

Response of chestnut phenology in China to climate variation and change



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ABSTRACT

Climate change has affected the phenology of plants and animals throughout the world, but few studies have evaluated climate responses of fruit trees in East Asia. In particular, the response of tree phenology to warming during different parts of the year has not been explored. We evaluated long-term records (1963–2008) of chestnut (*Castanea mollissima* Blume) first flowering, leaf coloring and length of the growing season from Beijing, China. Phenological dates were related with daily temperatures (subjected to an 11-day running mean) for the 12 months leading up to the respective events, using Partial Least Squares (PLS) regression. For each phenological indicator, regression results identified two relevant phases, during which temperatures were correlated with event timing or growing season length.

First flowering dates in Beijing advanced by 1.6 days per decade over the length of the record, whereas leaf coloring showed no significant trend. The growing season expanded by 4.3 days per decade. First flowering was advanced by high temperatures between January and June, but delayed by warm conditions during the chill accumulation phase (late October through early January). Leaf coloring was advanced by warm conditions during most of the growing season, but delayed by high temperatures in fall. Variation in the length of the growing season was strongly correlated to variation in spring phenology.

All phenological indicators of chestnut appeared to respond to high temperatures during certain parts of the growing season in a way that ran counter to currently dominant effects. For instance, warming during the period of chill accumulation delayed rather than advanced spring phenology. These secondary temperature responses may explain responses of certain plants and ecosystems that are not in line with general trends of advanced spring and delayed fall phases. It seems possible that the importance of these effects may increase as warming continues.

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1. Introduction

Climate change has affected the timing of life events of plants and animals in recent decades. A number of methods have been used to examine these responses, including species-level ground observation, satellite remote sensing and direct warming experiments (Badeck et al., 2004; Cleland et al., 2007; Wolkovich et al., 2012). Most studies have indicated that spring phenological events (e.g. leaf unfolding and first flowering) and fall phenological events (e.g. leaf coloring and fall) have been advanced

and delayed, respectively, resulting in longer growing seasons (Matsumoto et al., 2003; Menzel and Fabian, 1999). However, some exceptions to these general observations have been detected at high latitudes and high altitudes (e.g. Iceland, Kola Peninsula of Russia, and the Tibetan Plateau of China), where delayed spring events, advanced fall phenology or shortened growing seasons appeared (Frich et al., 2002; Kozlov and Berlina, 2002; Yu et al., 2010).

The majority of published studies have focused on phenological changes in natural vegetation. Relatively few reports are available on the response of fruit trees to climate change despite the high economic and agricultural values of these crops (Chmielewski et al., 2004). In Germany, first flowering dates of apple and sweet cherry advanced by about 2.1 days per decade from 1961 to 2000. Bloom dates there were significantly correlated with mean temperatures between February and April, with tree phenology advancing by about 5 days per 1 °C increase during this period (Chmielewski

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et al., 2004). In France and Switzerland, advanced flowering has also been observed in apple and pear trees over the last 40 years (Guédon and Legave, 2008). In the northeastern United States, flowering of apple and grape was advanced by 2.0 and 1.5 days per decade, respectively, from 1965 to 2001 (Wolfe et al., 2005). In South Africa, full bloom dates of apple and pear have advanced on average by 1.6 days per decade from 1973 to 2009, and by 3.6 days per 1 °C rise in mean spring temperature (Grab and Craparo, 2011). Relevant reports from Asia are scarce. In Japan, the combined effect of advanced budding and delayed leaf fall for ginkgo extended the growing season by 12 days between 1953 and 2000 (Matsumoto et al., 2003). In China, researchers at the Institute of Geographic Sciences and Natural Resources Research at the Chinese Academy of Sciences (IGSNRR-CAS) investigated the response of woody plants to climatic change in Beijing, North China, as well as in the entire country, mentioning phenological changes of certain fruit trees (Bai et al., 2011; Ge et al., 2011; Xu et al., 2005; Zheng et al., 2006, 2003; Zhong et al., 2010).

Generally, most of the above studies conduct regression analyses between monthly or annual mean temperatures and phenological events to estimate the response of phenology to climate change. However, climate data at a monthly or annual scale might not be detailed enough for considering specific temperature effects on phenology that are restricted to particular parts of the year (Matsumoto et al., 2003). For example, there is evidence that only temperature increases during certain periods advance spring events, while warming during some stages of winter dormancy might have a phenology-delaying effect (Luedeling et al., 2012). For flowering and leaf emergence, temperate fruit and nut trees require the fulfillment of a chilling requirement (Campoy et al., 2011; Luedeling, 2012). Particularly in warm growing regions, but possibly also in colder places, warming during the chill accumulation phase should cause a delay in the fulfillment of chilling requirements, which could precipitate into a delaying effect on spring phases. The abundance of reports on advanced bloom and leaf emergence (Fitter and Fitter, 2002; Menzel et al., 2006; Parmesan, 2007) indicates that the effect of winter warming has thus far been small compared to the impact of rising temperatures in spring. Yet theory dictates that the winter warming effect exists and could become important, as temperatures increase further. Severe future losses in winter chill have been projected for many places, indicating future problems for several important fruit producing regions (Darbyshire et al., 2013; Luedeling et al., 2011a, 2009c). Commonly reported linear models of advancing phenology are not normally capable of accounting for such effects. It is noteworthy in this context that many studies of spring phenology trends that considered large numbers of species, while showing advancing phenology for most, have often included a sizeable number of 'diverging species' (Cook et al., 2012), which have either shown no change in phenology or even displayed delays. Cook et al. (2012) recently linked these diverging responses to winter warming. While less information is available on fall events, it also seems likely that the timing of leaf coloring or leaf fall is driven by temperature responses during certain periods only (Menzel, 2003).

Our analysis was based on an observational record of chestnut phenology from Beijing, China, where bloom, leaf unfolding and leaf coloring have been recorded since 1963. A novel method (Partial Least Squares regression) was used to correlate the phenology dates to temperature variation at daily resolution. The objective of the present study is to identify the relevant periods influencing chestnut phenological stages and to comprehensively evaluate the responses of spring event (first flowering), fall event (leaf coloring) and the length of the growing season to temperature variation during the relevant periods.

2. Materials and methods

2.1. Study area

Located on the North China Plain, Beijing has the longest and most abundant records of phenology in China (Zhang et al., 2005). Compared to American and European zones at similar latitude, climatic variation in Beijing is substantially greater, leading to greater variation in the timing of phenological events and providing valuable information for elucidating climate responses of species (Lu et al., 2006).

In Beijing, species-level phenological observations of plants were conducted in Beihai Park and Summer Palace. Both parks are former royal gardens with a long history of more than 150 years. The former is located in the city center, and the latter is in the suburbs. To reduce the influence of the urban heat island effect, we chose the Summer Palace (40°01' N, 116°20' E, 50 m a.s.l.) as the research site.

2.2. Phenology data

Phenological data of chestnut (*Castanea mollissima* Blume) at Beijing Summer Palace during 1963–2008 were acquired from the Chinese Phenological Observation Network (CPON) – a nationwide system of monitoring stations that has conducted standardized, systematic and comprehensive phenological observations of plants and animals across China since 1963. Details of the phenological observation method have been described by Wan and Liu (1979) and Lu et al. (2006). All observations were carried out daily during the growth period on the southern side of the trees. For analysis of the relationship between chestnut phenology and climatic variation during the whole year, we chose first flowering as indicator of spring phenology, and leaf coloring as indicator of fall events. First flowering was registered when 10% of flowers were open, corresponding to stage 61 on the BBCH ('Biologische Bundesanstalt Bundessortenamt und Chemische Industrie') scale for pome and stone fruits (Meier et al., 1994; applied here, because we are not aware of a scale for chestnuts). Leaf coloring dates (BBCH stage 95) were recorded when 50% of leaves had changed color (Chen et al., 2005). For calculating the length of the growing season, we interpreted first leaf unfolding (stage 11 on the BBCH scale) and leaf coloring as signs of start and end of the growing season (Chen et al., 2005; Dai et al., 2012).

2.3. Climatic data

Daily minimum and maximum temperatures in Beijing during 1963–2008 were obtained from the Beijing Meteorological Station which is only 2.5 km from the Summer Palace, so that temperatures recorded there should closely mirror conditions at the observation site. Mean daily temperatures were computed as the arithmetic mean between minimum and maximum temperatures (Luedeling et al., 2012). To ensure the emergence of recognizable temperature response patterns of phenological stages in subsequent statistical analyses, we subjected daily temperatures to an 11-day running mean (Luedeling and Gassner, 2012; Luedeling et al., 2012).

2.4. Identification of relevant periods influencing chestnut phenology

Partial Least Squares (PLS) regression was used to analyze the response of chestnut phenology (first flowering, leaf coloring, and length of growing season) to variation in mean daily temperatures during all 365 days of the year, based on data for 1963–2008. PLS regression, a procedure commonly used in chemometrics (Wold et al., 2001) and hyperspectral remote sensing (Luedeling et al.,

2009b), is a regression technique that can be used reliably in situations, where independent variables are highly auto-correlated and where the number of independent variables exceeds the number of observations. Such situations are encountered in relating variation of plant phenology to temperature records at high temporal resolution, and recent work has shown that PLS regression can effectively be used in this context (Luedeling and Gassner, 2012; Luedeling et al., 2012; Ranjitkar et al., 2013; Yu et al., 2012, 2010). The two major outputs of PLS analysis are the variable importance in the projection (VIP) and standardized model coefficients. The VIP values reflect the importance of all independent variables for explaining variation in the dependent variables. The VIP scores are based on a weighted sum of squares of the PLS loadings and calculated for each variable. The threshold for the importance of VIP is commonly set to 0.8 (Wold, 1995), so we adopted this threshold for our analyses. The standardized model coefficients indicate the strength and direction of the impact of each variable in the PLS model. Centering and scaling of dependent and independent variables is necessary to allow comparison between different variables (Luedeling and Gassner, 2012).

PLS regression was used to relate chestnut phenological stages to daily temperatures between 1963 and 2008. Dependent variables were thus the phenological dates (expressed in day of the year), while independent variables used for building PLS models were mean daily temperatures for 365 days preceding the typical timing of the respective phenological stage. The root mean square errors (RMSE) of the regression analyses were calculated to clarify the accuracy of PLS models. In all PLS analyses, the number of latent factors was defined through cross-validation as the smallest number of factors that explained 30% or more of the variation in the independent (temperature) variables. Periods with VIP scores greater than 0.8 and high absolute values of model coefficients represent the relevant phases influencing chestnut phenology timing. Two distinct phases were determined for each phenological stage. These phases were marked by accumulation of important variables ($VIP > 0.8$), which were either predominantly negative or positive for extended periods of time. Positive coefficients indicate that warm temperatures during the respective period are related to delayed phenology, while negative coefficients imply a correlation between warm conditions and earlier occurrence of phenological events.

2.5. Response of chestnut phenology to mean temperatures during the relevant periods

Linear regression was used to analyze temporal trends in chestnut phenology, based on data between 1963 and 2008. Trends were tested for statistical significance using the Mann–Kendall test (Tao et al., 2006). Since PLS regression indicated that plant event timing was related to temperature variation during distinct phases, we explored relationships between phenological event timing and mean temperature during the relevant periods using linear regression. Results were assessed for significance using analysis of variance. We also calculated the RMSE to evaluate the regression results.

For all PLS analysis results, two distinct relevant phases emerged, during which independent variables were mostly important and model coefficients were either consistently negative or consistently positive. To investigate the relationship between phenology timing and mean temperatures during these two relevant periods, we constructed three-dimensional temperature response surfaces. These surfaces were produced using the Kriging technique to interpolate phenology timing as a function of temperatures during both relevant periods. For Kriging, we assumed an exponential relationship between phenological dates and distance in the

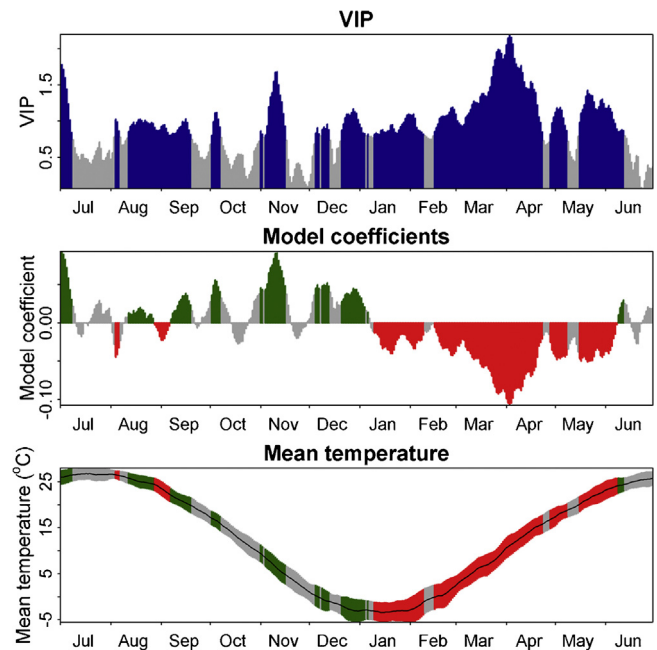


Fig. 1. Results of Partial Least Squares (PLS) regression correlating first flowering dates for chestnut at Beijing Summer Palace with 11-day running means of daily mean temperatures from the previous July to June. Blue bars in the top panel indicate VIP values greater than 0.8, the threshold for variable importance. In the middle and bottom panels, red color means the model coefficients are negative (and important), while the green color indicates positive (and important) relationships between flowering and temperature. The black line in the bottom figure stands for the mean temperatures, while the gray, green and red areas represent the standard deviation of daily mean temperatures for each day of the year. (For interpretation of the references to color in figure legend, the reader is referred to the web version of the article.)

climatic space. Default settings of the Kriging procedure in the R package ‘fields’ (Furrer et al., 2012) were used in the interpolation.

All analyses were implemented in the R 2.15.2 programming language (R Development Core Team, 2012). We included all procedures used in this study into the package ‘chillR’ (Luedeling, 2013), which relies heavily on the ‘pls’ package (Mevik et al., 2011).

3. Results

3.1. Relevant periods for chestnut first flowering

During 1963–2008, the average first flowering date of chestnut at Beijing Summer Palace was the 2nd of June. The 365 daily temperatures between the previous July and June were used as independent variables in the PLS regression, while dependent variables were chestnut first flowering dates, expressed in day of the year. A low root mean square error (RMSE) of 2.33 days for the resulting PLS model indicated that the model was a good fit for the data. Based on the VIP and standardized model coefficients of the PLS regression, we identified two periods, during which temperatures showed significant correlations with chestnut first flowering (Fig. 1).

Between 25 October and 7 January, model coefficients were mostly positive and VIP values mostly exceeded 0.8 (the threshold for variable importance), indicating that higher temperatures were related to a delayed first flowering of chestnut. This effect was clearly visible between 5 and 17 November, between 4 and 13 December, and between 21 December and 7 January. Model coefficients varied during this phase, which also included a short spell with negative model coefficients and VIP values less than 0.8. This variation might indicate that the timing

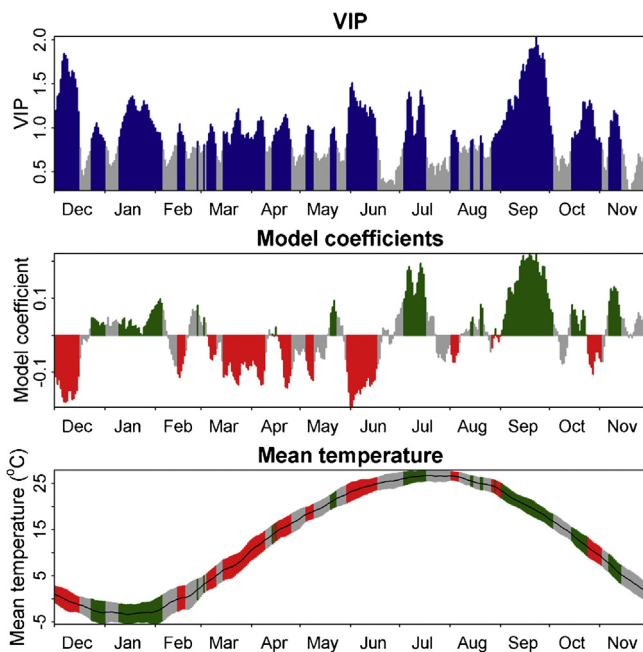


Fig. 2. Results of Partial Least Squares (PLS) regression correlating leaf coloring for chestnut at Beijing Summer Palace with 11-day running means of daily mean temperatures from the previous December to November. See caption of Fig. 1 for a full explanation.

of this temperature response varied from year to year. Alternatively, it seems possible that the strength of the temperature effect varied throughout the dormancy period, with cool temperatures at the beginning and end of the above-mentioned phase being more strongly related to early bloom than temperatures in the middle of the phase. Taking a broader view at model coefficients and VIP scores during this period, we interpreted the entire period (25 October to 7 January) as one relevant phase for the timing of chestnut first flowering.

Between 8 January and 8 June, model coefficients were consistently negative and VIP values were almost always important, justifying consideration of the entire period as a homogeneous block, during which high temperatures were correlated with earlier chestnut flowering.

3.2. Relevant periods for chestnut leaf coloring

During 1963–2008, the average leaf coloring date of chestnut was the 1st of November. The 365 daily temperatures between the previous December and November were used as independent variables in the PLS analysis. These were related to the timing of chestnut leaf coloring, expressed in day of the year. The resulting model was a good fit for the data, with RMSE of 2.34 days. Based on the VIP and standardized model coefficients of PLS regression, relevant periods for chestnut leaf coloring were identified (Fig. 2).

While distinct phases could be distinguished in the PLS output figures, the relationship between temperature and leaf coloring was not as clear-cut as for first flowering. During the winter (1 December to 4 March), no consistent responses could be identified. Positive responses were almost offset by negative ones. So we did not take this period into consideration for explaining variation in chestnut fall phases.

During spring and early summer (5 March to 27 June), most model coefficients were negative and VIP scores were greater than 0.8, indicating that higher temperatures advanced leaf coloring. This observation led us to consider this period as a relevant phase for chestnut leaf coloring. After 27 June (especially in fall), most

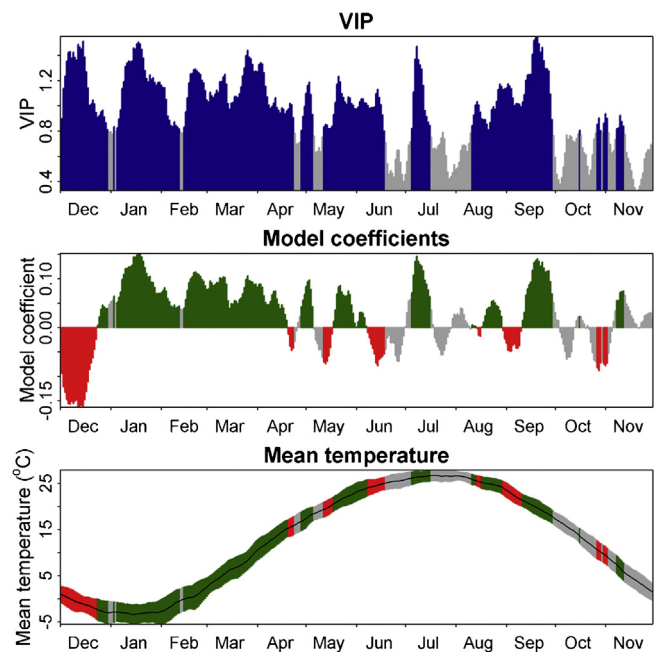


Fig. 3. Results of Partial Least Squares (PLS) regression correlating growing season length for chestnut at Beijing Summer Palace with 11-day running means of daily mean temperatures from the previous December to November. See caption of Fig. 1 for a full explanation.

model coefficients were positive. Model coefficients and VIP values were both greatest between 2 September and 6 October. Since effects appeared particularly pronounced for the latter phase, we regarded 2 September to 6 October as another relevant phase for chestnut leaf coloring.

3.3. Relevant periods for chestnut growing season length

The length of the growing season was defined as the period between first leaf unfolding and leaf coloring. During 1963–2008, the average first leaf unfolding date of chestnut was 23rd of April and the average leaf coloring date was 1st of November. The 365 daily temperatures between the previous December and November were used as independent variables for the PLS analysis, while the dependent variable was the length of the chestnut growing season. The RMSE for this model was 4.60 days. Relevant periods for chestnut growing season length are shown in Fig. 3. Between 1 December and 23 December, higher daily temperatures were related to shortening of the chestnut growing season. Between 24 December and 19 April, all model coefficients were positive and VIP scores greater than 0.8. This indicated that in winter and spring, high daily temperatures extended the length of the season. After 19 April, there was no consistent relationship between daily temperatures and growing season length. Relevant periods considered for further analysis were thus 1 December to 23 December and 24 December to 19 April.

3.4. Response of chestnut phenology to mean temperatures during the relevant periods

At the Summer Palace, chestnut flowering date showed a significant advancing trend, by 1.6 days per decade ($p < 0.01$, RMSE of 4.04 days) between 1963 and 2008 (Fig. 4). The advance in blossoming was significantly related to mean temperatures during 8 January and 8 June. First flowering advanced by 2.4 days per 1°C rise of mean temperature during this period ($p < 0.01$). Temperatures

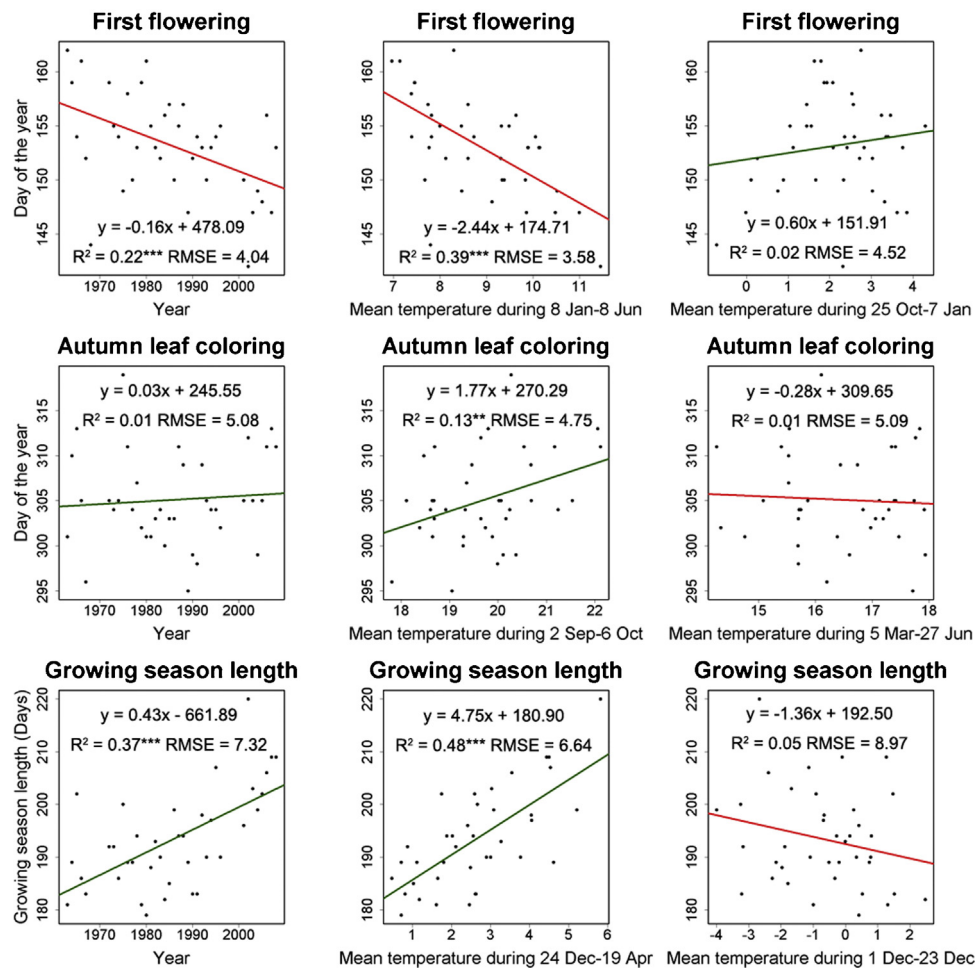


Fig. 4. Trends of chestnut phenology, and relationships between chestnut phenology and mean temperatures in the relevant periods from 1963 to 2008 at Beijing Summer Palace. Panels in the first column show trends of chestnut phenology over time, whereas the middle and right columns contain relationships between the timing of phenological events and mean temperatures during relevant periods. Green lines indicate positive, while red lines indicate negative relationships between the independent variables and dependent variables. Trends are significant with * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$. Root mean square errors (RMSE) are given in days. (For interpretation of the references to color in figure legend, the reader is referred to the web version of the article.)

between 25 October and 7 January were not significantly related to first blossoming ($p > 0.1$).

Chestnut leaf coloring did not show a significant trend. There was, however, a significant positive relationship between leaf coloring dates and fall temperatures (2 September to 6 October), showing a delay by about 1.8 days/°C ($p < 0.05$). The correlation between spring-early summer temperatures (5 March to 27 June) and leaf coloring was not significant, but exhibited a very slight phenology-advancing tendency of warm temperatures.

The length of the chestnut growing season expanded by 4.3 days per decade ($p < 0.01$). This increase was mainly caused by a response to warming between 24 December and 19 April, which lengthened the growing season by 4.8 days/°C ($p < 0.01$). The shortening effect of rising mean temperatures during 1 December and 23 December on the length of growing season was not significant ($p > 0.1$).

In the preceding analysis, we examined the response of phenological dates separately for both relevant periods identified for each phenological stage. Yet results from the PLS regression, as well as ecological theory, indicate that the timing of growth stages should be related to temperatures during both periods (Figs. 5–7).

Plotting first flowering dates as a function of temperatures during both relevant periods (Fig. 5) clearly showed that early flowering (blue colors) occurred not only in response to high temperatures during the forcing phase (8 January to 8 June), but also

as a result of cool conditions during the forcing phase combined with cool temperatures during chill accumulation (bottom left corner of Fig. 5). In particular for relatively cool forcing phases, temperatures during the chilling phase were a major determinant of bloom dates. At higher spring temperatures, bloom was generally advanced. Temperatures during the chill accumulation phase seemed to reduce in importance, as forcing temperatures rose above 10°C, but few observations of such warm springs are available to support this conclusion.

Leaf coloring was also clearly related to mean temperatures during the two phases identified by PLS analysis (Fig. 6). Warmer conditions during spring-early summer (5 March to 27 June) had a phenology-advancing effect, probably caused by earlier and more vigorous leaf growth in spring. The main climatic factor responsible for a delay of leaf coloring, however, appeared to be warmth between 2 September and 6 October. The relevance of these two factors indicated that leaf coloring might to a small extent be determined by accumulated heat during the early growing season, but was primarily triggered by conditions during a relatively short period just before leaf coloring occurred.

The length of the growing season also responded to temperature variation during the two relevant phases (Fig. 7), but the response was dominated by a season-extending effect of warm conditions between late December and April. This was indicated

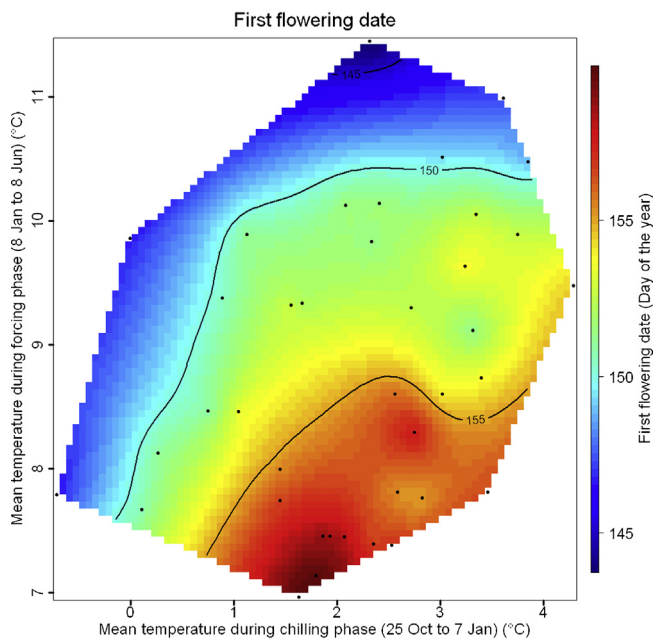


Fig. 5. First flowering dates of chestnut at Beijing Summer Palace, as a function of temperatures during the chilling (25 October to 7 January; x-axis) and forcing (8 January to 8 June; y-axis) phases. Variation in color reflects variation in bloom dates, while black dots indicate phenological observations between 1963 and 2008.

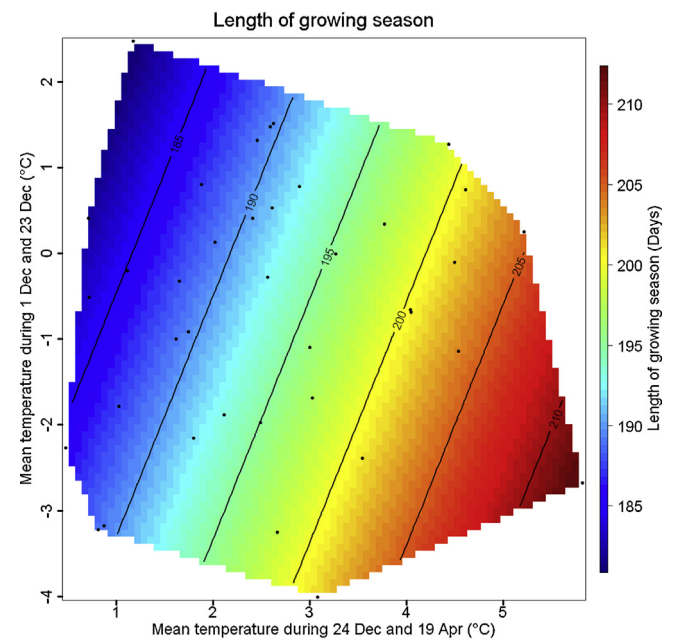


Fig. 7. Growing season length of chestnut at Beijing Summer Palace, as a function of temperatures during 24 December to 19 April (x-axis) and 1 December to 23 December (y-axis). Variation in color reflects variation in growing season length, while black dots indicate phenological observations between 1963 and 2008.

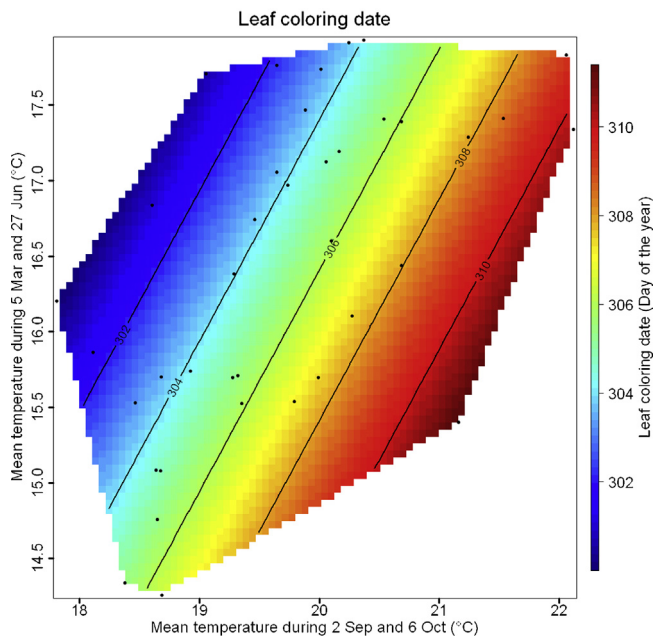


Fig. 6. Leaf coloring dates of chestnut at Beijing Summer Palace, as a function of temperatures during 2 September to 6 October (x-axis) and 5 March to 27 June (y-axis). Variation in color reflects variation in leaf coloring dates, while black dots indicate phenological observations between 1963 and 2008.

by the steep incline of the contour lines drawn in the figure. The season-shortening effect of warm December conditions was also recognizable, but clearly less important.

4. Discussion

4.1. Chestnut bloom trends

Our analysis indicated that chestnut bloom at the Summer Palace in Beijing has advanced by 1.6 days per decade since 1963.

These observations are in line with results for the majority of species in most major analyses of phenological trends conducted to date, such as [Fitter and Fitter \(2002\)](#) analysis of 385 species in England (76% of species showed an advancing trend), [Lesica and Kittelson \(2010\)](#) evaluation of 656 species in the Rocky Mountains (USA; 72% of species with advanced phenology) and the analysis by [Bai et al. \(2011\)](#) in Beijing (71% of species indicated early flowering). In total, chestnut bloom advanced by about one week (7.5 days) over the last 50 years, similar to changes in the timing of various spring events in Wisconsin between 1936 and 1988 ([Bradley et al., 1999](#)) and in the Mediterranean region between 1952 and 2000 ([Peñuelas et al., 2002](#)).

Chestnut bloom responses were dominated by an advancing effect of warming during the forcing phase (8 January to 8 June), with a temperature sensitivity of 2.4 days/°C. This rate is somewhat lower than the sensitivity of fruit trees (apple and sweet cherry) in Germany, where one degree of warming was found to advance bloom by 5 days ([Chmielewski et al., 2004](#)). Our results are, however, comparable to responses of cherry flowers on Mt. Takao in Japan (3.1 days/°C; [Miller-Rushing et al., 2007](#)) and mountain peach (*Prunus davidina* Franch) blossom in Beijing (2.8 days/°C; [Zhang et al., 2005](#)).

While there was an overall advance in chestnut spring phenology, there was also a clearly recognizable phenology-delaying effect of warming during the chill accumulation phase (25 October to 7 January). Like all other deciduous trees from temperate or cold climates, chestnuts fall dormant in winter to avoid frost damage to sensitive growing tissue ([Campoy et al., 2011](#)), and they require the fulfillment of chilling and heat requirements in order to break dormancy and resume growth in spring. It is commonly assumed that these requirements are fulfilled sequentially, with a phase of chill accumulation followed by a phase of heat accumulation ([Luedeling, 2012](#)). While this concept is likely a simplification of more complex climatic needs, it serves to explain our results. The phenology-delaying effect of warming in fall-early winter indicates that chestnuts accumulate chill during this time. Warming may then

slow chill accumulation, delay the fulfillment of chilling requirements and ultimately lead to later spring phases. Such delayed spring phenology events have been reported by several authors, who speculated that reduced winter chill may have caused the delays (Cook et al., 2012; Yu et al., 2010). Of particular interest for the present study are observations by Legave et al. (2013), who found that apples in Mediterranean locations in Europe have displayed a tendency toward later bloom. They also suspect that reduced rates of chilling are the cause of this phenomenon. Increasing temperatures during the subsequent phase then accelerate the accumulation of heat, leading to advancing bloom dates. Thus far, the latter trend has dominated net effects on tree phenology in most places.

It also seems possible that during the initial stage of the second relevant phase (8 January to 8 June), the bloom-advancing effect of warm temperatures may be related to chill rather than heat accumulation. Horticultural studies on winter chill typically assume that freezing temperatures are not effective for chill accumulation (Luedeling and Brown, 2011). Since mean temperatures in Beijing during January and February are frequently below 0 °C, warming during this phase may thus accelerate rather than slow chill accumulation. Using horticultural chill models, Luedeling et al. (2011b) showed that warming during certain periods of the winter increased the amount of chill that was accrued per time unit in Germany. These considerations imply that the chilling phase of chestnuts in Beijing may not be restricted to fall, but could extend later into the winter. Assuming that freezing conditions are really not effective for chilling, PLS regression can thus not ultimately decide the timing of plant responses during periods with frequent frost.

From our results, it seems advisable to keep potential decreases of winter chill in mind when projecting the effects of global warming on tree phenology. Under present climatic conditions, these effects are attenuated or eliminated by warming in spring (Körner and Basler, 2010; Murray et al., 1989), but further chill decreases have been projected (Baldocchi and Wong, 2008; Luedeling et al., 2011a,b, 2009a,c) and these might exert a stronger influence in the future.

The results of our analysis cannot exclude the possibility that factors other than temperature affected phenological dates. In particular the effects of daylength, which does not vary much between years for any given calendar date, cannot be detected with PLS regression, because the method relies on variation in independent variables. It is also possible that reduced photosynthetically active radiation (PAR) caused by air pollution affected tree phenology in Beijing. While for PAR, PLS regression did not show a meaningful effect that could not be explained by the correlation of PAR and temperature (data not shown), it seems likely that changes in air quality could have modulated the timing of plant phenology stages. This signal appears to have been relatively weak in the past, but further reductions in PAR might cause this factor to have a bigger effect in the future.

4.2. Chestnut leaf coloring trends

Leaf coloring of chestnuts did not show a significant trend over time in our analysis. It responded with a significant delay to warming in September, shortly before the occurrence of the phenological event, but this effect alone did not lead to a significant overall trend. These findings mirror results from studies elsewhere, which have generally found less pronounced and more heterogeneous temperature response patterns for fall phases than for spring phases (Bai et al., 2009; Menzel et al., 2001; Walther et al., 2002). In Europe and on the loess plateau of Gansu in China, leaf coloring has shown a progressive delay of 0.3–1.6 days per decade (Chmielewski and Rötzer, 2001; Menzel and Fabian, 1999; Menzel, 2000; Menzel et al.,

2001; Peñuelas and Filella, 2001; Pu et al., 2008; Walther et al., 2002). However, advancing trends in fall phases were reported in Latvia and Lithuania, and on the Kola Peninsula in Russia (Kalvāne et al., 2009; Kozlov and Berlina, 2002). In general, the response of fall coloring to climate change appears unclear and complex (Menzel, 2003; Menzel et al., 2006).

Our analysis of temperature responses during relevant phases indicated that leaf coloring resulted from the interplay of conditions during two distinct phases. Warming during much of the growing season caused a slight advance in fall phenology. This observation may indicate that leaf coloring becomes more likely with increasing accumulation of heat units over several months. Since this effect integrates over temperature changes during an extended period of time, effects of a long-term warming trend should be detectable. Yet this advancing effect was relatively small compared to the delay in phenology caused by warm fall conditions. The reason why the latter effect has not led to a significant trend in leaf coloring over the entire study period is probably that it works during a shorter period of time—only between 2 September and 6 October. For such short phases, random effects of climate variability are likely much more pronounced than the long-term signal of climate change. Phenological events that occur in response to short-term climatic cues are thus much less likely to show recognizable long-term trends than those that depend on integration of climatic conditions over many months.

4.3. Length of the chestnut growing season

The chestnut growing season expanded by 4.3 days per decade between 1963 and 2008. This value is within the range reported in earlier studies elsewhere. Estimates for Europe indicated an overall lengthening of the growing season by 2.7 days per decade (Menzel, 2000), with extensions by 0.7–2.1 days per decade in the Nordic region (Carter, 1998), 1.5 days per decade in the Greater Baltic area (Linderholm et al., 2008), 1.1–4.9 days per decade in Germany (Menzel, 2003) and 5 days per decade in Austria and Switzerland (Linderholm, 2006). For North America, Peñuelas and Filella (2001) reported an extension by 6 days per decade, while Matsumoto et al. (2003) showed that the growing season had lengthened by 2.4 days per decade in Japan. Khanduri et al. (2008) found that the growing season of 650 temperate plants has expanded, on average, by 3.3 days per decade in recent years. However, an opposite trend of growing season contraction has been reported for locations at high latitudes and high altitudes, most notably in Iceland, on the Russian Kola Peninsula, and on the Tibetan Plateau in China (Frich et al., 2002; Kozlov and Berlina, 2002; Yu et al., 2010).

The main driver of the growing season expansion of chestnuts in Beijing was warming in winter and spring (24 December to 19 April), when the growing season responded with a lengthening by 4.8 days/°C. Temperature increases in early winter (1 December to 23 December) appeared to be working in the opposite direction, but the effect was not very strong. Both of these phases modulate the beginning of the growing season rather than the end. The longer chestnut growing season was thus due almost entirely to the advancing spring phases rather than a delay in fall phenology. These results are in line with findings by Chmielewski and Rötzer (2001), Menzel (2003) and Robeson (2004), who identified warming early in the year as the main driver of growing season expansions in Germany, Europe and North America, respectively.

4.4. Past and potential future trends in Beijing chestnut phenology

Over the time period analyzed in this study, chestnuts at the Summer Palace have exhibited an advance in spring phases, while the timing of fall phases has remained relatively unchanged,

possibly with a slight tendency toward later occurrence. The timing of all phases was related to warm and cool conditions during distinct phases of the year, with particular periods effecting advances and delays in phenology. Based on past records, it is evident that for spring phases, the phenology advance caused by spring warming was greater than the delaying effect of reduced chilling. For fall phases, the impact of warmer conditions in fall was slightly greater than the influence of increasing temperatures during the spring and summer.

In the future, the current balance of temperature effects may shift. It seems possible that climatic influences that are currently swamped by greater impacts of opposite effects will increase in importance, as warming continues. Fall and winter temperatures in Beijing are currently low enough that chilling requirements are fulfilled every year for chestnut. Given that temperature increases during certain parts of the winter, when temperatures are around the freezing point, are likely to even increase the rate of chill accumulation, the dominance of spring warming will probably continue for some time into the future, even as the impact of reduced chilling becomes gradually more important. In the near future, temperate trees grown in regions that are substantially warmer than their native ranges are more likely to be affected by reductions in chilling (Luedeling et al., 2011a,b). All studies on past trends in spring phenology that involved large numbers of species included diverging responders that did not adhere to the general trend of advancing spring phases (Fitter and Fitter, 2002; Lesica and Kittelson, 2010; Parmesan, 2007). These responses may also be related to reductions in chill. Environments that have seen particularly strong temperature increases in recent years may also already display signs of a shift toward greater influence of phenology-delaying effects. This seems particularly likely for species at high altitudes and latitudes, where delayed spring phenology has recently been reported (Frich et al., 2002; Kozlov and Berlina, 2002; Yu et al., 2010).

Regarding fall phenology, past trends as well as future directions are quite unclear. Our analysis showed evidence that leaf coloring was a response to conditions during most of the growing season, as well as to short-term temperature triggers shortly before leaf coloring. The former effect indicates that the duration of photosynthetic activity of chestnut leaves is predetermined to some extent, with leaf coloring probably determined by a certain amount of accumulated heat. If this is truly the case, future warming should cause leaf coloring to occur earlier. This effect may then come to dominate the impact of the period of thermally favorable conditions in fall, but such trends will likely continue to be obscured by the erratic nature of the late-season temperature signal, which is much more strongly affected by short-term climatic variability – i.e. weather – than by the systematic impact of global warming.

5. Conclusions

Spring phenology of chestnuts at Beijing Summer Palace has advanced by 1.6 days per decade since 1963. The length of the growing season has expanded by 4.3 days per decade. While spring phase-advancing and growing season-extending factors have clearly dominated past temperature responses, it is unclear whether or not these trends will continue into the future. For all analyzed phenological stages, certain phases during the year were identified when warm conditions were related with effects that ran counter to general trends. These effects were a reduction in winter chill, which may delay rather than advance spring phenology, as well as an accelerated accumulation of heat during spring-summer, which may shorten the life time of chestnut leaves, leading to shortening rather than extension of the growing season. At present, these secondary warming effects on tree phenology are swamped by the dominant impacts of heat accumulation in spring and

prevalence of warm conditions in fall. Further warming may shift this balance, however, and eventually lead to substantial changes in plant responses to warming. We therefore recommend increased scientific attention to such secondary climate responses, especially for species grown outside their native ranges (e.g. fruit trees or ornamentals) and plants in environments exposed to particularly pronounced temperature increases.

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