Warming-induced increase in carbon uptake leads to earlier spring phenology

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Abstract

Under global warming, advances in spring phenology due to rising temperatures have been widely reported. However, the physiological mechanisms underlying the warming-induced earlier spring phenology remain poorly understood. Here, using multiple long-term and large-scale phenological datasets between 1951 and 2018, we show that warmer temperatures during the previous growing season led to earlier spring phenology in the Northern Hemisphere, with an average advancement of 2.5 days °C⁻¹. Correspondingly, we observed an earlier spring phenology with the increase in photosynthesis of previous growing season. Furthermore, we found a significant decline in the advancing effect of warming in previous growing season on spring phenology from cold to warm periods. These findings reveal that the observed warming-induced earlier spring phenology is driven by increased photosynthetic carbon assimilation in the previous growing season, while the slowdown in the advanced spring phenology may arise from decreased carbon assimilation when warming exceeds optimal temperatures for photosynthesis. Therefore, the vital role of warming-induced changes in carbon assimilation should be considered to accurately project spring phenology and carbon cycling under future climate warming conditions.

Introduction

Plant phenology influences the fitness of individual plants and functioning of terrestrial ecosystems, including water and energy fluxes and food web dynamics¹⁻⁶. Since phenological events are highly sensitive to climate variations, monitoring changes in plant phenology can provide early visible signals of the impact of climate change on terrestrial ecosystems^{6,7}. Under global warming, advanced spring phenological events (e.g., leafing and flowering) due to rising temperature have been widely reported over recent decades⁸⁻¹². However, important questions regarding the physiological mechanisms underlying this response remain unanswered¹³⁻¹⁷. This largely hinders the prediction of spring phenology under future, warmer conditions.

Generally, spring phenology is considered to be driven by temperatures in winter and spring because plants need to accumulate sufficient winter chilling units to end endodormancy and spring forcing units to break ecodormancy before spring phenological events¹⁸⁻²². Although warming-induced earlier spring phenology has been observed across multiple taxa, recent studies show that the response of earlier spring phenology to climate warming may be declining^{17,23}. However, the mechanisms behind the slowdown in the warming-induced spring phenology are not well understood.

Plants need to assimilate and store sufficient carbohydrates in the preceding growing season to resist low temperatures in winter and support growth reactivation in spring²⁴⁻²⁷. In temperate regions, nonstructural carbohydrate (NSC) concentrations, such as soluble sugar and starch, often reach maximum levels in autumn before winter dormancy, but become depleted by early summer after spring growth²⁸⁻³⁰. Girdling experiments demonstrated that a later budbreak is often associated with a lower

NSC availability^{31,32}. Timing of spring phenology is therefore likely to depend on the photosynthetic carbon assimilation during the previous growing season, yet this has received little attention across large spatial and temporal scales.

Under global warming, increasing temperatures may alter photosynthetic carbon assimilation, leading to changes in spring phenology in the following year³³. Photosynthetic carbon uptake tends to show a peaked response to temperature at the leaf and canopy scale^{12,34–37}. As such, an increase in temperature might increase photosynthesis in cold and temperate regions, and advance spring phenology in the following year^{38,39}. Also, temperature increases above the optimal threshold for photosynthesis could explain the slowdown in warming-induced advancement in spring phenology. However, previous studies have largely overlooked the links between previous growing season climate, photosynthesis, and the timing of spring phenology in the following season^{40–43}.

Using long-term phenological observations, remote-sensing and flux data collected in the Northern Hemisphere (Fig. 1), we analyzed the effect of warming during the previous growing season on spring phenology. We hypothesized that timing of spring phenology may depend on the photosynthetic carbon assimilation in the previous growing season prior to leaf senescence. According to this carbon-based assumption, we expected warmer temperatures during the previous growing season in cold and temperate regions to increase photosynthetic carbon uptake and trigger earlier spring phenology.

Materials And Methods

PEP725 phenological network

Phenological observation data were acquired by the European phenology database PEP725 (<http://www.pep725.eu/>). PEP725 contains phenological observations of temperate species across central Europe starting in 1951⁴⁴. We selected the date when the first leaf stalks were visible (BBCH11 in PEP725) to represent the start of spring phenology (SOS) and date when 50% leaves had their autumnal color (BBCH94 in PEP725) to represent the end of season (EOS). Data exceeding 2.5 times of median absolute deviation (MAD) were considered outliers and removed⁴⁵. We selected 466,988 records of nine temperate tree species (Table S1) at 2,300 sites, for a total of 171,202 species-site combinations with at least 30 years of observations.

PhenoCam network

The PhenoCam network (<https://phenocam.sr.unh.edu/>) is a cooperative database of digital phenocamera imagery that provides the dates of phenological transition between 2000 and 2018 worldwide^{46,47}. In the PhenoCam network, the 50% and 90% of the Green Chromatic Coordinate (G_{CC}) were calculated daily to extract the date of greenness rising and falling based on the following formula:

$$G_{CC} = \frac{G_{DN}}{R_{DN} + G_{DN} + B_{DN}}, (1)$$

where R_{DN} , G_{DN} and B_{DN} are the average red, green and blue digital numbers (DN), respectively.

We selected 50% threshold of G_{CC-90} (G_{CC} reaches 90th quantiles of its seasonal amplitude) as SOS⁴⁸. We removed outliers according to the above-mentioned procedure, and we selected sites with at least 8-year observations between 2000 and 2018. We also excluded agricultural ecosystems to avoid the impact of human-controlled planting dates. The final dataset had a total of 738 records at 78 sites from three vegetation types: deciduous broadleaf forests, evergreen forests, and grasslands.

GIMMS NDVI3g phenological product

The Normalized Difference Vegetation Index (NDVI), a proxy of vegetation greenness and photosynthetic activity, is commonly used to derive phenological metrics⁴⁹. We derived SOS from the third generation GIMMS NDVI_{3g} dataset (<http://ecocast.arc.nasa.gov>) from Advanced Very High Resolution Radiometer (AVHRR) instruments for the period 1982-2014 with a spatial resolution of 8 km and a temporal resolution of 15 days⁵⁰.

We only kept areas outside tropics (latitudes >30 °N) that have a clear seasonal phenology⁵¹ and excluded bare lands with annual average NDVI <0.1 to reduce bias. We applied a Savitzky-Golay filter⁵² to smooth the time series and eliminate noise of atmospheric interference and satellite sensor, and used a Double Logistic 1st order equation to extract phenology dates⁵¹ according to the formula:

$$y(t) = a \left(\frac{1}{1 + e^{k(t-m)}} + \frac{1}{1 + e^{\varepsilon(t-n)}} \right) + b, (2)$$

where a , k , m , and n are parameters of logistic function and a is the initial background NDVI value, $a + b$ represents the maximum NDVI value, t is time in days, and $y(t)$ is the NDVI value at time t . The second-order derivative of Eq. (2) was calculated to extract SOS and EOS at the first and second local maximum point, respectively^{53,54}.

FLUXNET dataset

The flux dataset was downloaded from FLUXNET (<https://fluxnet.org/data/>). The data were released in November 2016 (Total: 212 sites worldwide)⁵⁵. The dataset was processed with a processing pipeline to reduce uncertainty by improving the data quality control. The pipeline generates uniform and high-quality

derived data products suitable for studies that compare multiple sites⁵⁵. We selected 39 sites with at least 5-year observations and > 300 daily records for each year between 1992 and 2014. The Singular Spectrum Analysis (SSA) filter method⁵⁶ was used to smooth the time series of gross primary productivity (GPP) to minimize the noise. To describe the seasonal GPP variation⁵⁷, we used mean GPP and GPP_{max} (the maximum daily GPP) during previous growing season to evaluate the photosynthetic carbon fixation at the ecosystem scale^{57–59}.

Climate data

Gridded daily mean temperature, precipitation, solar radiation and air humidity during 1950-2015 in Europe were downloaded from the database E-OBS (<http://www.ecad.eu/>)⁶⁰ at 0.25° spatial resolution. Gridded monthly soil moistures during 1979-2015 were downloaded from World Meteorological Organization (http://climexp.knmi.nl/select.cgi?id=someone@ somewhere&field=clm_wfdei_soil01) at 0.5° spatial resolution and banded with PEP725 dataset. Global monthly mean temperatures during 1981-2017 were downloaded from Climate Research Unit (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.04/; <http://www.geodata.cn>) at 0.5° spatial resolution to match the PhenoCam and GIMMS NDVI_{3g} datasets. Bilinear interpolation method was used to extract climate data of each site or pixel using the *raster* package⁶¹ in R⁶². Environmental variables, including daily mean temperature (°C), shortwave radiation (Wm⁻²), CO₂ (ppm), and precipitation (mm) were also extracted from the FLUXNET dataset.

The detailed information of all the datasets used in our study was listed in Table S4.

Statistical analyses

To test our hypotheses, we primarily used the observations from the PEP725 network corresponding E-OBS climate dataset, while we used the PhenoCam and GIMMS NDVI_{3g} datasets to test the robustness of our PEP725 results. We did this because PEP725 data was relatively more reliable than the extracted phenological metrics from images in the PhenoCam network and GIMMS NDVI_{3g} product because its phenological records were taken manually *in situ*. In addition, the PEP725 network covered a longer period (between 1951 and 2015) than PhenoCam (between 2000 and 2018) and GIMMS NDVI_{3g} dataset (between 1982 and 2014).

We calculated the temperature sensitivity (S_T , change in days per degree Celsius) based on mean temperatures during the previous growing season (T_{GS}) and timing of spring phenology using the three complementary datasets (PEP725, PhenoCam, GIMMS NDVI_{3g}) in the Northern Hemisphere. S_T was defined as the slope of a linear regression between the dates of phenological stages and the

temperature^{22,63,64}. The length of growing season was defined as the period between SOS and EOS. The mean dates of SOS and EOS from the PEP725 network were DOY 120 and DOY 280. Therefore, the period between May and September was selected to represent the growing season. A similar time period was used for complimentary analyses of PhenoCam and GIMMS NDVI_{3g} data. Linear regression models were used to calculate S_T of leaf unfolding for each species at each site. In the model, the response variable was the leaf unfolding date while the predictor was the T_{GS} .

In addition to temperature, other climate factors (e.g., radiation and precipitation) may influence spring phenology by altering leaf photosynthesis. Partial correlation analysis has been frequently used to exclude confounding effects in order to isolate the relationship between two variables⁶⁵. Using partial correlation analysis, here we excluded potential covariate effects of a set of climate variables of growing season, including radiation, precipitation, soil moisture, humidity, on leaf unfolding and further examined the relationship between T_{GS} and leaf unfolding dates in PEP725 network. Then, we quantified and compared effects of these climate variables on leaf unfolding dates using boosted regression trees, an ensemble statistical learning method⁶⁶ that has been frequently applied in ecological modeling and prediction^{67,68}. Because radiation and soil moisture data were only available since 1980, we selected phenology and climate datasets between 1984 and 2015 to perform partial correlation analysis and boosted regression trees. We performed partial correlation analysis using *ppcor* package⁶⁹ in R⁶². We conducted boosted regression trees using *gbm* package⁷⁰ in R⁶², where 10-fold cross validation was used to determine the optimal number of iterations.

Commonly, temperatures in winter and spring act as the dominant driver of spring phenology by influencing the accumulation of chilling and forcing units⁷¹. To ensure the robustness of results, using partial correlation analysis, we further excluded the effects of chilling and forcing on spring phenology, and tested the relationship between T_{GS} and leaf unfolding dates in PEP725 network. In addition, a positive correlation between autumn phenology and spring phenology has been reported^{72,73}. As such, we also calculated the partial correlation coefficient between T_{GS} and leaf unfolding date after excluding the covariate effects of autumn leaf senescence date and accumulations of chilling and forcing units. Accumulations of chilling and forcing units were calculated during the period between November 1st and mean leaf unfolding date across years for each species at each site⁷⁴. The chilling units were calculated as the number of chilling days when daily mean temperature ranged from 0 to 5°C^{75,76}. The forcing units were calculated as the accumulated growing degree days when the daily mean temperature was above the threshold temperature 5°C^{75,76}.

To clarify the underlying physiological mechanisms, we further examined the relationships between GPP (both average GPP and GPP_{max}) of the previous growing season and SOS between 1992 and 2014 using FLUXNET data. Because the site-averaged daily GPP from FLUXNET started to increase from DOY 120, peaking at DOY 180, then decreased until DOY 300 (Fig. S2), the period between May and September was also selected as the growing season for calculating the climate variables. This is also consistent with the

period of growing season identified by the dates of leaf unfolding and leaf senescence in PEP725 network. We extracted the GPP_{max} of each year from the smoothed GPP curve by the SSA-based denoising smoothing method at individual sites⁷⁷. The average GPP was calculated as the mean daily GPP during growing season between May and September. SOS was extracted from smoothed daily GPP curve based on the threshold method⁵². The spring threshold was defined as 15% of the multi-year daily GPP maximum following previous studies^{78,79}, and SOS was defined as the turning point when the smoothed GPP was higher than spring threshold. Correlation analysis was used to examine the relationships between SOS and GPP during previous growing season.

We further used piecewise structural equation models (SEM) to analyze the relationships between climate, GPP (both average GPP and GPP_{max}) and SOS from the FLUXNET sites⁸⁰. To test our carbon-based hypothesis, we constructed a conceptual model that includes both the direct and indirect effects of climate factors in growing season on spring phenology. In the SEM model, we hypothesized that climate during the growing season is likely to directly influence the timing of spring phenology, i.e., plants can directly sense the change in climate factors and determine the onset of spring phenology, indicated by the arrows from each climate factor directly point to the SOS. Also, they can indirectly influence spring phenology by altering the photosynthetic carbon assimilation, indicated by the arrows from each climate factor firstly directly point to GPP or GPP_{max} then to the SOS. The piecewise SEM was fit using the *piecewiseSEM* package⁸⁰ in R⁶².

Following Fu et al.¹⁷, we assessed the effects of past climate warming on spring phenology. First, we calculated the T_{GS} across all the 2,300 sites in Europe from 1951 to 2015. Using a 15-year smoothing window, we identified the coldest and warmest periods: 1955-1969 and 2000-2014 over the past 65 years. We calculated the S_T of leaf unfolding in response to the T_{GS} during the two periods for each species at each site. One-way analysis of variance (ANOVA) was used to test the difference in the S_T of leaf unfolding during 1955-1969 and 2000-2014.

All data analyses were conducted using R version 4.0.3⁶².

Results

The calculated S_T of spring phenology based on three datasets is shown in Fig. 2. Using the PEP725 network, the mean S_T of leaf unfolding across nine temperate tree species between 1951 and 2015 was $-2.50 \text{ days} \cdot ^\circ\text{C}^{-1}$ (Fig. 2a). This suggested that a warmer previous growing season advanced leaf unfolding dates. The S_T was negative across all selected nine temperate tree species (Fig. 2b). The response of *Quercus robur* to T_{GS} was the strongest, with an average of $-2.82 \text{ days} \cdot ^\circ\text{C}^{-1}$, significantly stronger than those of *Tilia cordata* ($-1.04 \text{ days} \cdot ^\circ\text{C}^{-1}$) and *Tilia platyphyllos* ($-1.16 \text{ days} \cdot ^\circ\text{C}^{-1}$). After excluding covariate effects of other climate variables, autumn leaf senescence, and chilling and forcing units, we consistently observed that leaf unfolding dates were advanced by increasing temperature during previous growing season (Fig. S1a). Using boosted regression tree, we found the temperature had the strongest

effect on leaf unfolding dates (84.67%), followed by radiation (6.33%), soil moisture (3.93%), precipitation (3.32%), humidity (1.75%) (Fig. S1b).

Our PEP725 results were corroborated by PhenoCam and remote sensing data. Specifically, we observed a negative effect of T_{GS} on SOS in deciduous broad-leaved forests, evergreen forests and grasslands using phenological metrics extracted from the PhenoCam network between 2000 and 2018 (Fig. 2c). According to the calculated S_T , the SOS in response to warming of the previous growing season was the strongest in deciduous broad-leaved forests, followed by evergreen forests and grasslands (Fig. 2c). Using the phenology metrics extracted from the remote sensing dataset between 1982 and 2014, we also observed that increasing T_{GS} advanced SOS across different vegetation types in the Northern Hemisphere (Fig. 2d). Among all vegetation types, the S_T of the Tundra was the lowest, followed by Temperate Broadleaf & Mixed Forests and Savannas & Shrublands (Fig. 2d).

We found that the timing of SOS showed a significant negative correlation with the GPP_{max} during previous growing season between 1992 and 2014 (correlation coefficient = -0.47 , $P < 0.01$, Fig. 3a). We also observed a significantly negative correlation between SOS and averaged GPP in previous growing season (correlation coefficient = -0.39 , $P < 0.01$, Fig. S3a). This suggested that spring phenology occurred earlier when photosynthetic carbon assimilation was greater during the previous growing season. To further test the carbon-based hypothesis, we constructed a piecewise structural equation model to explore the direct and indirect effect of climate factors on spring phenology (Fig. 3b and Table S2). We found that spring phenology (SOS) was advanced directly by temperature (slope = -0.18 , $P < 0.05$), but delayed by radiation (slope = 0.243 , $P < 0.01$) and precipitation (slope = 0.11 , $P < 0.05$). In addition, the direct effect of CO_2 on SOS was not significant (slope = 0.05 , $P > 0.05$, Fig. 3b). These direct effects are likely occurring due to spatiotemporal climate variation. We found that increased temperature, precipitation, and CO_2 significantly increased GPP_{max} . Then, the spring phenology (SOS) was significantly advanced by increased GPP_{max} (slope = -0.68 , $P < 0.001$, Fig. 3b), providing evidence for indirect effects of temperature, precipitation, and CO_2 on SOS. We obtained similar results based on the averaged GPP in previous growing season (Fig. S3 and Table S3).

To examine the potential effects of climate warming on leaf unfolding, we used the PEP725 dataset to calculate and compare the S_T between the coldest and the warmest 15-year periods: 1955–1969 and 2000–2014, respectively (Fig. 4). We found that the S_T of leaf unfolding decreased by 63.1% from -1.76 ± 0.04 days $\cdot^{\circ}C^{-1}$ during 1955–1969 to -0.65 ± 0.04 during 2000–2014 (Fig. 4a). Between 1955 and 1969, the S_T of early-successional species is -2.37 days $\cdot^{\circ}C^{-1}$ and -1.23 days $\cdot^{\circ}C^{-1}$ for late successional species. Between 2000 and 2014, S_T of the early- and late-successional species were -0.13 days $\cdot^{\circ}C^{-1}$ and -0.92 days $\cdot^{\circ}C^{-1}$, respectively. The S_T of the early successional species decreased more from the coldest to the warmest periods (-2.24 ± 0.15 days $\cdot^{\circ}C^{-1}$) than that of late successional species (-0.31 ± 0.16 days $\cdot^{\circ}C^{-1}$) (Figs. 4b and S4).

Discussion

Global warming has advanced budbreak and leaf-out worldwide^{22,81–84}. Using three long-term and large-scale phenological datasets, we show that warmer temperatures of the previous growing season drive earlier phenology in the following spring in the Northern Hemisphere. We also find that warming increased seasonal photosynthetic carbon assimilation, suggesting a physiological mechanism by which global warming is triggering earlier spring phenology (Fig. 5).

In deciduous tree species, carbon gained through photosynthesis can be stored in the form of non-structural carbohydrates (NSC-soluble carbohydrates and starch), in part to support the growth of buds and leaves in the following spring before newly grown leaves can supply photosynthate^{85–87}. For instance, 95% of starches stored in the branches of *Fagus sylvatica* and *Quercus petraea* were consumed when spring bud-break occurred⁸⁶. Needle growth of *Larix gmelinii* in spring drew nearly 50% of the carbohydrates fixed in the previous year^{88,89}. Phloem girdling showed that deficient carbon storage can significantly delay the timing of spring budbreak and reduce bud size²⁸.

During winter dormancy, temperate tree species also need to store sufficient carbohydrates prior to leaf senescence for respiration to maintain baseline functions and protect cells from frost damage and ensure survival^{90,91}. Therefore, warmer temperatures in the previous growing season may advance spring phenology by increasing carbon storage, supported by the negative correlations we observed between spring phenology and GPP in the previous year. To further test the carbon-driven hypothesis, we constructed a carbon-based SEM model to analyze the relationships between climate factors, GPP and spring phenology. We found that climate has both a direct effect on phenology, as has been shown previously, but also an indirect effect through GPP. This again suggested that warming in the previous growing season may influence spring phenology by altering the photosynthetic carbon assimilation.

Recently, Zani et al.³³ has reported that increased carbon assimilation during the growing season drives earlier autumn leaf senescence in temperate ecosystems. When leaf senescence occurred earlier, trees advanced endodormancy^{5,92}. In this context, the requirement of chilling units may be also fulfilled earlier. As a result, earlier autumn phenology facilitates an earlier spring phenology⁹³. Therefore, increased carbon assimilation may directly drive autumn phenology, and, in turn, influence spring phenology. Furthermore, spring phenology is also influenced by chilling and forcing units in winter and spring⁷¹. After excluding the co-variate effect of other climate factors in growing season, autumn phenology, chilling and forcing units on leaf unfolding, we also observed that spring leaf unfolding was advanced by increasing temperature during the previous growing season. This provided additional support for our hypothesis that increased carbon assimilation in the previous season triggers an earlier spring phenology.

We observed that early-successional species showed a stronger response to warming during growing season as compared to late-successional species. In addition to temperature, spring phenology is also under photoperiodic control⁹⁴. Because photoperiod remains stable regardless of climate change, plants are expected to show relatively conservative climatic responses when they rely on photoperiod to

determine spring phenology. However, photoperiod sensitivity often varies among species⁹⁴. For example, late-successional species are reported to have a higher photoperiod sensitivity compared to early-successional species^{94,95}. The higher photoperiod sensitivity of late-successional species may, therefore, explain their conservative climatic responses compared to early-successional species^{94,96}.

Recent studies have reported that the warming-induced earlier spring phenology has slowed over time^{22,97,98}. Fu et al.¹⁷ reported that S_T of leaf unfolding decreased by 40% from $4.0 \pm 1.8 \text{ days} \cdot ^\circ\text{C}^{-1}$ during 1980–1994 to $2.3 \pm 1.6 \text{ days} \cdot ^\circ\text{C}^{-1}$ during 1999–2013. The observed declining effect of warming on spring phenology is generally considered a result of chilling reductions in winter⁹⁹. However, we found that the carbon-based earlier spring phenology effect is also slowing down in recent decades, especially for early-successional species. Duffy et al.¹² showed that the mean temperatures in the warmest quarter passed the optimal for photosynthesis over the past decade, with a sharp decline in photosynthesis. The increase in heat and water stress over time may lead to a spreading growth decline of forests^{100–102}. Therefore, the observed decline in the S_T may involve reductions in carbon assimilation by heat waves and/or drought events under global warming^{103,104}.

Conclusion

Despite the warming-induced spring phenology observed worldwide, the underlying causes and physiological mechanisms still remain unclear. In this study, we used multiple long-term and large-scale datasets to provide evidence that spring phenology is advanced by warmer temperatures in the previous growing season. Correspondingly, we observed that leaf unfolding occurred earlier with greater previous season photosynthetic capability. These findings suggest that an increase in carbon assimilation under global warming could be involved in the observed earlier leafing out of trees. In addition, we observed a decline in the carry-over effect of growing-season warming on spring phenology, which likely resulted from temperatures that have become supra-optimal. With an increase in projected drought frequency under warming scenarios^{100,105}, we expect that temperate trees will slow down the advancement of spring phenology. This may reduce the strength of forest carbon sinks under future climate conditions¹⁷. Our study provides new insights into the warming-induced change in spring phenology under global climate change to predict spring phenology and vegetation-atmosphere feedbacks under future climatic scenarios.

Declarations

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Conflict of interest

The authors declare no conflict of interest.

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Figures

Figure 1

Distributions of the phenological observation sites in this study. Orange dots represent the 2,300 sites selected from the PEP725 dataset across central Europe. Green dots and blue diamonds represent 78 sites in North America from the PhenoCam network and 39 FLUXNET sites, respectively.

Figure 2

Temperature sensitivities (S_T , change in days per degree Celsius) of spring phenology in response to increasing temperature during previous growing season. The calculated S_T was based on (a, b) records of spring leaf unfolding for nine temperate tree species at 2,300 sites in Europe, and phenological metrics extracted from (c) the PhenoCam network and (d) the GIMMS NDVI_{3g} products for different biomes. DB, EN and GR in (c) represents deciduous broad-leaved forests, evergreen forests and grasslands, respectively. In (d), the biomes included Boreal Forests/Taiga (BFT), Flooded Grasslands & Savannas (FGS), Temperate Broadleaf & Mixed Forests (TBM), Temperate Conifer Forests (TCF), Temperate Grasslands, Savannas & Shrublands (TGS), Tropical & Subtropical Coniferous Forests (TSC), Tropical & Subtropical Grasslands, Savannas & Shrublands (TSG), Tropical & Subtropical Moist Broadleaf Forest (TSM) and Tundra (TUN). The black dash lines indicate when the S_T is equal to zero.

Figure 3

(a) Relationship between spring phenology (SOS) and GPP_{max} and (b) the piecewise structural equation model (SEM) using the data of 39 FLUXNET sites between 1992 and 2014. In (a), black dash line

represents the fitted linear regression line, r value represents the correlation coefficient between SOS and GPP_{max} . **(b)** The model includes climate factors (temperature, radiation, precipitation, and CO_2) and GPP_{max} to explore the direct (arrows from each climate factor directly point to the SOS) or indirect (arrows from each climate factor firstly directly point to GPP_{max} then to the SOS) effects of climate factors on spring phenology. Standardized coefficients between variables are shown next to lines, blue lines indicate a negative effect while red lines indicate a positive effect. The solid lines represent significant ($P < 0.05$) relationships between variables, and dashed lines represent no significant ($P > 0.05$) relationships between variables. R^2 values represent the goodness of fits of the responses.

Figure 4

(a) Distributions of temperature sensitivities (S_T , change in days per degree Celsius) of leaf unfolding during the coldest (1955-1969) and the warmest (2000-2014) periods and **(b)** differences of S_T between early- and late-successional species during these two periods. The calculated S_T was based on the temperature during previous growing season and leaf unfolding dates obtained from the PEP725 database. The length of each box indicates the interquartile range, the horizontal line inside each box the median, and the bottom and top of the box the first and third quartiles respectively. The asterisks indicate a significant difference in the S_T 1955-1969 and 2000-2014 ($P < 0.001$). The black dashed horizontal line indicates when the S_T is equal to zero.

Figure 5

A schematic diagram of the earlier leaf-out in response to warming during previous growing season. Warmer temperatures during the previous growing season drivers earlier spring leaf-out by increasing photosynthetic carbon assimilation.

Supplementary Files

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