







## RESEARCH ARTICLE

# Global warming is increasing the discrepancy between green (actual) and thermal (potential) seasons of temperate trees

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## Abstract

Over the past decades, global warming has led to a lengthening of the time window during which temperatures remain favorable for carbon assimilation and tree growth, resulting in a lengthening of the green season. The extent to which forest green seasons have tracked the lengthening of this favorable period under climate warming, however, has not been quantified to date. Here, we used remote sensing data and long-term ground observations of leaf-out and coloration for six dominant species of European trees at 1773 sites, for a total of 6060 species–site combinations, during 1980–2016 and found that actual green season extensions (GS:  $3.1 \pm 0.1$  day decade<sup>-1</sup>) lag four times behind extensions of the potential thermal season (TS:  $12.6 \pm 0.1$  day decade<sup>-1</sup>). Similar but less pronounced differences were obtained using satellite-derived vegetation phenology observations, that is, a lengthening of  $4.4 \pm 0.13$  and  $7.5 \pm 0.13$  day decade<sup>-1</sup> for GS and TS, respectively. This difference was mainly driven by the larger advance in the onset of the thermal season compared to the actual advance of leaf-out dates (spring mismatch:  $7.2 \pm 0.1$  day decade<sup>-1</sup>), but to a less extent caused by a phenological mismatch between GS and TS in autumn ( $2.4 \pm 0.1$  day decade<sup>-1</sup>). Our results showed that forest trees do not linearly track the new thermal window extension, indicating more complex interactions between winter and spring temperatures and photoperiod and a justification of demonstrating that using more sophisticated models that include the influence of chilling and photoperiod is needed to accurately predict spring phenological changes under warmer climate. They urge

caution if such mechanisms are omitted to predict, for example, how vegetative health and growth, species distribution and crop yields will change in the future.

#### KEYWORDS

autumnal foliar senescence, climatic warming, green season, spring leaf-out, thermal season

## 1 | INTRODUCTION

The last three decades were the warmest on Earth over at least the last 800 years (Legg, 2021), leading to a lengthening of the time window during which temperatures remain favorable for carbon assimilation and tree growth in the extra-tropical regions. This favorable time window (potential thermal season, TS) plays a key role in the forest vitality (Hicke et al., 2012; Trumbore et al., 2015), crop yields (Ketring & Wheless, 1989; Zimmermann et al., 2017), vegetation growth and the geographic distribution of species (Chuine, 2010; Fang & Lechowicz, 2006). Recent warming has extended the latitudinal and altitudinal distributions of tree species (Lenoir & Svenning, 2015; Vitasse et al., 2021), albeit at a slower rate than the shift of their thermal niche due to demographic processes and interspecific competition (Huang et al., 2017; Scherrer et al., 2020; Vitasse et al., 2021). Phenology is highly sensitive to temperature and plays a key role in driving the distributions of plant species (Chuine, 2010; Körner et al., 2016). Global warming has also led to a lengthening of the growing season for plants at mid- to high latitudes of the Northern Hemisphere, which in turn has affected the carbon (a longer growing season could increase the carbon uptake) and water cycles (a longer growth season reduced the runoffs and a scale different between phenology and water flux) of terrestrial ecosystems and thereby influences land feedbacks to the climate system (Chen et al., 2022; Cleland et al., 2007; Keenan & Richardson, 2015; Kim et al., 2018; Peñuelas et al., 2009; Piao et al., 2019). Nevertheless, some researches indicated that it is more the conditions that prevail during the growing season than the actual length that matters (Ueyama et al., 2014; Zhang et al., 2020). It is still unclear the coupling extent of vegetation green seasons and the lengthening of this favorable period during this abrupt warming. Yet, it is essential for us to understand how trees' phenological cycles adapt to a rapidly warming climate, which will ultimately improve projections of future changes in the forest system and the multiple ecosystem services it provides.

Climatic warming is currently extending the vegetation growing season in the extra-tropical regions by advancing spring leaf-out and delaying autumnal foliar senescence (Chmielewski & Rötzer, 2001; Liu, Piao, et al., 2018; Piao et al., 2019; Zhu et al., 2012). Many studies have documented these responses of vegetative activity to a changing environment (Friend et al., 2014; Peaucelle et al., 2019; Wu et al., 2015), but increasing evidence also suggests that the sensitivity of phenology to climatic warming is decreasing. For example, the spring leaf phenology of six common species of European deciduous trees has become less sensitive to warming

in recent decades (Fu, Zhao, et al., 2015). Accordingly, the heat accumulation required for leaf-out in temperate European trees has increased by 50% with climatic warming (Fu, Piao, et al., 2015). Similarly, even though the timing of foliar senescence in autumn has been reported to be less responsive to temperature than the timing of spring leaf-out, the heat accumulation for autumnal phenology has also increased in recent decades (Menzel et al., 2020; Zani et al., 2020). These findings indicate that climatic warming-induced increases in TS do not necessarily translate to a linear extension of the actual vegetation green season extensions (GS). In other words, the thermal requirement of plants is likely to change under warmer environments, introducing large uncertainties and possibly errors in the predictions of future vegetation productivity and species distributions when constant thermal sums are used or when the growing season length is only limited by the climatic conditions without explicitly accounting for tree physiological processes (Chuine, 2010; Chuine & Beaubien, 2001; de Sauvage et al., 2022; Dow et al., 2022; Etzold et al., 2022). Investigating the temporal overlap and potential lag between vegetation phenology and favorable climatic conditions is critical to improving our understanding of vegetation responses to the ongoing climate change (Linderholm, 2006; Piao et al., 2020).

In this study, we examined whether the GS, defined as the period from leaf-out in spring to foliar senescence in autumn, has been tracking the ongoing lengthening of the TS, classically defined as the period from the first day of the year when daily air temperatures are  $>5^{\circ}\text{C}$  for more than five consecutive days to the last day of the year when daily air temperatures are  $<5^{\circ}\text{C}$  for more than five consecutive days. We used long-term phenological observations of six widely distributed tree species at 1773 sites in central Europe and a satellite-derived phenology dataset between 1980 and 2016 (Site locations and distribution of each species detailed in Figure S1) to address the following questions: (1) to what extent have GS and TS changed over 1980–2016 and (2) if the discrepancy between the thermal and actual season has increased, what are the underlying mechanisms for possible increases in the discrepancy between the thermal and actual season?

## 2 | MATERIALS AND METHODS

### 2.1 | Dataset and definition

In situ phenological data were obtained from the open-access Pan European Phenology Network (PEPN, <http://www.pep725.eu/>) and

applied to carry out the main analysis (without specifically declaration of source of data). We selected totals of 1773 sites and six tree species with dates for both leaf-out (BBCH 11, first leaves unfolded) and foliar senescence (BBCH 94, 50% of leaves discolored, which represents the percentage of discolored leaves in the entire canopy, indicating that the canopy is undergoing a process of leaf senescence) in 1980–2016. We defined the actual vegetation-based green season (hereafter designated as GS) as the period between leaf-out (start of green season) and foliar senescence (end of green season). Climatic data were derived from a gridded climatic dataset which fully considers the impact of topography and with a spatial resolution of 0.25° (Beer et al., 2014; Haylock et al., 2008; Van den Besselaar et al., 2011), including daily mean air temperature, daily cumulative precipitation, and daily shortwave radiation. The temperature index has been widely used in meteorological and modeling studies (Table S3). We used meteorological data from the grid closest to an in situ phenological site to calculate the thermal start/end of growing season of that site. The start of thermal season was defined as the first day of the year when daily mean temperatures were >5°C for more than five consecutive days, and the end of thermal season was defined as the day when daily mean temperatures were <5°C for more than 5 days after 1 July, which is a simplify way that ignores the asymmetrical driving mechanism between spring and autumn phenology (Frich et al., 2002; Zhou et al., 2018). The thermal season length (TS) was determined as the interval between the start and end of the thermal season. To further test the sensitivity of the TS estimation to the temperature thresholds, we estimated the TS and the difference between TS and GS ( $\delta$ GS) using temperature thresholds from 1 to 10°C with one-degree step. We found similar results across temperature thresholds (Figure S4), that is, larger TS than GS, but interestingly the  $\delta$ GS was largest when we chose the 5°C as the temperature threshold, which is precisely the threshold generally used in previous studies (Carter, 1998; Lallukka et al., 1978; Sarvas, 1972).

With the emergence and rapid development of remote sensing techniques, phenology observations are no longer limited to traditional in situ ground observation. To compare with the in situ-based species-level results, that is, difference in GS and TS, at the community level (across species), remote sensing-based phenology data, that is, vegetation-based start and end of season, with a spatial resolution of 0.25°, covering 1982–2015 were estimated using five different phenological extraction methods, which include multiple fitting procedures to improving data quality and reduce uncertainty (i.e., the HANTS-Maximum method, Spline-Midpoint method, Gaussian-Midpoint method, Timesat-SG method, and Polyfit-Maximum method), that were used in previous studies with an extract threshold of 0.5 (Cong et al., 2012; Fu et al., 2021), from the GIMMS<sub>3g</sub> NDVI data (<https://climatedataguide.ucar.edu/climate-data/ndvi-normalized-difference-vegetation-index-3rd-generation-nasagfsc-gimms>).

Spring warming model is a one-phase model that only considers the forcing process, which calculates the accumulated daily rates of forcing ( $R_f$ ) applying a logistic function as below:

$$S_f = \sum_{t_0}^t R_f = \sum_{t_0}^t \frac{A_f}{1 + e^{\alpha(T-\beta)}}$$

where  $S_f$  represents a daily sum of forcing rates;  $A_f$ ,  $\alpha$ , and  $\beta$  are the parameters take effect during forcing. The  $S_f$  begins to accumulate start from  $t_0$ , which is January 1st of the current year.

The Sequential model is a two-phase model which assumes that the accumulation of forcing ( $S_f$ , a daily sum of forcing rates) starting after the chilling requirement ( $C_{crit}$ ) is reached (Kramer, 1994). While another two-phase model (Parallel model) assumes that the accumulation of forcing functions when a critical threshold ( $C_{crit}$ ) of chilling state ( $S_c$ , a daily sum of chilling rates) has not been attained (Landsberg, 1974). A triangular function and a logistic function with a competence function ( $K$ ), note that the Parallel model introduces another parameter ( $K_{min}$ ) which determining the minimum potential of an unchilled bud to respond to the forcing temperature, were used to calculate the rate of chilling ( $R_c$ ) and  $R_f$ , respectively. So, the state of chilling and forcing is increasing simultaneously over time:

$$R_c = \begin{cases} 0, & T \leq T_a \\ \frac{T - T_a}{T_b - T_a}, & T_a < T < T_b \\ \frac{T - T_c}{T_b - T_c}, & T_b < T < T_c \\ 0, & T \geq T_c \end{cases}$$

$$R_f = \begin{cases} 0, & T \leq T_d \\ K \frac{A_f}{1 + e^{\alpha(T+\beta)}}, & T > T_d \end{cases}$$

$$K_{Sequential} = \begin{cases} 0, & S_c < C_{crit} \\ 1, & S_c \geq C_{crit} \end{cases}$$

$$K_{Parallel} = \begin{cases} k_{min} + \frac{1 - k_{min}}{C_{crit}} S_c, & S_c < C_{crit} \\ 1, & S_c \geq C_{crit} \end{cases}$$

where  $T_{a-d}$  are the parameters associated with chilling, and  $A_f$ ,  $\alpha$ ,  $\beta$ , and  $K_{min}$  represent the parameters take effect during forcing. The  $S_c$  and  $S_f$  begin to accumulate after September 1 of the previous year.

We parameterized these models of each site through PSO (Particle swarm optimization) algorithm by setting the swarm number as 50, maximum number of iterations as 1000, and the expected value of the objective function (RMSE, root mean square error) as 1, based on the in situ SOS records before 1998, which splits 1980–2016 into two periods of the same length (Marini & Walczak, 2015). And then, we applied three models to estimate the SOS of six species in each site during 1980–2016.

## 2.2 | Statistical analysis

### 2.2.1 | Determination of the temporal trend of long time-series data and the latitudinal trend

We used a simple linear regression analysis to retrieve the long-term trend of variation in phenology (with year as the independent variable and phenological date as the dependent variable) and the spatial patterns of the main variables (e.g.,  $\delta$ SOS,  $\delta$ EOS,  $\delta$ GS, temporal changes in chill days, seasonal precipitation, standard deviation of phenological dates) by setting latitude as the independent variable. We also used mixed-effects models (lmer function from the lme4 package in R) to determine if  $\delta$ GS was affected by  $\delta$ SOS and  $\delta$ EOS by taking species and sites into consideration as random effects. Mixed-effects models were of the general form as:

$$y_{\text{effect}} = \beta_0 + \beta_1 x_{\text{fixed}} + b + \varepsilon,$$

where  $y_{\text{effect}}$  is the effect size;  $\beta_0$  is the intercept;  $\beta_1$  is the coefficient associated with the fixed effect,  $x_{\text{fixed}}$ ;  $b$  is the coefficient of the random effect (species and sites); and  $\varepsilon$  is the remaining variation.

### 2.2.2 | Determination of optimal preseason

To exclude the covariate effects of other environmental factors, we obtained partial correlations between phenological dates and average temperature during a specific period (ranging from 15 to 120 days, with steps of 15 days) before the mean phenological dates, using cumulative precipitation and shortwave solar radiation as control variables. The optimal preseason was determined as the period for which average temperature had the largest absolute partial correlation coefficient with the phenological dates ( $R_{\text{r}}$ ). We adopted the optimal preseason for specific sites and species in the subsequent analysis. The mean pre-seasons for the spring and autumn (Although the main drivers that control autumn leaf senescence are photoperiod and autumn nighttime temperature, recent studies have found that summer climate involved the autumn leaf senescence processes (Liu, Chen, et al., 2018; Zani et al., 2020)) vegetation phenologies across all species and sites were  $53 \pm 26$  day (mean  $\pm$  SD) and  $64 \pm 36$  day, respectively (Figure S14).

Apparent sensitivity to temperature ( $S_{\text{T}}$ ) was defined as the advance (spring) or delay (autumn) of phenological date for every one degree increase in air temperature and was determined using reduced major-axis regression between the phenological dates and average air temperature during the optimal preseason.

### 2.2.3 | Quantification of the relative contributions of spring and autumn phenology to the overall changes in growing season length

The relative contribution (CON) of spring and autumn phenology to the overall changes in green season length was calculated as (Garonna et al., 2014):

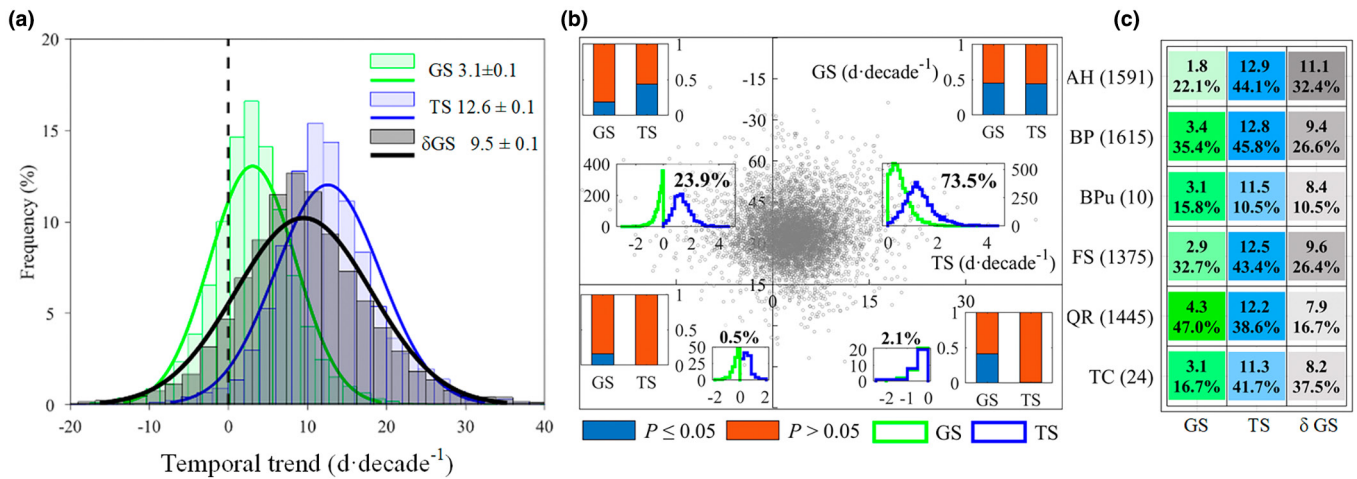
$$\text{CON} = (\text{abs}(\text{Tr.SOS}) - \text{abs}(\text{Tr.EOS})) / (\text{abs}(\text{Tr.SOS}) + \text{abs}(\text{Tr.EOS})),$$

where Tr.SOS and Tr.EOS are the temporal trends of spring and autumn phenology, respectively, expressed in  $\text{day decade}^{-1}$ . A negative CON indicates that the changes in green season length were mostly attributed to the changes in autumn phenology, whereas a positive CON indicates that the shift of spring phenology contributed more to the changes in green season length.

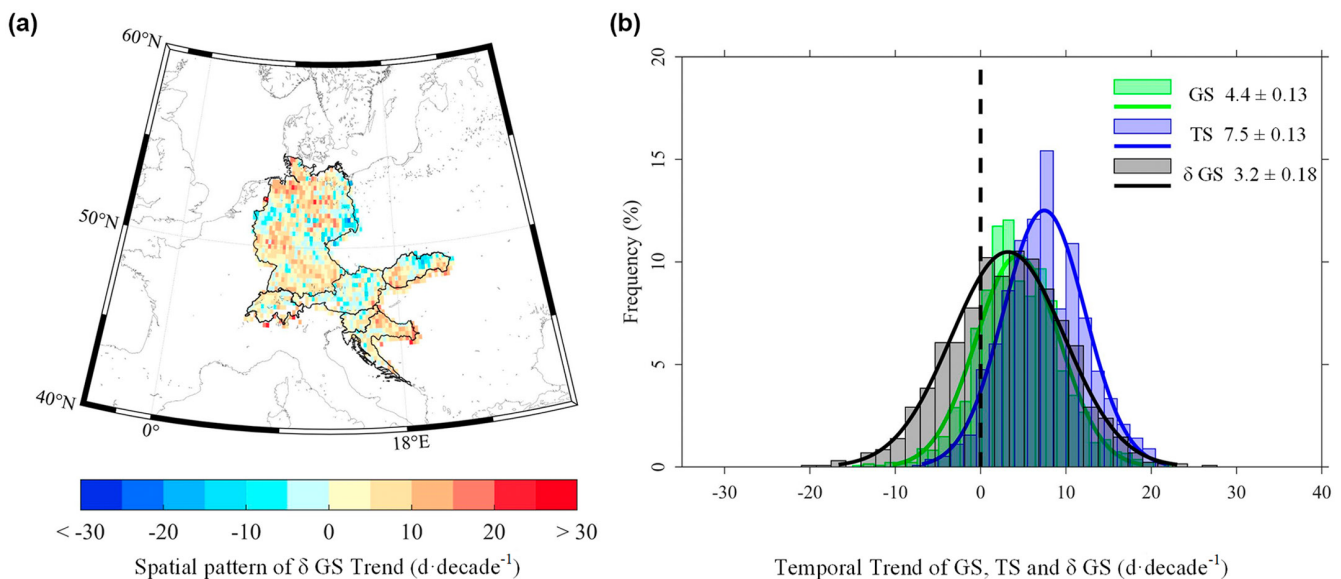
Chill days was defined as the number of days when temperature within a specific range (base temperature). In the present study, we counted the chilling days when daily mean temperature falls into the range between 0 and 5°C following previous study (Fu, Zhao, et al., 2015; Wang et al., 2020), and spanned from the previous 1 November to the average phenological date for spring leaf-out. Although the average daily mean temperature can fluctuate between -3 and +15°C when the average daily mean temperature is between 0 and 5°C, some studies suggest that there is actually a much wider range of temperatures that chilling function (Baumgarten et al., 2021). We used the same methodology to estimate the cold days for autumnal phenology and calculated the days from the summer solstice (21 June) to the average date of foliar senescence (base temperature of 25°C) (Dufrène et al., 2005) during 1980–2016 for each site.

## 3 | RESULTS AND DISCUSSION

The mean annual temperature in the study area increased at an average rate of  $0.39 \pm 0.11^\circ\text{C decade}^{-1}$  during 1980–2016 (Figure S2). Based on the in situ phenology observations and temperature records, both GS and TS lengthened during this period, but the lengthening of TS was four times greater than the one GS extensions ( $12.6 \pm 0.1$  vs.  $3.1 \pm 0.1$  day  $\text{decade}^{-1}$ , respectively), leading to an increase of  $9.5 \pm 0.1$  day  $\text{decade}^{-1}$  in the mismatch between TS and GS ( $\delta$ GS, Figure 1a). Both TS and GS extended across 73.5% of the 6060 species–site combinations, with ~50% of these extensions showing significant trends at  $p \leq .05$  (Figure 1b). Similar results were found for each of the six studied species, with  $\delta$ GS ranging from 7.9 to 11.1 day  $\text{decade}^{-1}$  across species (Figure 1c and Figure S3). To compare with the in situ species-based results, we also explored the  $\delta$ GS across the study region using gridded climate data and satellite-based phenological observations (see Section 2), and we found similar patterns, with GS and TS extending by  $+4.4 \pm 0.13$  and  $+7.5 \pm 0.13$  day  $\text{decade}^{-1}$ , respectively (Figure 2). Nevertheless, the differences between GS and TS were smaller for the remote sensing-based results than for the in situ results, which can likely be attributed to differences in species composition (satellite-based phenological dates mainly reflect the mean phenological dates across species) and to larger uncertainty in the satellite-derived phenological dates, for example, pixel mixing effect. Furthermore, the six widely distributed European tree species used for the in situ observations might not be the dominant species across all regions in the study area, which



**FIGURE 1** Changes in the temporal trends of the thermal season length (TS) and actual green season (GS) during 1980–2016. (a) Frequency distributions of the temporal trend of GS, TS, and the difference between them ( $\delta$ GS) across all sites and species. The dashed line denotes no trend. (b) The distributions and relationship between GS and TS. The subpanels show the frequency and distribution of significance of the data in each quadrant. (c) Changes in the temporal trend of the length of the green season for each species. The data in the boxes represent averages and the fraction of the data with significant temporal trends. AH, *Aesculus hippocastanum* (horse chestnut); BP, *Betula pendula* (silver birch); BPu, *Betula pubescens* (white birch); FS, *Fagus sylvatica* (beech); QR, *Quercus robur* (oak); TC, *Tilia cordata* (lime). The number of sites for each species is in brackets below the species name. [Colour figure can be viewed at wileyonlinelibrary.com]



**FIGURE 2** Changes in the temporal trends of the thermal season length (TS) and remote sensing-based green season (GS) during 1982–2015. (a) Spatial pattern of  $\delta$ GS (the difference between TS and GS) trend. (b) Frequency distributions of the temporal trend of GS, TS, and the difference between them ( $\delta$ GS) in study area. The dashed line denotes no trend. [Colour figure can be viewed at wileyonlinelibrary.com]

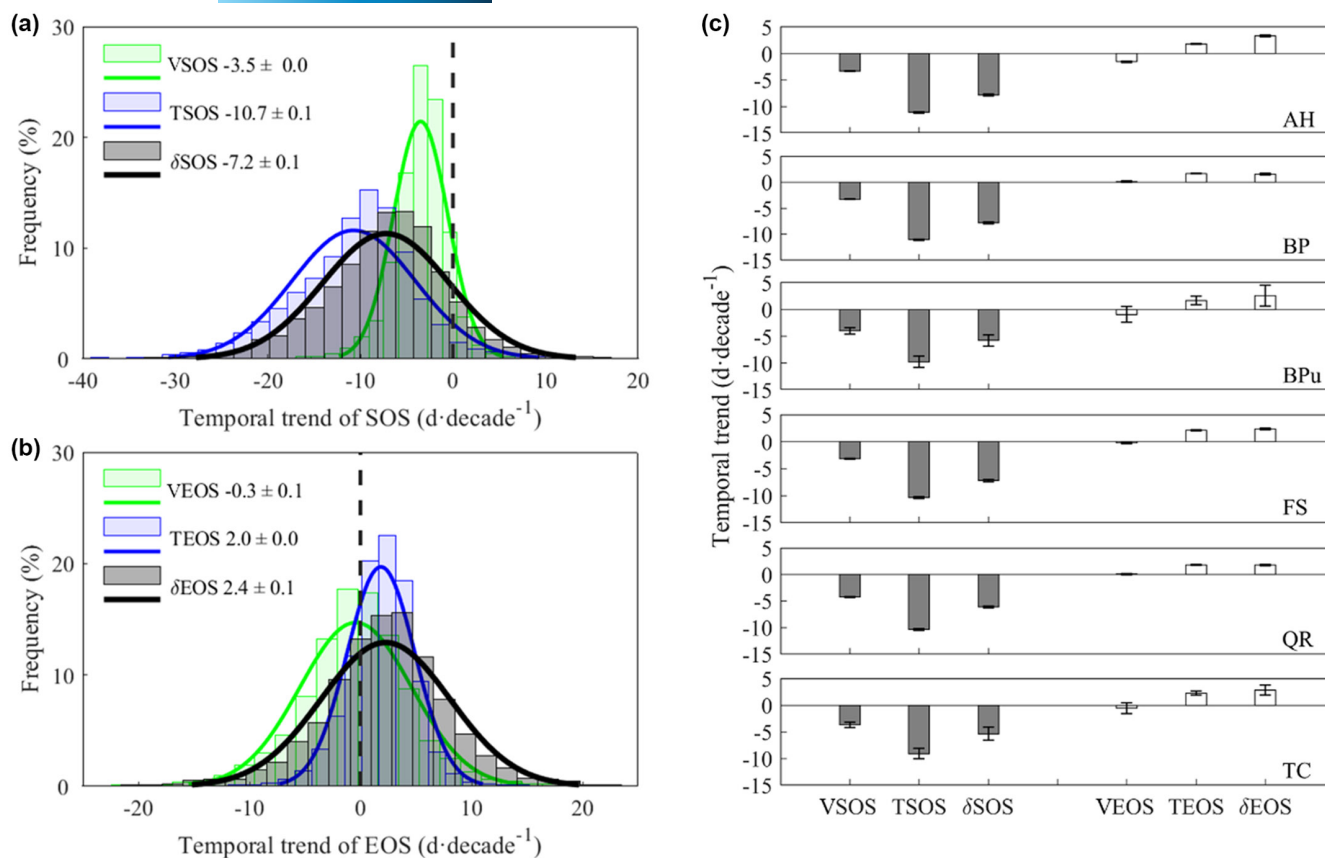
may further explain differences between the ground-sourced and satellite-derived results.

To test the sensitivity of the GS estimation to the choice of the temperature threshold used to estimate TS, we estimated the  $\delta$ GS using temperature thresholds from 1 to 10°C with one degree interval. Interestingly, we found that the temporal change in the difference between TS and GS ( $\delta$ GS) was the largest when using TS threshold of 5°C, which is the most common temperature threshold used in previous studies. These new results therefore justified previous methods and highlighted that the selection of the temperature

threshold can largely affect the inferred temporal trends in TS (Figures S4 and S5).

Based on the in situ phenology observations, both the onsets of the green season and the thermal (potential) season have advanced substantially over recent decades, at a speed of  $-3.5 \pm 0.1$  and  $-10.7 \pm 0.1$  day  $decade^{-1}$ , respectively, leading to an increasing mismatch between the trajectories of the start of the thermal and the start of the green seasons ( $\delta$ SOS) of  $7.2 \pm 0.1$  day  $decade^{-1}$  (Figure 3a). Based on the results of Spring Warming model, Sequential model, and Parallel model, we found a larger difference



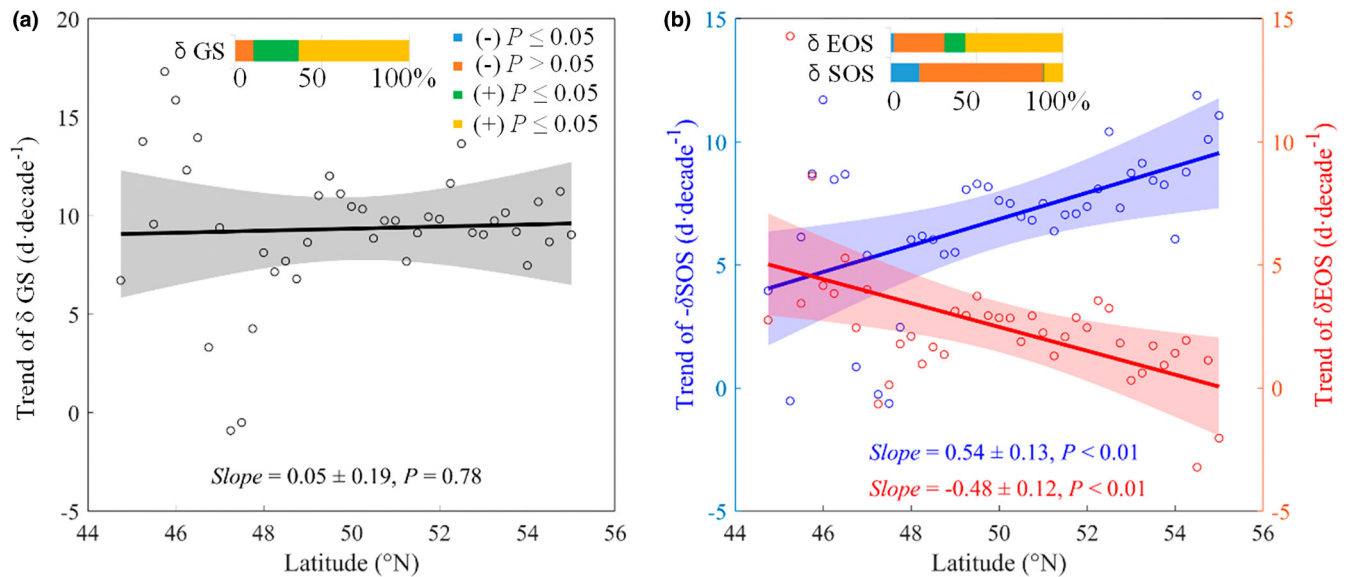


**FIGURE 3** Changes in the temporal trends of the start (SOS) and end (EOS) of the growing season during 1980–2016. (a) Frequency distributions of the temporal trends of the start of the vegetative growing season (VSOS), start of the thermal growing season (TSOS), and the difference between them ( $\delta$ SOS) for all sites and species. (b) Frequency distributions of the temporal trends of the end of the vegetative growing season (VEOS), end of the thermal growing season (TEOS), and the difference between them ( $\delta$ EOS). The dashed lines in (a) and (b) denote no trends. (c) Temporal trends of the start and end of the growing season for each species. AH, *Aesculus hippocastanum* (horse chestnut); BP, *Betula pendula* (silver birch); BPu, *Betula pubescens* (white birch); FS, *Fagus sylvatica* (beech); QR, *Quercus robur* (oak); TC, *Tilia cordata* (lime). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

between the trend of predicted SOS and TSOS, and this is mainly because we used the vegetation phenology dates (VSOS) to parameterize these models (see Section 2 and Figure S6). The temporal changes of the end of green season and the end of thermal season differed in both magnitude and direction. The end of thermal season was delayed by  $2.0 \pm 0.04$  day decade<sup>-1</sup>, and the end of green season advanced at an average rate of  $-0.3 \pm 0.1$  day decade<sup>-1</sup>, causing an increasing mismatch between the end of thermal and green season ( $\delta$ EOS) of  $2.4 \pm 0.1$  day decade<sup>-1</sup>. Note that, the leaf coloration (only part of an autumnal hardening syndrome of the entire tree, driven by its genome and executed by hormones) may have large uncertainty for presenting the leaf senescence. Recent studies have reported that solar-induced chlorophyll fluorescence (SIF) values are closely linked to growth stage, and thus provided an alternative method to quantify autumn phenology in the future (Jeong, 2020; Zhang et al., 2022).  $\delta$ EOS was smaller than  $\delta$ SOS (Figure 3b) implies that the increasing difference between TS and GS is mainly due to the large mismatch in spring rather than autumn. Further quantification of the relative contribution of spring and autumn phenology dates to the overall changes in GS and TS (see

Section 2) confirmed that  $\delta$ SOS contributed more than  $\delta$ EOS to the increased mismatch between GS and TS ( $\delta$ GS) in 70% of the 6060 species–site combinations (Figure S7). These results were similar across all six species (Figure 3c and Figure S7). To account for species and site effects, we applied a mixed-effects model, including both species and sites as random factors and the results are similar as before (see Table S1).

In a next step, we explored the spatial variation in  $\delta$ GS,  $\delta$ SOS, and  $\delta$ EOS, which showed that  $\delta$ SOS increases with latitude, whereas  $\delta$ EOS decreases with latitude, resulting in a constant  $\delta$ GS across latitude for all species and sites (ANCOVA,  $F = 4.186$ ,  $p < .001$ ; Figure 4). At lower latitudes,  $\delta$ SOS and  $\delta$ EOS were similar (increasing mismatch of  $\sim 5$  day decade<sup>-1</sup>), but at higher latitudes,  $\delta$ SOS and  $\delta$ EOS showed significant increase ( $0.54 \pm 0.13$  day decade<sup>-1</sup> °N<sup>-1</sup>,  $p < .01$ ) and decrease ( $-0.48 \pm 0.12$  day decade<sup>-1</sup> °N<sup>-1</sup>,  $p < .01$ ), respectively. At higher latitudes,  $\delta$ GS was mainly driven by the change in  $\delta$ SOS, while at lower latitudes, it was mainly caused by the changes in  $\delta$ EOS (Figure S8). The latitudinal distribution of the study species is uneven (Figure S1), and we accounted for this by excluding *Betula pubescens* and *Tilia cordata*, which resulted in very similar results (Figure S9),



**FIGURE 4** Spatial variability of the temporal trends in  $\delta$ GS,  $\delta$ SOS, and  $\delta$ EOS with latitude. (a) Changes in the temporal trend of the difference between the canopy duration of temperate trees and thermal growing season length ( $\delta$ GS) with latitude. (b) Changes in the temporal trend of the difference between the start and end of the vegetation-based and thermal growing seasons ( $\delta$ SOS and  $\delta$ EOS) with latitude. All data were averaged every  $0.25^\circ$  northward.  $\delta$ SOS was the opposite of the original data. The shading represents the 95% confidence intervals. The subpanels show the proportion of positive and negative values of the site and species data and their significance. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16545)]

suggesting that the species distribution did not drive the latitudinal patterns.

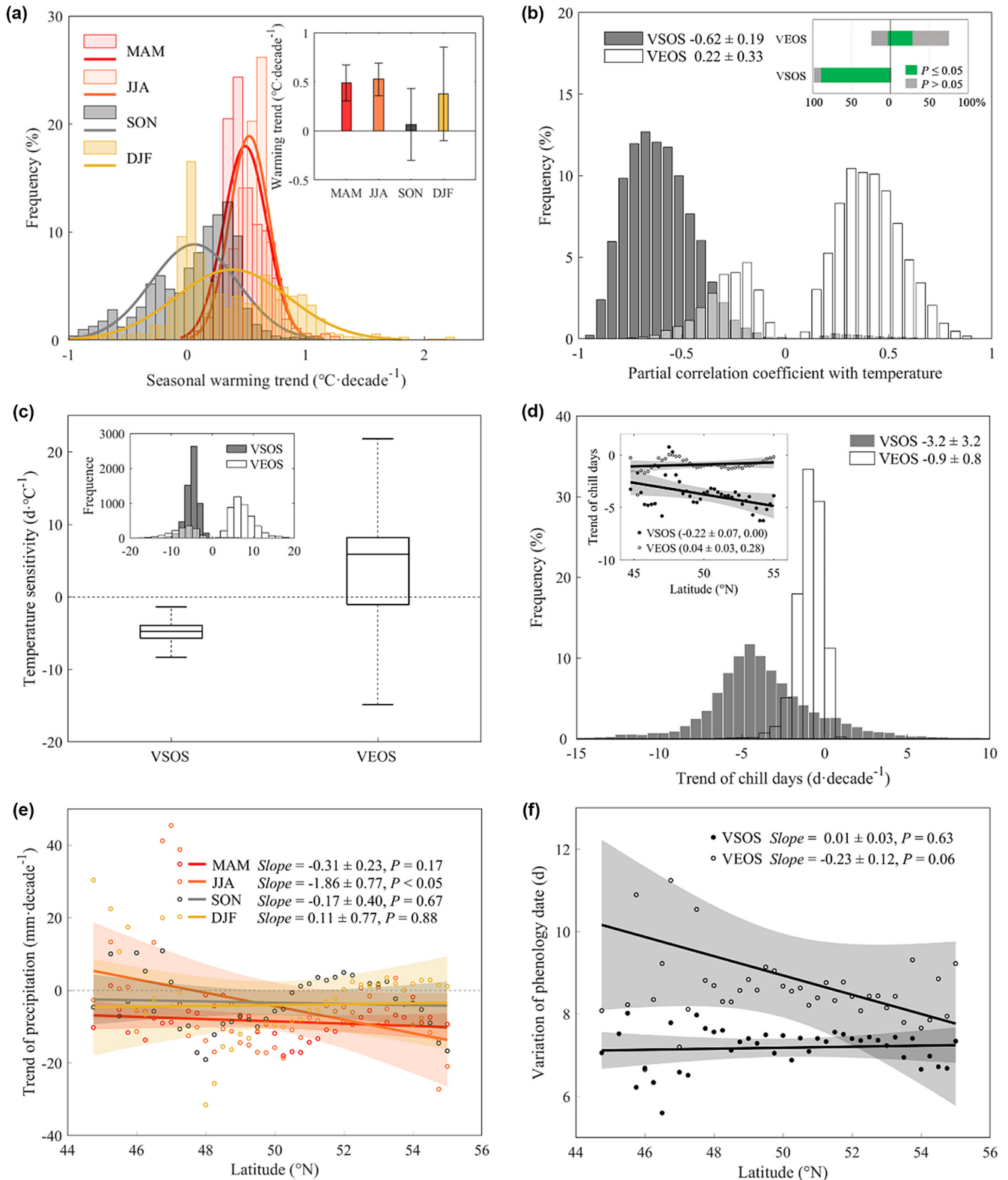
That larger increase in TS than GS implies that an increased mismatch between the thermal season during which trees could be active (favorable conditions) and the vegetation green season. This increasing mismatch might be the result of plant already acclimatized to a warmer environment (Hoffmann & Sgrò, 2011; Mora et al., 2015). Plants compromise maximizing their growing season length to compete for resources with minimizing potential exposure to frost in spring and autumn (Augspurger, 2013; Fu et al., 2019; Körner et al., 2016; Vitasse et al., 2019).

Interestingly, the increased mismatch between TS and GS was mainly due to  $\delta$ SOS rather than  $\delta$ EOS, suggesting that the spring phenology of tree species did not linearly track the occurred temperature rise. The differences between  $\delta$ SOS and  $\delta$ EOS are mainly attributed to seasonal differences in the amplitudes of warming and the phenological responses between spring and autumn. A higher rate of warming in spring than autumn (Legg, 2021; Renner & Zohner, 2018), and a lower sensitivity of spring than autumnal phenology to temperature, may have together led to a larger  $\delta$ SOS than  $\delta$ EOS. This increasing discrepancy between the thermal and the actual start of season may affect ecosystem functioning, for example, by lowering frost damage risk due to thermal adaptation, impacting the synchronization between insects and their food plants (Maino et al., 2016), and increasing the risk of pest damage (Hicke et al., 2012; Trumbore et al., 2015), which subsequently might induce a short-term slump in forest productivity or niche changes (Heberling et al., 2019; Kellermann & van Riper, 2015; Liu, Piao, et al., 2018).

To test this, we analyzed the trends in seasonal temperature and indeed found different warming trends among seasons

(spring > winter > autumn, Figure 5a), explaining the larger changes in thermal start than the end of the season. We also estimated the partial correlation between the dates of vegetative phenology and preseason temperature (see Section 2). The mean partial correlation coefficient between the start of green season and preseason temperature across all sites and species ( $-0.62 \pm 0.19$ , 89% being significant) was significantly larger than that of the end of the green season ( $+0.22 \pm 0.33$ , with only 30% significant) (Figure 5b), suggesting that spring phenology is more controlled by temperature than the onset of senescence which is likely under strong photoperiodic control to remobilize nutrients before the occurrence of critical low temperatures. Previous studies have reported a positive correlation between spring and autumn phenology (Fu et al., 2014; Keenan & Richardson, 2015), which may offset the autumn temperature effect on autumn phenology, and partially contribute to constraint delays in the end of green season. As a result, this is likely to reduce the overall difference between TS and GS. We further estimated the apparent sensitivities of spring and autumn phenology to temperature (see Section 2) and found that the start of the green season advanced by  $-4.8 \pm 1.9$  day for each degree Celsius increase in spring temperature, whereas the end of green season was delayed by only  $1.9 \pm 7.1$  day  $^\circ\text{C}^{-1}$  (Figure 5c). These results indicate that both the faster warming in spring and the higher, rather than lower, sensitivity of spring phenology to temperature have contributed to the larger shift (advance) in the start of green season compared to the shift (delay) in the end of green season (which is mainly controlled by photoperiod and temperature fluctuations) (Descals et al., 2022).

The sensitivity of spring phenology to temperature has been reported to decrease with climatic warming, likely due to



progressively insufficient chilling to fully break winter dormancy or photoperiodic constraints slowing down bud development (Fu et al., 2019; Fu, Zhao, et al., 2015; Garonna et al., 2016; Preve et al., 2017). In line with this, we found that the chilling accumulation for the start of the green season has decreased significantly by  $-3.2 \pm 3.2$  day  $\text{decade}^{-1}$  (Figure 5d), which might lead

to reduced temperature sensitivity and thus contribute to the increase in  $\delta\text{SOS}$  over the study period.

As mentioned above, the magnitude of warming was much smaller in autumn than in spring (Figure 5a), and the end of thermal season occurs only slightly later than in the past. These findings, however, cannot account for the slight advances in the end of green



**FIGURE 5** Possible effects of environmental variables. (a) Temporal trend of seasonal temperature in spring (MAM; March, April, and May), summer (JJA; June, July, and August), autumn (SON; September, October, and November) and winter (DJF; December, January, and February). The subpanel shows the average and standard deviation of the seasonal warming trends. (b) Frequency distribution of the correlation coefficient between phenological date and temperature determined using a partial correlation analysis that excluded the influence of precipitation and shortwave radiation. The subpanel shows the proportion of positive and negative values and the significance. (c) Apparent sensitivities to temperature for the start and end of the vegetation-based growing season (VSOS and VEOS, respectively). The central marks indicate the medians, and the bottom and top edges of the boxes indicate the 25th and 75th percentiles, respectively. The subpanel shows the frequency distribution of the sensitivities to temperature. (d) Distribution of the temporal changes in chill days for VSOS and VEOS. The subpanel shows the spatial pattern of temporal changes in chill days. The values in brackets indicate the slope and significance ( $p$  value) of the linear fitting. (e) Spatial pattern of temporal changes in seasonal precipitation. (f) Variation of the deviation of phenological dates with latitude. The data for (e), (f), and the subpanel in (d) are averaged every  $0.25^\circ$  northward. The shading represents the 95% confidence intervals. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

season over recent decades and instead suggest that factors other than autumnal temperature have played a role (Fu et al., 2019; Zani et al., 2020). For example, previous studies have found that changes in spring leaf-out affect the dates of autumnal foliar senescence (Fu et al., 2014; Keenan & Richardson, 2015), whereby an earlier start of the season translates to advances in the end of the season, offsetting (at least partly) the retarding effect of a warming autumn. Similarly, it was found that the dates of foliar senescence advanced with increased vegetative productivity/growth due to an earlier spring phenology, increasing growing season temperature, and/or increasing atmospheric  $\text{CO}_2$  concentrations (Asshoff et al., 2006; Zani et al., 2020). Increased cumulative water deficits from either warming-induced enhanced evapotranspiration or from decreased precipitation could also potentially advance foliar senescence (Li et al., 2021), though contrasting results have been found depending on the drought intensity (Estiarte & Peñuelas, 2015; Xie et al., 2018). Indeed, we found that seasonal precipitation over the study period (1980–2016) tended to decrease in all seasons, that is, spring ( $-9.9 \text{ mm decade}^{-1}$ ), summer ( $-9.3 \text{ mm decade}^{-1}$ ), autumn ( $-3.1 \text{ mm decade}^{-1}$ ), and winter ( $-7.9 \text{ mm decade}^{-1}$ ), and especially at higher latitudes (Figure S10 and Figure 5e), which is consistent with previous studies (Wang et al., 2022). We took the mean annual precipitation of 600 mm to separate the sites into areas with water deficit potentials and areas with sufficient water. We found that within sites with an annual precipitation of less than 600 mm, the  $\delta\text{GS}$  at sites with decreased precipitation were larger than those with increased precipitation. However, the difference is not obvious in the sites with annual precipitation greater than 600 mm (Figure S11).

The spatial patterns of  $\delta\text{SOS}$  and  $\delta\text{EOS}$  were of opposite direction, that is,  $\delta\text{SOS}$  increased but  $\delta\text{EOS}$  decreased toward higher latitudes, which may be due to spatial variations in warming trends and environmental constraints. The larger difference between advances in the start of thermal and green season ( $\delta\text{SOS}$ ) at higher latitudes may have been caused by the stronger warming trends that have occurred over recent decades at higher latitudes (larger advance in  $\text{TSOS}$ , Figure S12), whereas advances in the start of the green season show no clear latitudinal pattern. Indeed, the spatial differences in the temporal trends in the start of the green season were small (Figure S13), indicating that other environmental constraints, such as photoperiod and local microclimate, may have buffered

against warming-induced advances in leaf-out (Fu et al., 2019; Tang et al., 2016). To test whether the stronger buffering at higher latitudes could be due to the effect of photoperiod, we used the standard deviation of phenological dates as an indirect measure of the effect of photoperiod following previous studies (Geng et al., 2022; Zohner et al., 2016). This photoperiod index, however, was not significantly correlated with latitude (Figure 5f), suggesting that photoperiod alone cannot account for the spatial difference in temporal trends in the start of the thermal and green season. The spatial variation of  $\delta\text{SOS}$  may be mainly driven by spatial differences in the rates of warming and by local environmental constraints on the start of the green season.

$\delta\text{EOS}$  was large at low latitudes and small at high latitudes (Figure 4). The end of thermal season was consistently delayed across all latitudes, whereas the end of the green season varied with latitude, with temporal advances at low latitudes and slight delays at high latitudes ( $p < .01$ ) (Figure S13c). These results may indicate a larger photoperiod limitation of the end of the green season at higher latitudes, and we found that the standard deviation of the end of the green season decreased with increasing latitude ( $-0.23 \pm 0.12 \text{ day}^\circ\text{N}^{-1}$ ,  $p < .1$ ) (Figure 5f), suggesting a larger effect of photoperiod at high latitudes. Water stress has mainly increased in central-southern Europe (Spinoni et al., 2018; Vicente-Serrano et al., 2014), which may also partially account for the temporal advance in the end of green season at lower latitudes. These results indicate that spatial variation in  $\delta\text{EOS}$  can mainly be attributed to differences in local environmental constraints rather than to differences in the rates of autumnal warming.

## 4 | CONCLUSIONS

This study found that global warming is extending both the thermal (potential) and the green (actual) seasons, as rated by flushing date and autumnal color change, of temperate deciduous trees, but trees are not exploiting the full window opportunity of the potential green season. On average, trees' actual green season extensions lag behind extensions of the thermal potential by 7.9–11.1 days (65%–86% of total  $\text{TS}$  extension) during the period 1980–2016. We further demonstrated that the increased discrepancy

between the lengths of the thermal and green seasons was mainly driven by the decoupling between strong advances in the thermal onset of the season and advances in actual leaf-out dates. Our findings revealed that climate warming-induced northward expansions of the cold range limits and productivity isolines of forest trees (Keenan et al., 2014; Lucht et al., 2006; Richardson et al., 2010) are at a much slower pace relative to the northward advances of temperature isolines (Huang et al., 2017). These results suggest that thermal acclimation of trees needs to be accounted when estimating spring phenology in dynamic global vegetation models (Piao et al., 2014; Vickers et al., 2016) to capture the changes in spring onset, lengthening of growing season, shifting vegetation distribution and changes in ecosystem productivity. The mismatch between the responses of vegetation and the thermal growth potential is projected to increase as climatic warming continues. We therefore call for more studies to explore the underlying mechanisms of phenological shifts in response to the ongoing climate change, and highlight the issues of using thermal sums to predict future changes in plant vegetative growth or any processes involving plant development.

#### AUTHOR CONTRIBUTIONS

Yongshuo H. Fu conceived the ideas and designed methodology; Xiaojun Geng and Shouzhi Chen analyzed the data and Yongshuo H. Fu led the writing of the manuscript in corporation with Xuan Zhang, Xiaojun Geng, and Shouzhi Chen; all authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The in-situ phenological data that support the findings of this study are openly available in open-access Pan European Phenology Network at <http://www.pep725.eu/>, and the GIMMS3g NDVI data that support the findings of this study are openly available at <https://climatedataguide.ucar.edu/climate-data/ndvi-normalized-difference-vegetation-index-3rd-generation-nasagfsc-gimms>.

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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