerous. In terms of methods of analysis for phenology and climate change, it makes the case for avoiding reliance solely on simple linear regression and ordinary least squares to model and estimate the response of plant behavior to temperature changes. Simple linear regression using JMP 9 (SAS Institute Inc., Cary, NC, USA, 1989–2012) with our leaf-out data yielded a model with a probability of 0.5503, which would be judged as not significantly different from a model with a slope of zero. Thus, simple linear regression would have misinterpreted the trends in the data as leaf-out timing not changing over the last 60 years. Whether by Bayesian analysis, some other change point analysis, cluster analysis, or novel approaches (Zhang *et al.*, 2007; Gordo & Sanz, 2009; Schleip *et al.*, 2009a; Haiying *et al.*, 2010; Schwartz & Hanes, 2010), analyses need to allow for the possibility of a shift in the response to temperature changes after a specific year or thermal experience while not presuming there will certainly be one.

In terms of climate change in California, this study confirms that the climate has been changing in the Central Valley of California and that the phenological behavior of some plants (or organs of plants) has changed with it. It also suggests that for some varieties of walnuts and other varieties of species with high chilling requirements, the Central Valley may be shifting toward being an unsuitable area for cultivation and growth. More globally, but specific to walnuts, it suggests that the chilling requirement of the 'Payne' cultivar and similar genotypes is higher than reported by Aslamarz *et al.* (2009) and Luedeling & Gassner (2012).

Finally, from a much broader view, these findings suggest that conclusions based on previous findings of the forward march of spring may be misguided for some species and climates. As with many areas of climate change research, the story lies more in a tipping point than a linear progression. While the timing of spring phenology has been advancing in some cases, this trend should not be automatically projected into the future. For example, Crepinsek *et al.* (2009), having found that bloom had advanced 3–7 days (depending on cultivar) in walnut over the course of their 22-year record, speculated that the average bud-break date of walnut could advance as much as 4 weeks by 2060, triggering concerns regarding frost hazard. Our findings would instead suggest that advancement of bud break will likely be followed by a delay in the timing of bud break, and possibly eventually by bud failure resulting from a lack of chill.

The implications of this work in a global sense can be seen as devastating or hopeful. Certainly, it indicates that the continued warming of climates can have deleterious consequences for cultivated plants. As a species grown outside the range in which it evolved, however, cultivated walnuts may serve as a harbinger of the future, showing behavioral changes that are a step ahead of those that native temperate species will likely exhibit under increased temperatures. As global temperatures rise, many areas will experience warmer winters (Luedeling *et al.*, 2011). As winter chill decreases, more spring heat will be necessary to cause bud break. At a certain point, winter chill accumulation may shift from suboptimal, just causing delayed phenology, to below the requirement, eventually leading to loss of the species in specific areas.

There are still many unknowns in quantifying chilling requirements and optimal chill in temperate perennial species (Campoy *et al.*, 2011). Future work should focus on better quantifying chill and heat requirements and optimums for specific species and cultivars. Analyzing phenology records henceforth with a change point or similar analysis should also be undertaken, not only to better elucidate trends to-date but to gauge how

many species are near or below accumulation of optimal chill.

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