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Timing of cherry tree blooming: Contrasting effects of rising winter low temperatures and early spring temperatures

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ABSTRACT

Phenology reflects the interplay of climate and biological development. Early spring phenological phenomena are particularly important because the end of diapause or dormancy is related not only to heat accumulation in the early spring but also probably to winter low temperatures. Although a warmer winter can reduce overwintering mortality in many insects and plants, it also reduces the accumulation of chilling time that often triggers the end of diapause or dormancy. We examined a continuous 67-year time series of the first flowering date of cherry trees and compared three phenological models based on the temperature-dependent developmental rate: (i) the accumulated degree days (ADD) method, (ii) the number of days transferred to a standardized temperature (DTS) method, and (iii) the accumulated developmental progress (ADP) method. The ADP method performed the best but only slightly better than the DTS method. We further explained the residuals from the ADP method by an additive model using the mean winter minimum daily temperatures, the number of days with low temperatures (represented by daily minimum temperature) below a critical low temperature, and the minimum annual extreme temperature. These three temperature variables explained more than 57.5% deviance of the ADP model residuals. Increased mean winter low temperatures can delay the blooming of cherry trees by reducing the accumulation of chilling time, whereas reduced numbers of cold days can shift the blooming to become earlier. Overall, rising winter low temperatures will delay the flowering time, while rising early spring temperatures directly shift earlier the flowering time. The flowering time has been shifted to earlier, and the balance from the opposing effects of rising winter low temperatures and early spring temperatures explains this shift.

1. Introduction

Changes in phenological events are good proxy of climate change (Pau et al., 2011) and relevant for safeguarding agriculture and other natural ecosystem service (Fitter and Fitter, 2002; Fu et al., 2015; Guo et al., 2015). Temperatures are a crucial factor of developmental rate (Uvarov, 1931) and thus dictate the occurrence timing of many poikilotherm animals and plants (Gienapp et al., 2005; Kingsolver, 2009). At low temperatures, the developmental rate increases exponentially with temperature. In the middle range of temperatures, it increases linearly with temperature. At high temperatures, the developmental rate declines rapidly when approaching the lethal upper

thermal limit (Campbell et al., 1974). Rising temperatures have shifted many phenological events to occur earlier, potentially causing profound trophic cascades (Anderson et al., 2013).

Many right-skewed bell-shaped models are available for capturing the developmental rate as a function of temperature (Wagner et al., 1984; Shi et al., 2016, 2017). Some phenological studies have used the accumulated degree days (ADD) model (e.g., Ring and Harris, 1983; Ho et al., 2006), which is based on the hypothesis that developmental rate is a linear function of temperature in the middle range of temperatures (Campbell et al., 1974). In early spring (from early February to early April), daily mean temperatures in the temperate zone of Northern Hemisphere are usually below 20 °C, with only a few days having the

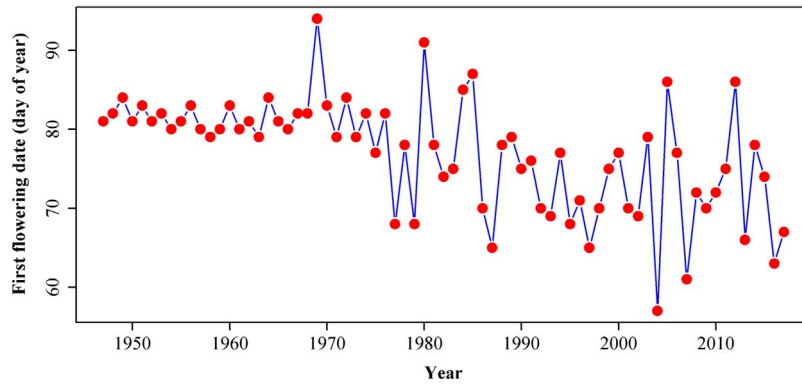


Fig. 1. Time series of the first flowering date of Japanese cherry trees (*P. yedoensis*) in Wuhan University campus from 1947 to 2017.

daily maximum temperature above 30 °C. However, the ADD model neglects the potential deviation from the linear relationship between developmental rate and temperature. To this end, Konno and Sugihara (1986) recommended the use of an exponential equation to replace the linear model by transferring the number of days to a standardized temperature; hereafter, the DTS model. Omoto and Aono (1989) used both the DTS and ADD models to estimate the blooming date of cherry trees (*Prunus yedoensis* Matsum) and found that the DTS model is superior to the ADD model. The DST model has been used to reconstruct the ancient springtime temperature of Kyoto, Japan using the phenological data series of the flowering of *Prunus jamasakura* instead of the ADD model (Aono and Kazui, 2008; Aono and Saito, 2010).

However, these models face challenges for predicting future phenological events under natural fluctuating thermal regimes. Controlled experiments that are often used for measuring the developmental time of insects and plants under constant temperatures have been criticized for lacking the natural thermal variability in ambient environment. To this end, Wagner et al. (1984) proposed a practical model for applying any nonlinear temperature-dependent developmental rates and predicting phenological events by accumulating the developmental progress (ADP). In this proposed ADP model, the expected occurrence date is the day when the accumulation of daily developmental rates from the starting date reaches 100%. Ungerer et al. (1999) have applied the ADP model to estimate the number of generations per year for the southern pine beetle (*Dendroctonus frontalis* Zimmermann) by integrating a nonlinear temperature-dependent developmental rate model proposed by Schoolfield et al. (1981). Ikemoto and Egami (2013) proposed a revision to the Schoolfield model and calculated developmental rates in a natural thermal environment from a controlled thermal experiment. However, to date, no studies have compared these methods in describing the phenological events of plants in early spring.

Besides temperature accumulation, winter low temperatures have been found to significantly affect the phenology of boreal and temperate plants in early spring (Hänninen, 2016). It is thus necessary to separate the effect of winter low temperatures from the effect of temperature/heat accumulation on occurrence time in early spring. Changes in winter extreme temperatures have been widely concerned for affecting the fitness and survival of organisms (Ungerer et al., 1999). Rising winter temperatures are believed to reduce the mortality of overwintering insects and plants, and shift the timing of phenological events to become earlier in spring (Parmesan and Yohe, 2003; Pau et al., 2011; Valtonen et al., 2014). It is important to examine the indirect effect of winter low temperatures on the occurrence time via affecting the dormancy, before considering the direct effect of early spring temperatures.

In this paper, we attempt to examine the effects of winter low temperatures on the first flowering date of cherry trees using a 67-year continuous time series. We further use this dataset to compare the strengths of the three models (ADD, DTS versus ADP). The best method

according to the goodness of fit was selected for prediction. Residuals were further explained by winter low temperatures. We also provide several practical computer codes for parameter estimates.

2. Materials and methods

2.1. Data collection

Japanese cherry trees (*P. yedoensis*) are a famous ornamental plant in East Asia. In 1939, 28 cherry trees from Japan were planted in the Wuhan University campus, then a Japanese military hospital. After the WWII, three additional plantings (in 1957, 1973 and 1985) were added to the cherry tree population in Wuhan. The first flowering date, defined as the day on which three to five flowers open in several trees (> 10) along an avenue in the Wuhan University campus (normally between March and April), has been continuously recorded since 1947 (Fig. 1). The cherry trees along the avenue always keep high synchronicity and close spatial proximity for the first flowering times, so the mean time was used to represent the first flowering time of each year. Microsite covariates were excluded because of high synchronicity in the first flowering time and close spatial proximity among cherry trees in the campus. If the observation area was larger and more heterogeneous, to use the microsite covariates would likely reduce prediction errors. Although the tree age (depending on the planting date) could affect the first flowering date, the long-term trend should be driven largely by climate. We obtained the daily mean temperature data of Wuhan from the China Meteorological Data Net (data.cma.cn) from 1 January, 1951 to 30 March, 2017; and the daily temperature data from 1 November to 31 December in 1950 was obtained from the Meteorological Service Center of Huibei Province (Fig. S1 in Appendix B). We did not use any other earlier daily climatic data as the accuracy cannot be guaranteed during the war time (the Chinese Civil War from June 1946 to June 1950 directly followed the WWII).

2.2. Three phenological models related to temperature-dependent developmental rates

2.2.1. Accumulated degree days (ADD) method

The developmental rate in the middle range of temperatures can be approximated by a linear function, $r = a + bT$, where r represents the developmental rate, T the constant temperature, and a and b model constants (Campbell et al., 1974). A lower developmental threshold ($T_0 = -a/b$; called the base temperature in phenology) exists, below which development halts (namely $r = 0$). Under the linear relationship hypothesis, the sum of effective temperatures (> T_0) required for completing a developmental stage is assumed a constant thermal time k , which has: $k = t \cdot (T - T_0)$, where t represents the developmental time. According to the definition of developmental rate that $r = 1/t$, we have $k = 1/b$. As T is a constant temperature, we can use the daily

mean temperature to replace the constant temperature for predicting the occurrence time of a phenological event:

$$k_i = \sum_{j=S}^{E_i} (T_{ij} - T_0) \quad (1)$$

where the subscript i represents the i th year, S the starting date where temperatures begin to be accumulated for completing the development (usually a constant), E the ending date of the phenological event, and T_{ij} represents the daily mean temperature on the j th day in the i th year. The value in parentheses is defined to be zero if $T_{ij} < T_0$. In practice, the daily mean temperature is known, whereas the base temperature and the required accumulated degree days (i.e., thermal time requirement) are to be estimated. If there are n available historical records for the occurrence date, we could use the average thermal time as the critical accumulated degree days $\bar{k} = \sum_{i=1}^n k_i/n$ that will trigger the occurrence of the phenological event. Using this critical accumulated degree days and the observed daily temperatures, we can predict the occurrence dates for different years.

The best combination of starting date and base temperature can be normally determined using the criterion of lowest resultant root mean squared error (RMSE in days). Although not ideal, this practice is feasible for some datasets. There are cases where the RMSE is a monotonic function of S or T_0 , and there is no combination of these two parameters that can minimize RMSE. An effective remedy is to optimize these two parameters separately (Ring and Harris, 1983; Aono, 1993). In general, the starting date is first determined by searching the smallest value of the negative correlation between the occurrence time and the mean of daily mean temperatures from a candidate starting date to the occurrence time. If the mean of the daily temperatures is large, the occurrence time will be expected to be moved to earlier time points. Using the approach, the smallest correlation coefficient might correspond to the starting date and is usually regarded as the desired starting date (Aono, 1993).

2.2.2. Number of days transferred to the standard temperature (DTS) method

Organisms with phenological events in early spring often experience several cold days during the development. In this case, an exponential model appears to be more suitable (Campbell et al., 1974; Wagner et al., 1984). For instance, Arrhenius' (1889) equation has been used to describe such a relationship:

$$r = A \cdot \exp\left(-\frac{E_a}{R \cdot T}\right) = \exp\left(B - \frac{E_a}{R \cdot T}\right) \quad (2)$$

Here, E_a represents the activation free energy (cal mol^{-1}); R the universal gas constant ($= 1.987 \text{ cal mol}^{-1} \text{ K}^{-1}$); A is a model constant and normally used after a logarithm transformation $B = \ln(A)$ (Ratkowsky, 1990); T denotes the absolute temperature in Kelvin. For calculating the developmental rate of cherry trees, parameters A and B are both unitless, but A has a 10^{12} order of magnitude. For convenience, we directly multiplied the right-hand side of Eq. (2) by 10^{12} to reduce the order of magnitude of A and the size of B . And we changed the unit of E_a from cal mol^{-1} to kcal mol^{-1} by multiplying E_a by 1000 in Eq. (2). Normally, we assume that the multiplication of developmental rate and developmental time is a constant (Konno and Sugihara, 1986; Omoto and Aono, 1989; Aono, 1993), that is, $r_1 t_1 = r_2 t_2 = \dots = \text{constant}$, where the subscript represents a particular developmental rate and time. Let the developmental time be t_s at a standard temperature T_s . When completing a particular developmental stage needs many days, the daily DTS can be obtained based as the follow:

$$(t_s)_{ij} = \exp\left\{\frac{E_a(T_{ij} - T_s)}{RT_{ij}T_s}\right\} \quad (3)$$

Here, $(t_s)_{ij}$ represents the number of days transferred to the standard

temperature on the j th day in the i th year. T_s is usually defined to be 298.15 K (i.e., 25 °C) (Konno and Sugihara, 1986; Omoto and Aono, 1989; Aono, 1993). To complete the whole developmental progress in the i th year would require the following number of days:

$$\text{AADTS}_i = \sum_{j=S}^{E_i} (t_s)_{ij} \quad (4)$$

where AADTS represents the annual accumulated DTS from the starting date to the actual first flowering date. If there are n -year phenological records on the occurrence dates of a particular event, we can obtain the mean of AADTS values for many years:

$$\overline{\text{AADTS}} = \frac{\sum_{i=1}^n \text{AADTS}_i}{n} \quad (5)$$

We refer to the above as the critical AADTS which can be used to predict the occurrence date of a given year.

The parameter E_a in Eq. (3) is a constant to be fitted. Aono (1993) found that E_a ranges from 5 to 30 kcal mol^{-1} for the blooming of cherry trees. In order to obtain the target starting date, we did (1) choose a combination of S and E_a , and calculate the AADTS for each year and the critical AADTS; (2) predict the occurrence date of a given year based on the critical AADTS by accumulating daily DTS values from the candidate starting date to a date when the accumulated daily DTS reaches the critical AADTS; (3) calculate the RMSE for the given combination of S and E_a ; (4) repeat the above steps by considering other combinations of candidate S and E_a values. The desired values of S and E_a are the combination that can result in the lowest RMSE.

2.2.3. Accumulated developmental progress (ADP) method

A problem of the DTS method is that it cannot estimate the parameter B in the Arrhenius' equation; consequently, the developmental rates at different constant temperatures cannot be predicted. However, we do sometimes need to know the curve shape of developmental rate that is difficult to derive from controlled experiments especially for trees. In addition, to predetermine the standard temperature is somewhat subjective, and for different species it could be challenging (Ikemoto, 2005; Shi et al., 2013) as the use of 298.15 K for all species might be problematic. The concept of developmental rate represents the speed of development per unit time. If the time unit is day, it denotes the proportion of completed developmental progress per day. Thus, the daily developmental rate will stop when the accumulation reaches or exceeds 100% (Wagner et al., 1984; Ungerer et al., 1999). This avoids the unnecessary transformation to a predetermined standard temperature. We refer to this method as the accumulated developmental progress (ADP) method. The daily ADP on the j th day of the i th year can be calculated as:

$$r_{ij} = \exp\left(B - \frac{E_a}{R \cdot T_{ij}}\right) \quad (6)$$

Here, we also directly multiplied the right-hand side of Eq. (6) by 10^{12} to reduce the size of B , which is helpful for carrying out parameter estimation, and changed the unit of E_a from cal mol^{-1} to kcal mol^{-1} by multiplying E_a by 1000. The annual accumulated ADP (hereafter, AAADP) of the i th year is then,

$$\text{AAADP}_i = \sum_{j=S}^{E_i} r_{ij} \quad (7)$$

The critical AAADP is theoretically equal to 1, namely completing 100% of developmental progress. We need to therefore find a date to which the accumulated daily ADP from the starting date equals or exceeds 1. The detailed operation steps for the ADP method are as follows: (1) provide a combination of starting date (i.e., S), B , and E_a , and calculate the AAADP for each year; (2) predict the occurrence date for each year by accumulating daily ADP values from the candidate

starting date to a date when the accumulated daily DTS reaches 1; (3) calculate the RMSE for the given combination of S , B , and E_a ; (4) repeat the above steps by considering other combinations of candidate S , B , and E_a . Because there are three variables that use the candidate values, we can use the optimization method proposed by Nelder and Mead (1965) to estimate the best target values of B and E_a . In this case, we also need to provide a group of candidate integer values for S .

2.3. Model assessment

To evaluate model validity, we divided the dataset into two parts: training set and test set. The training set was used to fit the models and estimate parameters, and the test set was used to evaluate the prediction errors. We calculated the RMSEs for the training set and test set using the three models, respectively. Because there is no general rule on how to choose the number of observations in each of the two parts (Hastie et al., 2009), the dataset was randomly divided into two parts based on the golden ratio (i.e., 0.618), which was repeated 100 times. There are totally 67 observations of the first flowering date, so the data length of the training set is 41 and that of the test set is 26 for every repetition. Then the RMSEs were calculated to compare three methods for the training set and test set.

2.4. Effects of winter low temperatures on the occurrence times

The blooming date of many plants in early spring can be affected by winter low temperatures (Hänninen, 2016). Winter low temperatures such as the mean daily minimum temperature, the minimum annual extreme temperature, and the number of days with low temperatures ($\leq$ a critical low temperature) have all been reported to affect the population densities of poikilotherms (Uvarov, 1931; Ungerer et al., 1999; Friedenberg et al., 2008). Many fruit and nut trees require a certain level of chilling accumulation during winter time before breaking the endodormancy (Luedeling and Brown, 2011; Guo et al., 2015). The effect of chilling can be captured by three indices: (i) the mean daily minimum temperatures from 1 November of the preceding year to the starting date, i.e., 27 January for the present studied plant, (x_1), (ii) the number of days with low temperatures $\leq$ a critical value (x_2), and (iii) the minimum annual extreme temperature (x_3). If winter chilling is independent from the heat (or rate) accumulation in early spring, the unexplained deviance in the heat or rate accumulation model can be reflected by the residuals (= observed occurrence times – predicted occurrence times). The predicted occurrence times using the rate accumulation model represents the theoretical occurrence times. If a residual is positive, it indicates a delayed (later) flowering time; if it is negative, an advanced (earlier) flowering time (see Fig. S2 in Appendix B). Although the residuals might also result from other factors such as randomness and environmental factors, the residuals could be largely affected by the winter chilling. Here we used the ADP method to represent the rate accumulation model and the generalized additive model to explore the effect of mean daily minimum temperatures from 1 November of the preceding year to the starting date, the number of days with low temperatures below a critical value during this period, and the minimum annual extreme temperature on the residuals between the observed and predicted occurrence dates. To find the critical low temperature below which the number of days are counted, we provided a group of candidate low temperatures ranging from -6 to 0 °C in 0.05 °C increments. Then the target critical low temperature is associated with the highest adjusted coefficient of determination from using the generalized additive model (Hastie and Tibshirani, 1986, 1990). All analyses were carried out on the platform of R software (version 3.2.2; R Core Team, 2015). We also developed R scripts for implementing the ADD, DTS, and the ADP methods (Appendix A).

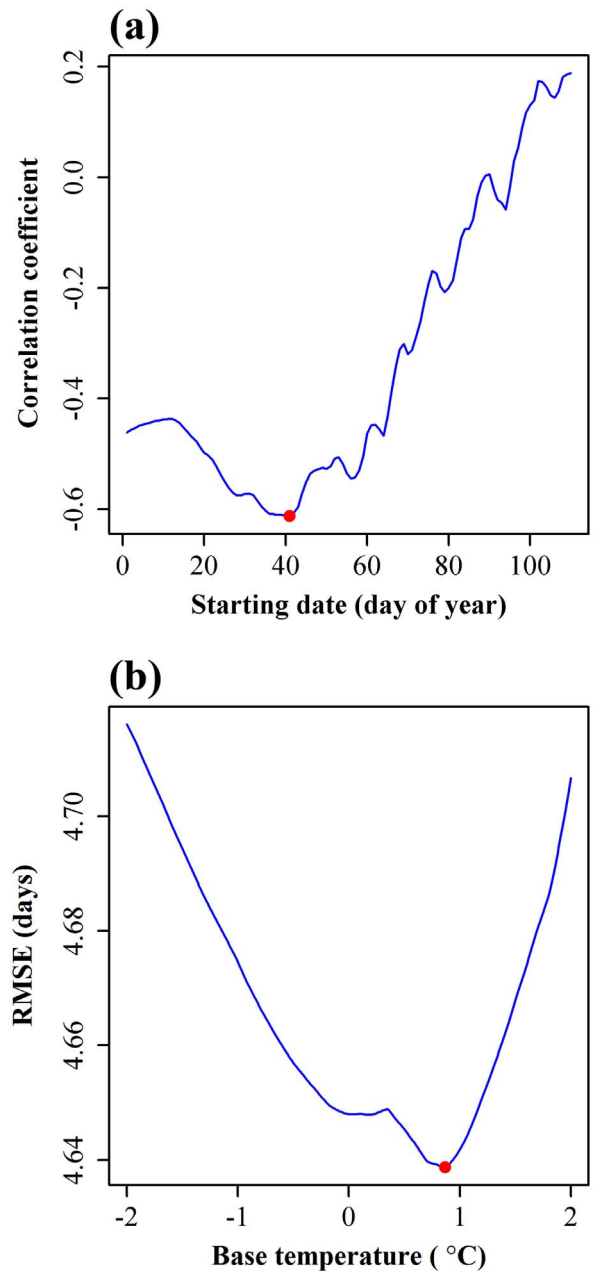


Fig. 2. Determination on the starting date and base temperature of first spring flowering of Japanese cherry trees using the accumulated degree days (ADD) method. (a) At different starting dates there are different correlation coefficients between the flowering times and the mean of daily mean temperatures from the starting date candidate to observed flowering time. The coefficient reaches the minimum when $S = 41$; (b) when $S = 41$, at 0.87 °C, the root mean squared error (RMSE) between the observed and predicted occurrence times reaches the minimum.

3. Results

The ADD method provides an estimate of starting date (in day of year) to be 41 (i.e., 10 February) and an estimate of base temperature to be 0.87 °C (Fig. 2). At the 41st day, the correlation coefficient between the flowering dates and the mean of daily mean temperatures from the candidate starting dates to the flowering dates is the lowest (= -0.61). That is, the higher the mean of daily mean temperatures during the period, the earlier the first flowering date of cherry trees in spring is. The RMSE is equal to 4.6387 days. Note in this method, we first estimated the starting date based on the smallest correlation coefficient, then estimated the base temperature using the lowest RMSE.

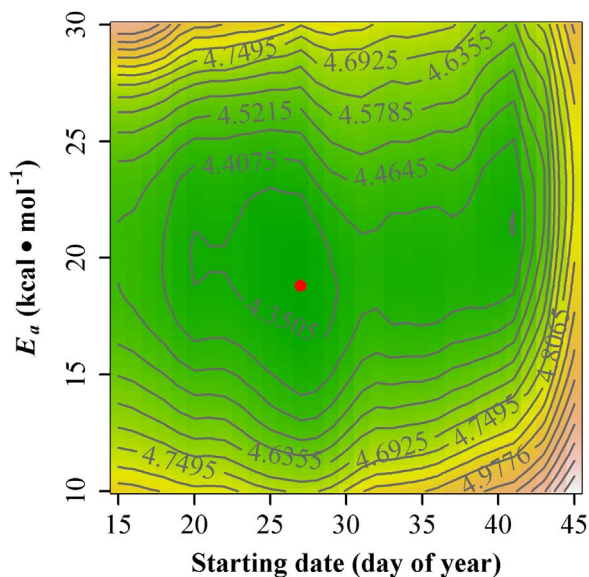


Fig. 3. The contour of root mean squared errors as a function of starting date and E_a using the number of days transferred to the 'standard' temperature (DTS). When $S = 27$ and $E_a = 18.77 \text{ kcal mol}^{-1}$, RMSE reaches the minimum.

The DTS method provides an estimate of the starting date around 27 (i.e., 27 January), and an estimate of the activation free energy (E_a) to be $18.77 \text{ kcal mol}^{-1}$, and the RMSE is equal to 4.2935 days, which is lower than that of the ADD method. It suggests the DTS method is better than the ADD method. Fig. 3 exhibits the RMSE contour in different combinations of S and E_a candidates.

The ADP method provides an estimate of starting date also around 27, the same as the estimate by the DTS method. However, the ADP method can provide the parameter estimates of B and E_a at the same time. $\hat{B} = 2.2668$, and $\hat{E}_a = 18.8840 \text{ kcal mol}^{-1}$ (where these hat symbols represent estimates for the parameters). The estimate of E_a of the ADP method is very close to that of the DTS method. The RMSE is equal to 4.2928 days, which is slightly lower than that of the DTS method. Fig. 4 exhibits the daily mean temperatures from the starting date to the first flowering date, the developmental rates based on the daily mean temperatures, and the comparison between the observed and predicted occurrence times of the first flowering in spring.

Fig. 5 shows the comparison of the prediction errors among three models using the training and test sets. Either the DTS or ADP method is better than the ADD method for both the training and test sets (Fig. 5a and b). For the test set, the ADP method is the best because it obtained the smallest median of RMSEs for 100 random divisions than the ADD and DTS methods. For the training set, it appears that the ADP and DTS methods can obtain the approximate prediction errors. In fact, we have limited the activation free energy (E_a) in the ADP method to be equal to the final estimate of the DTS method to make a balance comparison for the test set, and only the parameter B in the Arrhenius' equation was estimated using the optimization approach. If we also estimated E_a in the ADP method using the optimization approach, the RMSEs will be smaller than those using the DTS method. That is, for both the training and test sets, the ADP method is actually the best.

The optimal value of the critical low temperature is -5.6°C . Fig. 6 exhibits the effects of three indices of winter low temperatures on the residuals of occurrence dates unexplained by the ADP method. All three variables have significant effects on the residuals (all P values < 0.01 ; Table 1). The adjusted coefficient of determination is 0.471, and the deviance explained is 57.5%, that is, more than a half of the deviance of residuals that cannot be explained by the ADP method can be further explained by these three variables. Therefore, considering the influence of winter chilling is rather useful in further reducing errors in prediction (Fig. 7). After considering the influence of winter chilling,

the correlation coefficient between the observed and predicted occurrence times of the first flowering of cherry trees reaches 0.92 ($P < 0.001$), and the RMSE is only 2.7971 days for a 67-year time series. The secondary residuals (= observed occurrence dates – predicted occurrence dates – explainable residuals by using the above three winter low temperature variables) are obviously reduced (Fig. 7b). Using the Shapiro–Wilk test to examine whether the secondary residuals follow a normal distribution, we find that $W = 0.9849$ and $P = 0.5909 > 0.05$, which means that the secondary residuals are normal. We noted that there are smaller variations in flowering dates from 1951 to 1968 with 81.2 ± 1.5 days than the variations from 1951 to 2017 with 76.6 ± 7.2 days. However, the residuals from 1951 to 1968 do not exhibit smaller variations than those from 1951 to 2017 (Fig. 4c). After introducing the effects of winter low temperature and its duration, the most residuals from 1951 to 1968 largely decrease and the predicted occurrence times are on or approximate to the straight line of $y = x$ (Fig. 7a). It shows that winter low temperature and its duration explain why there are smaller variations in flowering dates from 1951 to 1968.

The increased winter low temperatures will result in the delay of the spring flowering of cherry trees by decreasing the chilling accumulation (Fig. 6a), while an increased number of days with low temperatures below a critical low temperature will also result in delayed spring flowering. However, these two variables are negatively correlated, with a correlation coefficient between x_1 and x_2 of -0.72 ($P < 0.001$). Thus, the increased mean winter low temperature will be followed by the reduced number of days with extreme low temperatures in winter, which will counteract the effect of the former by advancing flowering. Interestingly, the empirical critical value for the accumulation of chill hours is 7.2°C , which includes most daily minimum temperatures in winter, meaning that x_1 can reflect the traditional accumulation of chilling hours. From this, we draw the following conclusions: (i) if the mean of winter low temperatures is low, the number of days with extreme low temperatures will increase; (ii) if the mean of winter low temperatures is high, the number of days with extreme low temperatures will decrease; and (iii) these two variables will have converse effects on the occurrence dates of spring flowering of cherry trees. Whether a phenological event is delayed or advanced will to an extent rely on the trade-off between these two variables' effects. In order to judge which is more important in affecting the occurrence date, we dropped x_1 and x_2 separately and then together in the generalized additive model and checked the changes of the explained deviance. Without x_1 , the explained deviance is 26.9%; without x_2 , the explained deviance is 30.9%; without both these variables (with only x_3 remaining), the explained deviance is 12.6%. Obviously, the contribution of x_1 is greater than that of x_2 . Overall, the increase of mean winter low temperatures will delay the occurrence date of spring flowering of cherry trees by reducing the accumulation of chilling time.

4. Discussion

Compared with the ADD, DTS methods, the ADP method potentially has a wider use. It can apply to other nonlinear developmental rate curves that have a mathematical property of Jensen's inequality (Ruel and Ayres, 1999). There are many nonlinear equations in describing the temperature-dependent developmental rates of plants and poikilotherms (e.g., Wagner et al., 1984; Shi et al., 2016, 2017; Ratkowski and Reddy, 2017). For some phenological events occurring in summer or autumn, biological organisms experience extreme high temperatures in summer that can decrease the developmental rates. The Arrhenius' equation then need to be replaced by other non-linear equations such as the beta model (Yin et al., 1995), the square root model (Ratkowski et al., 1983). However, for the phenological events of early spring, the Arrhenius' equations appears to be suitable. In Eq. (2), we used a new parameter B that is the logarithm transformation of A to reduce the possibility of appearing a right long tail of distribution of model

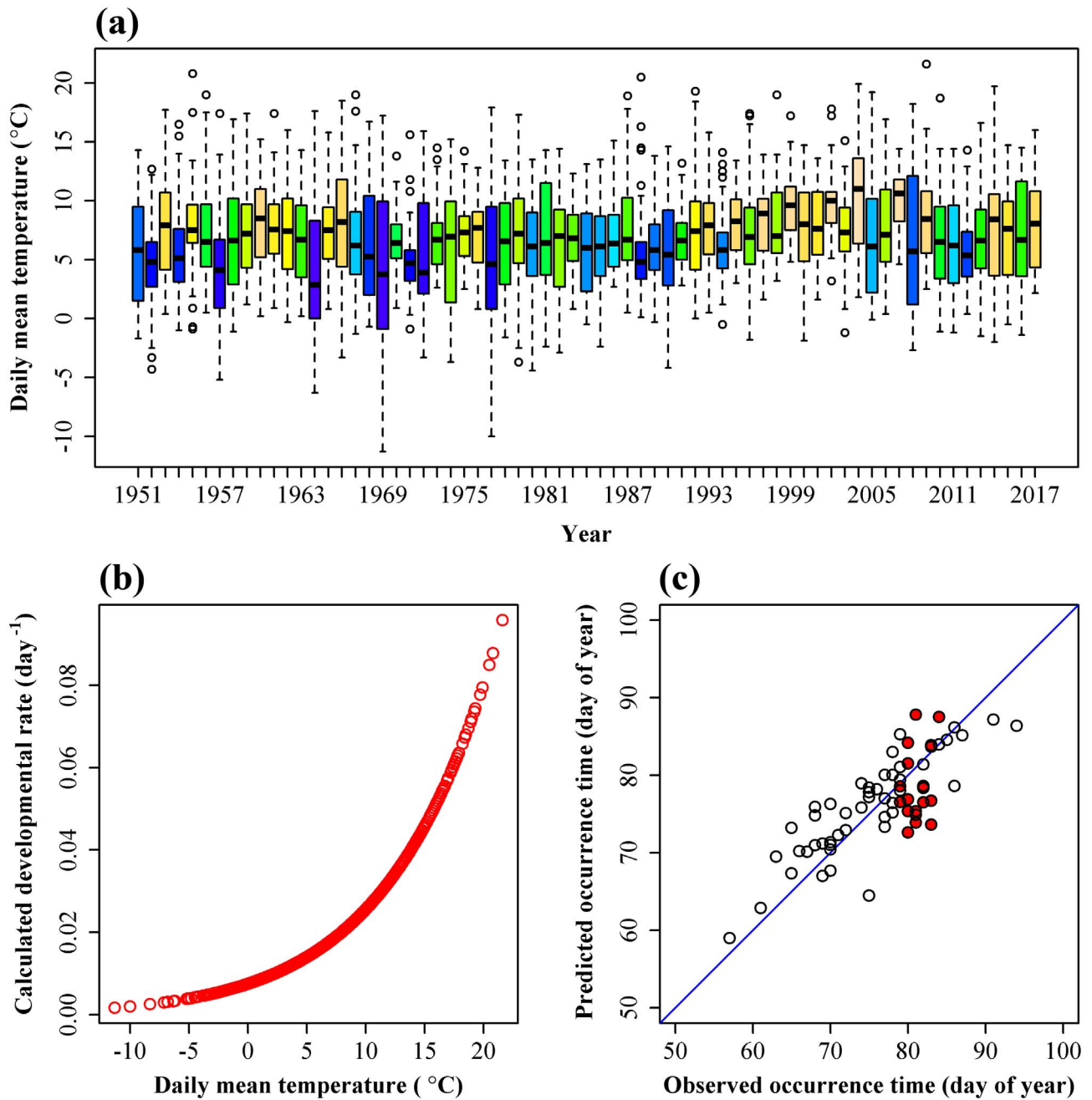


Fig. 4. Predicted results using the accumulated developmental progress (ADP) method based on Arrhenius' equation. (a) Boxplot of daily mean temperatures from the starting dates to the first observed flowering dates from 1951 to 2017, where different colors in boxes are used to help distinguish different medians of daily mean temperatures each year; (b) predicted developmental rate curve (namely Arrhenius' equation); (c) comparison between the observed and predicted occurrence times, where the red points represent the first flowering dates from 1951 to 1968. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

parameter. Here, we used the bootstrap method (Efron and Tibshirani, 1993) to check the robustness of parameter fitting using two cases of Arrhenius' equation with A and B , respectively. Fig. 8 exhibits the histograms of parameters' estimates in two cases using the 2000 bootstrap replications. The equation with parameter A apparently leads to a right long tail which deviates from a normal distribution (Fig. 8a), whereas another equation with parameter B has a better property of behaving close to a linear model. That is, the estimators of the set of parameters have distributions closely approximating a normal distribution (Ratkowsky, 1983; Fig. 8c and d). However, the 95% confidence interval of parameter E_a when using the equation with B shows wider than that with A (Fig. 8b and d).

Previous studies have suggested the accumulation of chilling hours to be linked to an empirical critical temperature, ranging from 7.2 to

10 °C (Aron and Gat, 1991). Luedeling and Brown (2011) compared three winter chill models (the dynamic model, the Utah model, and the chilling hours model) for fruit and nut trees, and found that the chilling time requirements were consistently defined most clearly by the dynamic model. If the hourly climatic data in a long-term time series are available, choosing a traditional winter chilling model might be ideal. Although several studies have proposed using the sine function based on the daily minimum and maximum temperatures to simulate hourly temperatures (Linville, 1990; Aron and Gat, 1991; Shi et al., 2012; Martínez-Lüscher et al., 2017), this could lead to large deviations from the actual readings. Indeed, many studies on winter chilling models have not provided a final comparison of predicted occurrence dates with the actual observations, probably due to the lack of long-term phenological records or the lack of hourly meteorological data

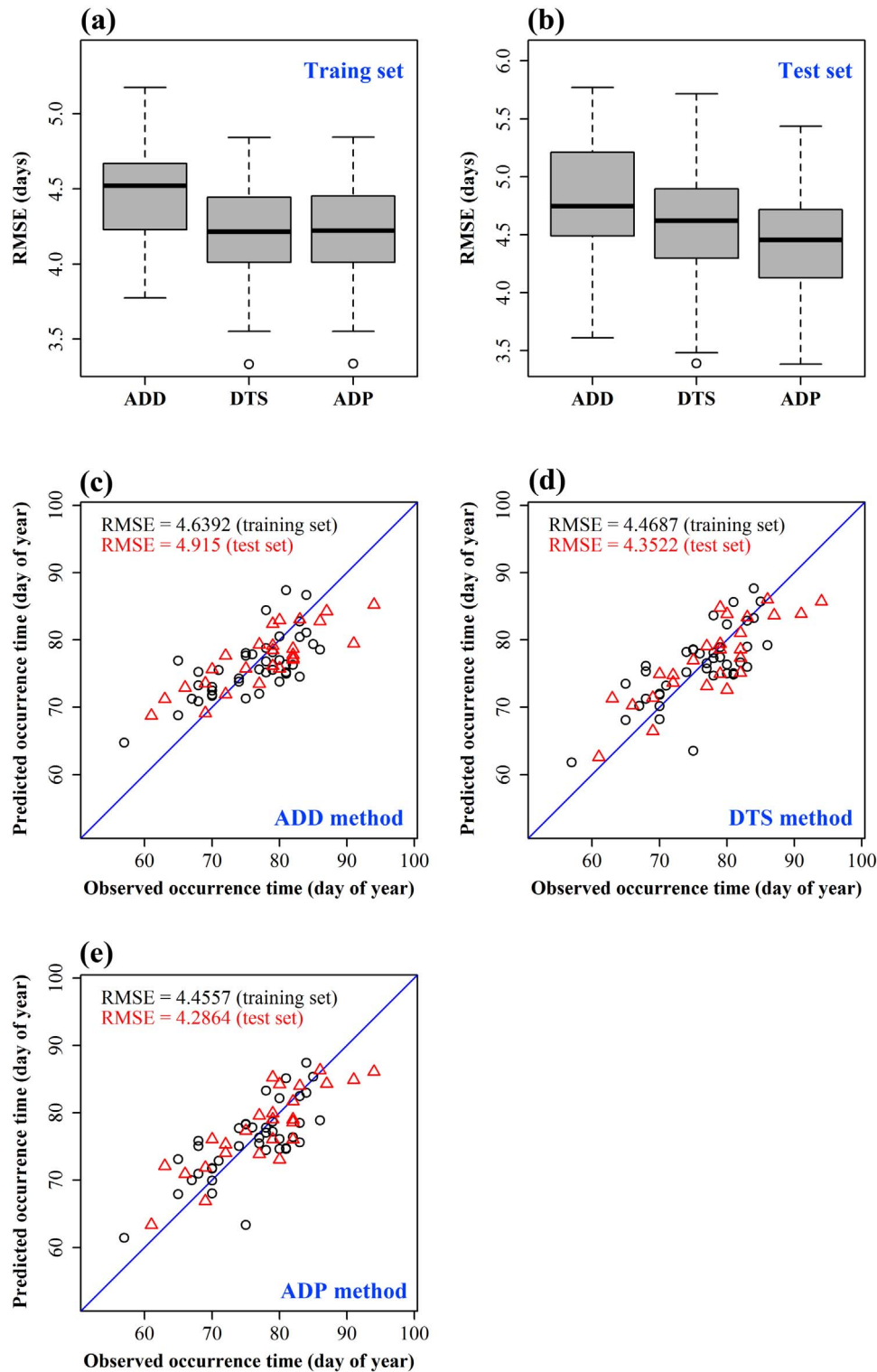


Fig. 5. Comparison of the prediction errors among three methods based on the 100 random divisions for training and test sets. (a) RMSEs for the training set; (b) RMSEs for the test set; (c) an example using the accumulated degree days (ADD) method; (d) an example using the number of days transferred to the 'standard' temperature (DTS) method; (e) an example using the accumulated developmental progress (ADP) method. The black open circles represent the training set, and the red open triangles represent the test set. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Guo et al., 2015). Therefore, it appears practical in the present study to use daily minimum temperatures in winter as the proxy for the accumulation of chilling time.

Under the scenario of global warming, winter temperatures are usually expected to rise (Ungerer et al., 1999; Fu et al., 2015). Fu et al. (2015) studied the effect of rising winter and spring temperatures on

the advance of spring leaf unfolding and found that a reduced accumulation of chilling time might counteract the advance of leaf unfolding caused by high early spring temperatures. Martínez-Lüscher et al. (2017) recently reported that with temperature increasing the flowering time of apricot in Southern UK remained relatively unchanged because the delayed chilling might counteract flowering

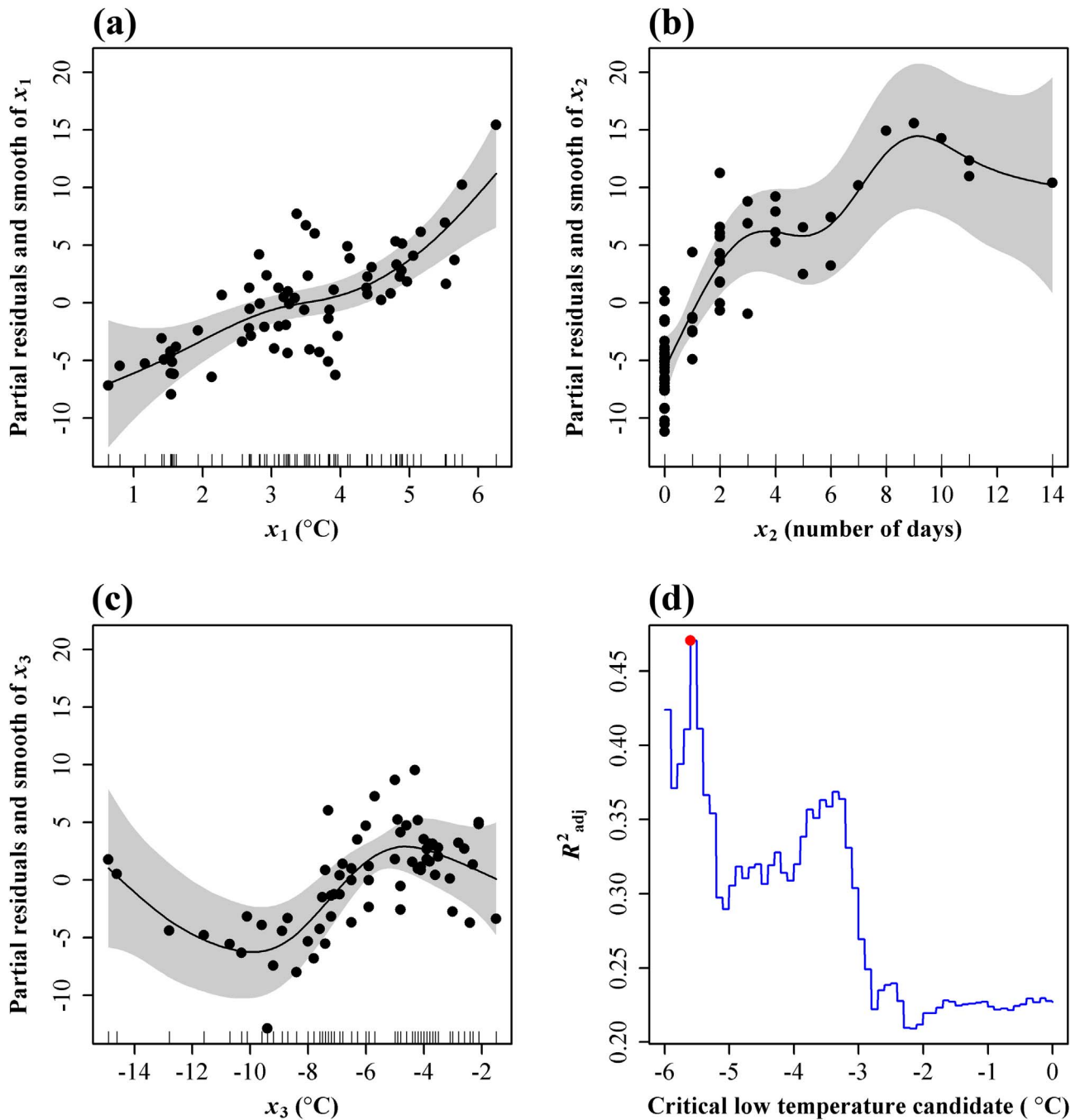


Fig. 6. Generalized additive model fit to: (a) x_1 , the mean of daily minimum temperatures from 1 November of the preceding year to the starting date (27 January); (b) x_2 , the number of days with daily minimum temperature ≤ -5.6 °C during the period from 1 November of the preceding year to the starting date; (c) x_3 , the minimum annual extreme temperature; (d) it exhibits the effects of different the low critical temperature candidates on the adjusted coefficient of determination of the generalized additive model fit. The critical low temperature in (b) is actually the consequence of (d).

advances. However, different from the results of [Fu et al. \(2015\)](#), [Martínez-Lüscher et al. \(2017\)](#) did not find that rising temperature decreased the chilling accumulation but it delayed the onset of chill accumulation and the completion of the average chill accumulation necessary to start heat accumulation. Our study here revealed a different counteracting pattern. There is a counteracting effect between the mean winter low temperatures and the number of days with extreme low temperatures. It indicates that winter low temperatures might have fewer influence on the first flowering time relative to the heat (or rate) accumulation in early spring because two key variables of winter weather counteracts each other.

Compared to other phenological models (e.g., [Hänninen, 1990](#); [Kramer, 1994](#); [Chuine, 2000](#); [Chuine et al., 2016](#); [Hänninen, 2016](#)), the

ADP method is simpler and easier to implement. The Arrhenius' equation has a clear thermodynamic meaning ([Eyring, 1935](#); [Sharpe and DeMichele, 1977](#); [Shi et al., 2017](#)), allowing us to divide the effects of temperature rise on the occurrence time of a phenological event into two parts: (1) the effect of winter low temperatures on the time for endodormancy release, and (2) the effect of early spring temperatures on the development (i.e., ecodormancy release) after completing the first stage. The effect of the chilling accumulation has not been consistently defined and explored in literature ([Chuine, 2000](#); [Hänninen, 2016](#)). For instance, [Chuine et al. \(2016\)](#) used 11–13 records for predicting the budbreak/flowering dates of three species, and the calculated RMSE values are rather high (see Table 2 in [Chuine et al. \(2016\)](#)). For walnut ($n = 11$), all the RMSE values exceed 5 days. The

Table 1
Fitted results using the generalized additive model ($n = 67$).

Item	Reference degrees of freedom	F	P	R^2_{adj}	Deviance explained
$s(x_1)$	4.189	7.391	< 0.01	0.471	57.5%
$s(x_2)$	6.557	3.993	< 0.01		
$s(x_3)$	5.217	3.425	< 0.01		

Here, $s(\cdot)$ represents smoothing function. x_1 represents the mean of daily minimum temperatures from 1 November of the preceding year to the starting date (27 January); x_2 represents the number of days with low temperatures $\leq -5.6^\circ\text{C}$ during the period from 1 November of the preceding year to the starting date; x_3 represents the minimum annual extreme temperature. The response variable is the residuals between the observed and predicted occurrence dates by using the ADP method.

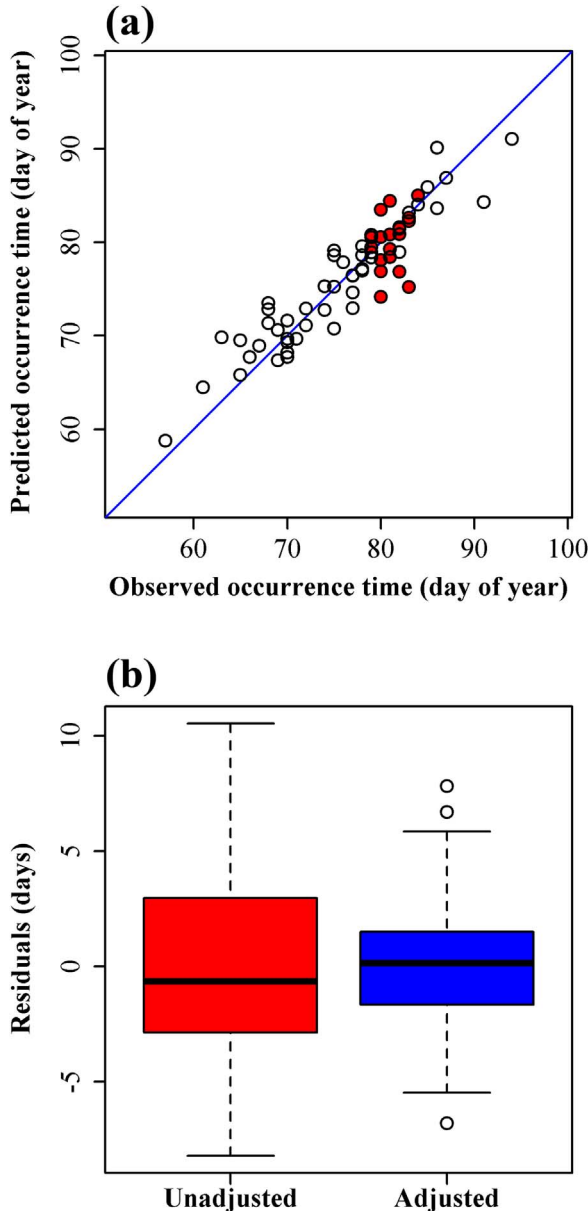


Fig. 7. Effect of winter low temperatures on the predicted residuals. (a) Comparison between the observed and predicted occurrence times before and after considering the effects of winter low temperatures on the residuals, where the red points represent the flowering dates from 1951 to 1968; (b) comparison of the predicted residuals between neglecting the effect of winter low temperatures (unadjusted) and considering the effect of winter low temperatures (adjusted). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

calculated RMSE in the present study is only 2.8 days for $n = 67$ after considering the effects of winter low temperatures.

Hänninen (1990) introduced a ‘competence’ function to consider the effect of chilling temperatures, as a weight between 0 and 1, when calculating the developmental rate under a given forcing temperature. Of the four models (sequential, parallel, deepening rest, and four phase) proposed for the competence function, the sequential model assumes that the development can only start when the chilling accumulation reaches a critical value, and the corresponding competence function is equal to 0 before this critical value and 1 thereafter. Other three models, however, lack support from rigorous experimental observations. It is, nonetheless, difficult to justify the weighted summation of the effects of chilling temperatures and forcing temperatures. We must also admit that the generalized additive model used in the present study also lacks a theoretical support of thermodynamics. However, the chosen variables can significantly reduce the residuals, signifying their contribution to variance explained.

To this end, Chuine et al. (2016) have proposed a ‘unified’ model for budburst of trees. However, their model combines many empirical formulae and assumes a negative exponential relationship between the critical state of forcing and the total state of chilling. This assumed negative exponential relationship could enhance calculation errors in practice. Interestingly, Chuine (2000) has demonstrated that the negative exponential relationship does not normally exist. There seems to be further some confusion on the definition of biological development in Chuine (2000) and Chuine et al. (2016). In the former reference, it was defined as the growing degree days (i.e., accumulated degree days); however, in the latter one, it was defined as the sum of the daily rates of development. As mentioned above, developmental rate can be defined as $r = a + bT = 1/k (T - T_0)$, where k represents the thermal time required for completing a developmental stage. In Chuine (2000), the developmental rate is defined as $T - T_0$, which mandatorily constrains all thermal times for different phenological events and for different tree species to a constant (i.e., $k = 1$). Chuine (2000) and Chuine et al. (2016) do not follow the method of Hänninen (1990, 2016) as no competence function was considered.

There is no convincing evidence to demonstrate the existence of an explicit and strong relationship between the effect of chilling accumulation and that of heat accumulation on the first flowering time. Also, there is no any general rule for defining the critical starting date and threshold temperature for chilling accumulation of the plants in different climatic zones. Sugiura et al. (2010) studied the threshold temperature for the chilling accumulation of the flower bud of the ‘Hakuho’ peach (*Prunus persica* L. Batsch) using 8 candidate temperatures from -6 to 15°C in 3°C increments, and found that 6°C with 1400-h chilling accumulation was most effective for breaking the endodormancy. However, such an elaborate experiment still cannot explicitly distinguish the effect of chilling accumulation from that of heat accumulation. 6°C might exceed the lower developmental threshold at which heat accumulation starts. With regard to the cherry tree in the subtropical monsoon region, its first flowering time was also largely affected by winter low temperatures as shown by the present study. Of course, a suitable method by correctly defining the chilling requirement without doubt can reflect the effects of winter low temperatures (e.g., Guo et al., 2015; Martínez-Lüscher et al., 2017), and vice versa. However, we argue that there is no relevant evidence to clearly elucidate the physiological mechanisms of the effect of chilling requirement on the first flowering time of cherry trees. In fact, the physiological mechanisms controlling bud burst and flowering of plants in early spring are not precisely known (Allen et al., 2014). Moreover, there is a flaming dispute on whether the effects of chilling accumulation and heat accumulation are overlapped in time (Allen et al., 2014; Chuine et al., 2016; Martínez-Lüscher et al., 2017). There are too much theoretical hypotheses and models around this question that were proposed to provide a key, but no one can state that their methods are absolutely correct and general for bud burst, flowering, leaf-unfolding

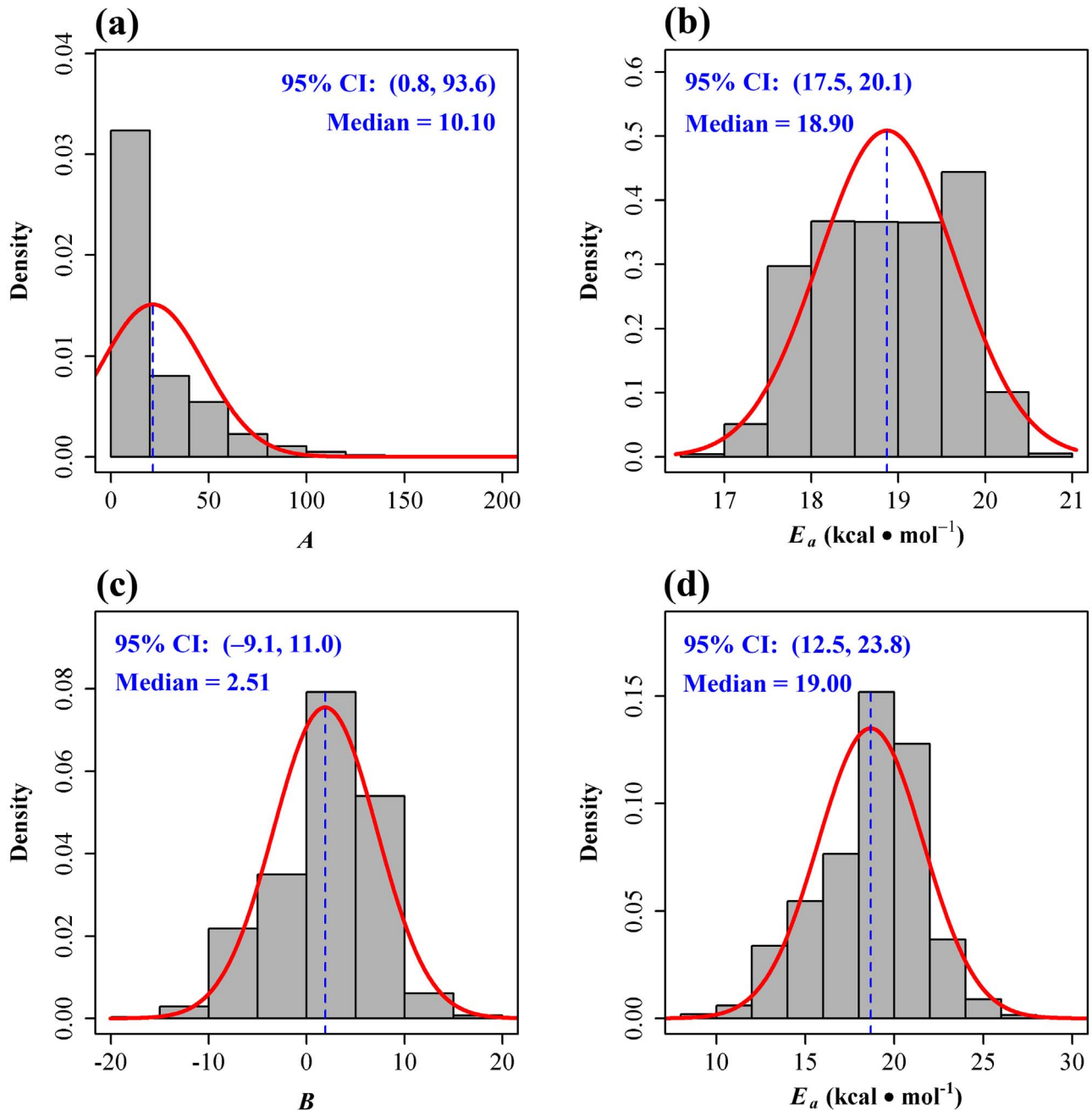


Fig. 8. Histograms of the bootstrap replications of model parameters. (a) and (b) come from the Arrhenius' equation with parameter A , whereas (c) and (d) come from that with parameter B . Please see Eq. (2) for details. The number of bootstrap replications is 2000 for every panel. The red bell-shaped curve represents the probability function of the normal distribution. 95% CI represents 95% confidence interval based on 2000 simulations.

of different plants (also shooting for many bamboo species) in spring. However, the effects of winter low temperatures on the development, growth and survival of plants and poikilotherms are empirically observed and explained (e.g., Uvarov, 1931; Ungerer et al., 1999; Shi et al., 2012; Hänninen, 2016). Our recent thermal experiment on the occurrence times of seedlings emergence and leaf-unfolding of four bamboo species has further demonstrated that there is a strongly linear relationship between temperature and developmental rate in the mid-temperature range (unpublished data). Liu et al. (2006) reported that the developmental time of bud sprouting of *Platanus acerifolia* Willd. decreased with increasing temperature (from 15 to 25 °C). For a whole thermal range (from the lowest threshold temperature to the highest threshold temperature), there is a right-skewed bell-shaped curve for the forcing temperature effect (Campbell et al., 1974). Sharpe and

DeMichele (1977), and Ratkowsky et al. (2005) already clearly provided detailed physiological and thermodynamic explanations. These explanations and predictions can fit the actual observations of temperature-dependent developmental rates for many species well (especially for crops, aquatic and terrestrial arthropods; e.g., Watts, 1972; Quinn et al., 2013; Ratkowsky and Reddy, 2017). In addition, we need point out that the previous models that combined the effect of chilling requirement and forcing requirement produced large prediction errors, which were reflected by large RMSEs between the observed and predicted occurrence times. We did not attempt to compare our methods with those in the present study, because there are too much 'integrated' models with different critical values for calculating the chilling accumulation. We must admit that an integrated phenological model combining the effects of winter low temperatures (or chilling

accumulation) and early spring temperatures (or heat accumulation) is probably better in further increasing the goodness of fit. However, we stopped such an attempt based on the following two points: (i) the physiological mechanism of winter low temperatures' effect is unknown, and (ii) some phenological events occurring in other seasons are not affected by winter low temperatures. In this case, to use a non-parametric fitting technique such as generalized additive model (Hastie and Tibshirani, 1990; Hastie et al., 2009) in the present study to fit the residual data is then reasonable. This technique need not know the interacting mechanism. In spite of a possibility of over-fitting, the plots of partial residuals still could reflect the impact tendencies of all predictors. Even though we did not develop an integrated model, the goodness of fit is still overall better than the reported results by the relevant references we have searched (e.g., Chung et al., 2011; Allen et al., 2014; Chuine et al., 2016).

Some phenological models have considered the effects of other factors, such as the age structure of trees, drought, photoperiod and precipitation, and some microsite covariates including aspect, slope and elevation of individual tree on the occurrence time (Gienapp et al., 2005; Ohashi et al., 2012; Allen et al., 2014). These factors are probably useful for further reducing the prediction errors for a short-term time series. However, microsite factors were less important predictors than climatic variables especially daily air temperature for a long-term time series (Allen et al., 2014; Martínez-Lüscher et al., 2017). In any case, the calculated correlation between observations and predictions has reached 0.92 in this study, demonstrating convincingly that temperature is still the cardinal determinant for early spring phenology of plants.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.04.001>.

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