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Growth Onset Rather Than Photosynthesis Strongly Regulates Autumn Senescence Termination Besides Climate Change

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ABSTRACT

Aim: Plant senescence largely influences the global carbon cycle by regulating the growing season length. However, the driving mechanisms of plant senescence remain unclear, particularly the role of developmental factors. This study aims to investigate how environmental and developmental factors drive autumn senescence and evaluate whether woody and herbaceous plants exhibit divergent responses to these drivers.

Location: Eurasia.

Time Period: 1982–2014.

Major Taxa Studied: Woody and herbaceous species.

Methods: Using 120,833 long-term ground phenological observations, we employed partial correlation analysis to investigate the influence of environmental and developmental factors on senescence termination. Experimental records from literature and pasture survey observations from China were separately utilised to further validate the influence of developmental factors on senescence termination. Structural equation modelling was applied to analyse the pathways of growth onset affecting senescence

[Correction added on 15 September 2025, after first online publication: The copyright line was changed].

termination. Additionally, multiple linear regression was used to examine the tendency of the sensitivity of senescence termination to plant development rate.

Results: We find that earlier growth onset primarily leads to earlier senescence termination directly in herbaceous plants, but indirectly in woody plants by accelerating early-season development. The sensitivity of senescence termination to plant development rate shows a declining trend, particularly in early-season negative effects on woody plants and late-season positive effects on herbaceous plants, suggesting diminished impacts of future warming on senescence timing. The impact of growing season photosynthetic activity on senescence termination is not pronounced for both woody and herbaceous plants.

Main Conclusions: The results demonstrate that growth onset may affect woody and herbaceous senescence termination through different pathways, whereas the carry-over effects of growing season photosynthetic activity are not widely discovered. This emphasises that the introduction of developmental factors into phenological models needs to be considered carefully according to plant type.

1 | Introduction

Vegetation phenology is a highly sensitive indicator of how terrestrial ecosystems respond to climate change (Piao et al. 2019; Rosbakh et al. 2021). In recent decades, significant shifts in both spring and autumn phenology have been observed in temperate and boreal ecosystems, leading to an extension of the growing season (Jeong et al. 2011; Park et al. 2018; Vitasse et al. 2022). These phenological changes have profound impacts on ecosystem carbon balance, with growing season extension being considered one of the primary drivers of increased vegetation productivity in the Northern Hemisphere (Peñuelas et al. 2009; Richardson et al. 2013). While there has been extensive research focused on spring phenology at various scales, autumn phenology has received comparatively less attention, and its driving mechanisms remain highly debated (Gallinat et al. 2015; Garonna et al. 2016; Bao et al. 2019). Therefore, a comprehensive understanding of the underlying mechanisms driving changes in autumn phenology is needed, which is crucial for accurately predicting the future carbon sequestration potential of terrestrial ecosystems.

Autumn phenology has been shown to be potentially regulated by multiple environmental factors. Traditionally, low temperature and short photoperiod in autumn were considered the primary factors driving leaf senescence in temperate trees (Lang et al. 2019; Wang et al. 2022). Additionally, water shortages in summer and autumn could hinder plant growth, potentially leading to earlier senescence (Xie et al. 2015; Vitasse et al. 2021; Wu et al. 2022). Nutrient supply (Fu et al. 2019; Vitasse et al. 2021), CO_2 concentration (Wang et al. 2019) and insolation (Renner and Zohner 2019) have also been found to play a role in regulating the timing of leaf senescence in temperate trees. Due to the multitude of drivers involved, the responses of plant autumn phenology to environmental changes are highly complex.

Recent studies suggest that plant senescence is regulated not only by environmental variables but also by the development status, including internal reserves, carbon acquisition and growth dynamics (Fu et al. 2014; Ren et al. 2022; Vitasse et al. 2022). Particularly, the timing of the growing season onset has emerged as a crucial factor affecting autumn senescence (Fu et al. 2014), with earlier spring leaf unfolding leading to earlier autumn leaf senescence in some woody temperate species (Fu et al. 2014; Keenan and Richardson 2015; Liu et al. 2016). Emerging evidence indicates that the key factor determining plant senescence timing may not be the advancement of spring phenology itself, but rather the accelerated plant development rate and increased productivity during the growing season resulting from this shift (Zohner et al. 2023). However, the impact of growing season productivity on plant senescence remains controversial. Earlier autumn leaf senescence linked to increased growing season productivity has been reported in European deciduous tree species using long-term phenology records and controlled experiments (Zani et al. 2020). Further study suggests that the enhancement of early-season photosynthesis due to spring warming may offset the delaying effect of warmer temperatures in autumn (Zohner et al. 2023). Nevertheless, the senescence period, from the start of leaf coloration to the end, is expected to extend due to slower pigment degradation under warmer conditions (Fracheboud et al. 2009; Zhang et al. 2023). The negative effect of growing season photosynthesis on leaf senescence has not been consistently observed in phenological records from flux tower measurements or Harvard Forest (Lu and Keenan 2022). In most free-air CO_2 enrichment and environmental control experiments, elevated CO_2 and altered hydrothermal conditions either delayed leaf senescence or showed no significant effect (Norby 2021; Yu et al. 2022).

The conflicting findings highlight the urgency of further investigating the mechanisms that trigger plant autumn phenology. Moreover, due to the lack of long-term ground observations, existing evidence on the driving factors of herbaceous plant phenology is still very limited, especially the impact of developmental factors on autumn phenology (Zani et al. 2020; Lu and Keenan 2022). Understanding the differences in senescence mechanisms between woody and herbaceous plants would contribute to accurate predictions of vegetation composition dynamics and ecosystem carbon sequestration. To address these knowledge gaps, we conducted a comprehensive analysis using three datasets: (1) 120,833 records from long-term ground observations at 1882 sites, (2) 190 experimental records collected through meta-analysis and (3) 34 time series at 12 sites from pasture survey datasets. Specifically, we aimed to (1) clarify the impact of environmental and developmental factors on plant senescence, (2) examine whether the timing of senescence in woody and herbaceous plants responds similarly to these drivers and (3) explore the potential pathways through which these factors influence senescence termination.

2 | Materials and Methods

2.1 | Phenology Datasets

In this study, we utilised three distinct phenological datasets: in situ phenological observations, phenology experiment data collected through literature, and pasture phenological data from China combined with biomass records.

2.1.1 | Long-Term In Situ Phenological Observations

Two in situ plant phenology datasets from temperate regions (30°–61° N) were employed in this study. First is the Pan European Phenology (PEP725) dataset, containing long-term phenology observations across European countries. The date of the first visible leaf stalk (BBCH code 11) and the date of 50% autumnal coloration of leaves (BBCH code 94) were selected to represent spring and autumn leaf phenology, respectively. The second phenology dataset was provided by the China Meteorological Administration (CMA), and recorded multiple phenology stages in common woody and herbaceous species across China. For this dataset, the 'leaf unfolding' and 'leaf coloration' stages were selected, representing the dates when new leaves begin to unfold and when at least two-thirds of aboveground organs have wilted and/or discoloured, respectively (China Meteorological Administration 1993).

We retained only the phenological time series for each site and species that simultaneously contained the corresponding leaf unfolding and leaf coloration dates and included only those with more than 15 years of continuous phenological time series. In total, 112,938 records of six woody species at 1694 sites from the PEP725 dataset during 1982–2014, 4812 records of 30 woody species at 118 sites, and 2588 records of 17 herbaceous species at 70 sites from the CMA dataset during 1982–2011 were used in this study. The spatial distribution of phenology observation stations can be found in Figure S1. The geolocation, species information and observation timespan for the CMA datasets are listed in Data S1.

2.1.2 | Phenological Records Based on Experimental Warming

The aboveground plant phenology data from experimental warming, collected through meta-analysis by Liu et al. (2022), were used to explore the impact of net shifts in the start-of-season (SOS) on the end-of-season (EOS), thereby enabling the accurate quantification of the independent influence of spring growth onset on leaf senescence timing. In this dataset, SOS and EOS were defined as the Julian days at which 10% and 90% of annual growth in aboveground dry matter, plant height or stem diameter were accumulated (Liu et al. 2022). The net shifts in SOS and EOS were calculated through multiplying 'temperature sensitivity' by 'warming magnitude'. In total, 144 woody phenological observations and 46 herbaceous phenological observations were analysed, primarily distributed across North America, Europe, China, Australia and Japan. For detailed information about species, please refer to Data S2.

2.1.3 | Pasture Survey Records in China

The historical pasture survey records from the CMA, including both phenology observations and biomass records, provide us with an unprecedented chance to probe the potential impact of real plant production on leaf senescence timing. The phenology metrics used here are also 'leaf coloration' and 'leaf unfolding', which share the same observation criterion with the above long-term phenology dataset from CMA. The pasture biomass is harvested within 1 m^2 grid in late August and expressed as the dry weight for each species. Before analysis, we removed outliers with three standard deviations away from the mean for both phenology and biomass observations and eliminated the time series with lengths less than 10 years. After data cleaning, we acquired a total of 34 individual time series for 22 common pasture species at 12 sites (see Data S3).

In this study, we focused on the mid to late stages of plant senescence. For consistency across different data sources, we uniformly referred to 'leaf unfolding' from in situ plant phenology datasets and pasture survey records, and SOS from warming experiments as 'growth onset', while 'leaf coloration' and EOS were collectively termed as 'senescence termination'.

2.2 | Gridded Climatic and Photosynthesis Proxy Datasets

We acquired monthly maximum temperature (T_{max}), minimum temperature (T_{min}) and precipitation (Pre) from the CRU TS v.4.01, monthly solar radiation (Solr) from CRUNCEP Version 7 at the spatial resolution of 0.5°, and monthly soil moisture (SM) from the Global Land Data Assimilation System (GLDAS) at a spatial resolution of 0.25°. SM data were resampled to 0.5° to keep consistent with other climate variables. The time range of all climate variables is from 1982 to 2014. To examine the role of photosynthesis in regulating autumn senescence termination, we applied two individual gross primary production (GPP) datasets generated from (1) a revised light use efficiency model (EC-LUE model) that integrates major environmental variables (i.e., atmospheric CO_2 concentration, radiation components and atmospheric VPD) at the spatial resolution of 0.05° and 8-day interval (Zheng et al. 2020), and (2) an empirical model based on near-infrared reflectance (an effective substitution of satellite solar-induced chlorophyll fluorescence) and eddy covariance GPP estimations at spatial resolution of 0.05° and one-month interval (Wang et al. 2021). As the two datasets were greatly consistent in interannual fluctuation (Figure S2), we averaged GPP values for further analyses.

2.3 | Statistical Analysis

First, temporal trends in senescence termination and growth onset from in situ plant phenology datasets, plant productivity during the growing season, and climate variables (i.e., average mean, maximum and minimum temperature; total precipitation; total solar radiation; and average soil moisture) during January–March (3 months before multi-year average growth onset) and June–August (3 months before multi-year average senescence termination) were calculated using the Theil-Sen method (Akritas et al. 1995). The non-parametric Mann-Kendall test at the level of 0.05 was employed to assess the significance of the trends (Mann 1945; Kendall 1948). Meanwhile, to examine whether environmental conditions differed preceding senescence termination and growth onset, we used Student's *t*-test to evaluate the differences in trends of climate variables between January–March and June–August.

Second, partial correlation analysis was implemented to assess the separate effect of each developmental and environmental factor on senescence termination using in situ plant phenology datasets. Before that, we identified the preseason length for each climate variable (i.e., average maximum and minimum temperature, total precipitation, total solar radiation and average soil moisture) that had the largest influence on senescence termination (Piao et al. 2015). Specifically, we calculated Spearman correlation coefficients for a range of preseason durations, from the month of multi-year average senescence termination to February at 1-month intervals, and selected the time period corresponding to the highest absolute correlation value (Liu et al. 2016). For each in situ phenological time series, the partial correlation coefficients between senescence termination and growth onset, photosynthesis (growing season summed GPP) and climate variables were separately obtained by controlling for the remaining variables. For obtaining the growing season total GPP, we beforehand interpolated GPP time series into 1-day resolution with a cubic spline function and then summed GPP values from yearly growth onset to the multi-year average senescence termination date (Zohner et al. 2023).

To further examine whether the plant development rate affects senescence termination, we characterised the plant development rate using growing degree days (GDD), calculated as the cumulative daily mean temperature above 0°C. Similar to a previous study (Zohner et al. 2023), we tested for seasonal differences in the effects of plant development rate and photosynthesis strength on senescence termination timing by computing the GDD and cumulative GPP for the pre-solstice growing season (from the yearly growth onset date to the summer solstice, named GDD_{pre} and GPP_{pre}) and the post-solstice growing season (from the summer solstice to the multi-year average senescence termination date, named GDD_{post} and GPP_{post}). The effect of plant growth rate on senescence termination was tested using partial correlation analysis by controlling for growth onset and environmental factors except for temperature. Finally, we established multiple linear regression models to obtain the sensitivity of senescence termination to plant development rate using a 15-year window (Wu et al. 2022) and examined whether it has changed over time using in situ plant phenology datasets. A significance level of 0.05 was employed to assess the significance of the trends.

To further support the findings on the effect of developmental factors on senescence termination, linear regression was performed to test the relationship between the net movements of EOS and SOS collected from the warming control experiments. Additionally, using pasture survey records from China, we employed partial correlation analysis to uncover the associations between senescence termination, growth onset and dry biomass.

2.4 | Path Analysis

To clarify the direct and indirect effects of growth onset, we conducted a path analysis using structural equation modelling (SEM) on in situ plant phenology datasets. SEM allows us to quantitatively compare the relative importance of all investigated factors and their influence path (Streiner 2005). We designed a conceptual model assuming that growth onset cannot only directly affect senescence termination but also indirectly trigger senescence termination by regulating GDD_{pre} and GPP. Moreover, GDD_{post}, Pre, Solr and SM directly influence senescence termination. We ran this model separately for each species, with site location as a random effect variable. The path coefficient and the model explanation rate (R^2) were then averaged across all species. This analysis was implemented using the "piecewiseSEM" package in R.

3 | Results

3.1 | Trends in Plant Phenology, Photosynthesis and Environmental Factors

During the period 1982–2014, long-term in situ observations showed earlier growth onset in 85.1% (38.8%, $p < 0.05$) of woody and 53.3% (21.0%, $p < 0.05$) of herbaceous time series (Figure 1a). The average rate of change was -4.0 ± 0.05 (mean ± standard error) and -1.0 ± 0.45 days decade^{-1} for woody and herbaceous plants, respectively. Delays in senescence termination were observed in 54.7% (15.0%, $p < 0.05$) of woody and 57.1% (23.8%, $p < 0.05$) of herbaceous time series (Figure 1b). The average rate of change in senescence termination was $+0.03 \pm 0.09$ days decade^{-1} for woody plants and $+1.1 \pm 0.68$ days decade^{-1} for herbaceous plants.

At the same time, the growing-season total GPP has increased in 72.3% (32.9%, $p < 0.05$) of the Northern Hemisphere (Figure 1c). Similar increasing trends in GPP were found before and after the summer solstice (Figure S3). For environmental factors, compared to the 3 months preceding growth onset (January–March), the increasing trend in mean temperature (+0.18°C vs. +0.15°C decade^{-1}), maximum temperature (+0.18°C vs. +0.13°C decade^{-1}), minimum temperature (+0.16 vs. +0.12°C decade^{-1}) and precipitation (+0.19 vs. +0.12 mm decade^{-1}) during the 3 months preceding senescence termination (June–August) was significantly greater (Figure 1, Figure S4). In contrast, the decreasing trend in solar radiation (−0.05 vs. −0.01 W m^{-2} decade^{-1}) and soil moisture (−1.24 vs. −0.55 kg m^{-2} decade^{-1}) was also significantly larger (Figure 1f,g). Generally, environmental conditions in the 3 months before senescence termination have changed more intensively than those preceding the growth onset period.

3.2 | Responses of Senescence Termination to Environmental and Developmental Factors

Earlier spring growth onset was predominantly associated with earlier autumn senescence termination (Figures 2 and 3, Figure S5). Using in situ plant phenology datasets, we found a positive correlation between growth onset and senescence

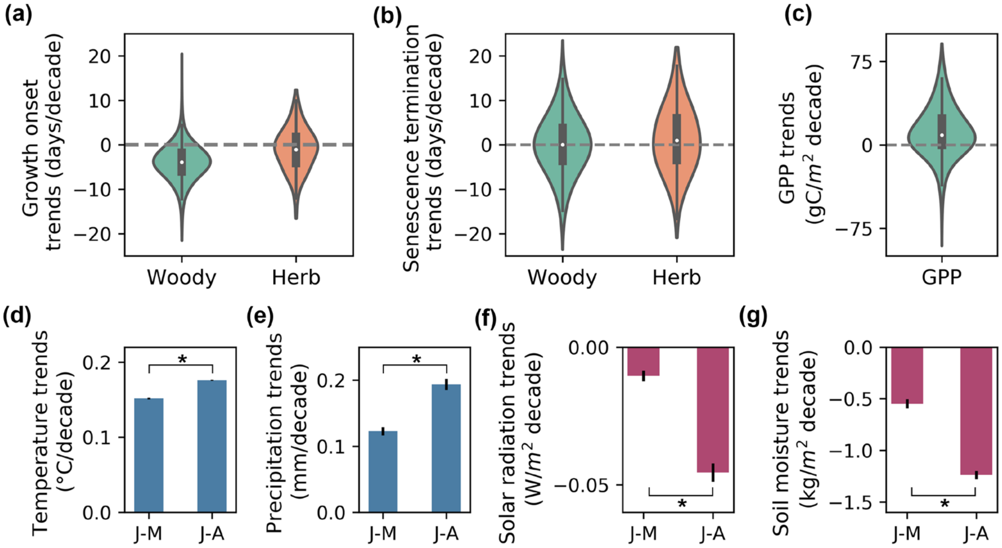

FIGURE 1 | Temporal trends in plant phenology, photosynthesis and environmental conditions. Trend frequency of (a) growth onset, (b) senescence termination and (c) growing season total gross primary productivity (GPP). Climate change trend comparison between the pre-growth onset period (January–March) and the pre-senescence termination period (June–August) across the Northern Hemisphere. (d) Air mean temperature; (e) Precipitation; (f) Solar radiation; (g) Soil moisture. * indicates a significant difference ($p < 0.05$) between pre-growth onset (January–March, named J–M) and pre-senescence termination (June–August, named J–A), performed with Student's *t*-test.

termination in 61.1% (6.2%, $p < 0.05$) of woody and 63.9% (8.3%, $p < 0.05$) of herbaceous time series when controlling for growing-season photosynthesis and environmental factors (Figure 2c and Figure S5). For the phenological records from warming experiments, the results also revealed a significant positive correlation between the shifts in growth onset and senescence termination for both woody ($r = 0.53$, $p < 0.001$) and herbaceous plants ($r = 0.60$, $p < 0.001$) across all site-species observations (Figure 3a,b). Individually, this positive relationship was also detected in 87% of woody species and 57.1% of herbaceous species (Figure 3a,b). Additionally, for pasture survey records, we also detected a predominant positive correlation (70.6%) between growth onset and senescence termination in herbaceous time series when controlling for ground-measured biomass and environmental factors (Figure 3c).

Regardless of the dataset used, photosynthetic activity exhibited little pronounced influence on senescence termination in either woody or herbaceous plants (Figures 2 and 3 and Figure S5). Using in situ plant phenology datasets, growing-season total GPP was significantly correlated with senescence termination in only 7.5% ($p < 0.05$, positive vs. negative: 4.1% vs. 3.4%) of woody time series and 5.5% ($p < 0.05$, positive vs. negative: 4.6% vs. 0.9%) of herbaceous time series (Figure 2c). Similarly, very few significant effects of GPP before and after the summer solstice were found (Figure S6). Results from pasture survey data also showed a minimal effect of harvest biomass on senescence termination, with very close proportions of positive (47.1%) and negative (52.9%) correlations and only 2 out of 34 time series being significant (Figure 3d).

Regarding the external environmental drivers of senescence termination, for woody plants, using in situ plant phenology datasets, preseason warming showed a predominantly positive correlation with senescence termination. Specifically, 58.0% (5.8%, $p < 0.05$) of woody time series were positively correlated with preseason maximum temperature, and 59.2% (7.7%, $p < 0.05$) were positively correlated with preseason minimum temperature (Figure 2c and Figure S5). By contrast, herbaceous plants showed a relatively larger proportion of significant negative correlations with preseason maximum temperature, accounting for 6.5% ($p < 0.05$) of time series, whereas preseason minimum temperature had a limited influence on senescence termination, with only 4.7% of herbaceous time series showing significant correlations ($p < 0.05$, positive vs. negative: 2.8% vs. 1.9%). Higher preseason solar radiation was associated with delayed senescence termination in 58.6% (5.5%, $p < 0.05$) of woody time series, while it was linked to earlier senescence termination in 59.3% (12.0%, $p < 0.05$) of herbaceous time series (Figure 2c).

3.3 | The Effect of Plant Development Rate on Senescence Termination

To further study whether and how plant development rate may affect autumn senescence, we tested the effects of GDD before and after summer solstice (GDD_{pre}, GDD_{post}), using in situ plant phenology datasets. Including the effects of GDD in the partial correlation model largely reduced the effect of growth onset in woody plants but not in herbaceous plants (Figure S6). Further, path analysis showed that GDD_{post} had a substantial delaying effect on senescence termination in both woody plants (mean ± standard error: 0.28 ± 0.04) and herbaceous plants (0.17 ± 0.07), stronger than the advancing effect of GDD_{pre} (Figure 4). Earlier growth onset could indirectly lead to earlier senescence termination by increasing GDD_{pre}. In woody plants, this indirect effect was greater than the direct effect of growth onset on senescence termination (0.04 ± 0.05), but in herbaceous plants, it was smaller than the direct effect (0.21 ± 0.10) (Figure S7). Furthermore, the effect of GPP on senescence termination was still not noteworthy in the path analysis in both woody plants (0.01 ± 0.05) and herbaceous plants (0.09 ± 0.05).

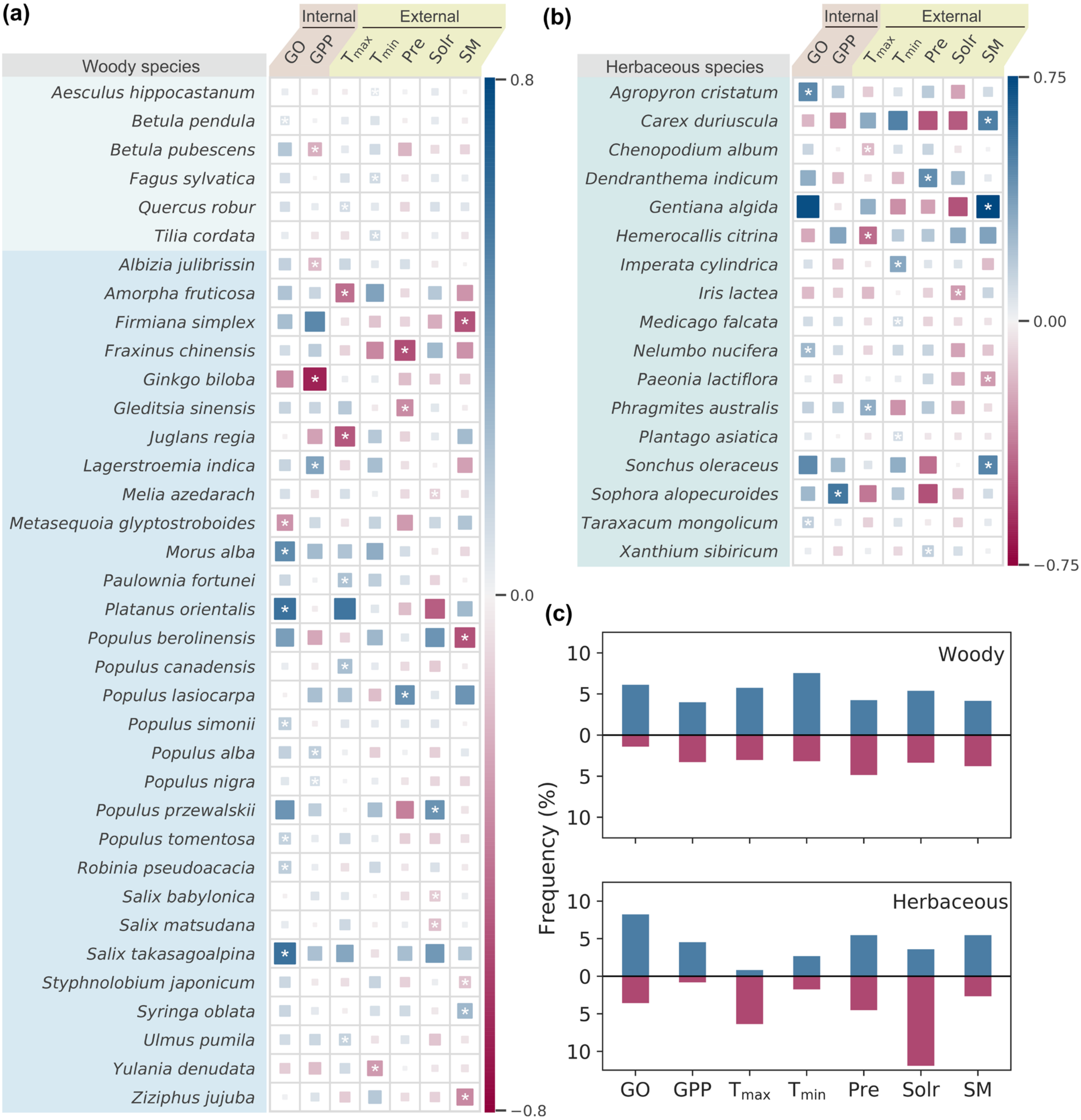

FIGURE 2 | Impacts of environmental and developmental factors on senescence termination using in situ plant phenology datasets. From left to right columns: Species-specific average partial correlation coefficient between senescence termination and growth onset (GO), growing-season total gross primary production (GPP), maximum temperature (T_{max}), minimum temperature (T_{min}), precipitation (Pre), solar radiation (Solr) and soil moisture (SM) for (a) woody species in Europe (first six species on light blue background) and China (the remaining 30 species on medium blue background), (b) herbaceous species in China. GO and GPP are two developmental or 'Internal' factors potentially regulating senescence termination, while T_{max}, T_{min}, Pre, Solr and SM are four environmental or 'External' factors considered to likely affect senescence termination. The square size and colour depth both refer to the average value of the partial correlation coefficient for each species across all sites. The white asterisks the species' maximum absolute mean partial correlation coefficient. (c), The frequency of partial correlation coefficients between senescence termination and GO, GPP, T_{max}, T_{min}, Pre, Solr and SM for woody and herbaceous time series passing the significance test ($p < 0.05$).

On average, compared to herbaceous plants, senescence termination of woody plants was more sensitive to GDD_{pre} (−0.014 vs. −0.001 days $°C^{-1}$) but less sensitive to GDD_{post} (+0.013 vs. +0.031 days $°C^{-1}$). The sensitivity of senescence termination to GDD_{pre} in woody plants has significantly decreased over recent decades ($R^2 = 0.74$, $p < 0.01$), while the effect of GDD_{post} has remained comparatively constant (Figure 5a). By contrast, for herbaceous plants, the sensitivity of senescence termination to GDD_{post} had significantly decreased ($R^2 = 0.83$, $p < 0.01$) during 1982–2011 (Figure 5b).

4 | Discussion

In this study, we investigated variations in senescence termination in response to growth onset, vegetation productivity and

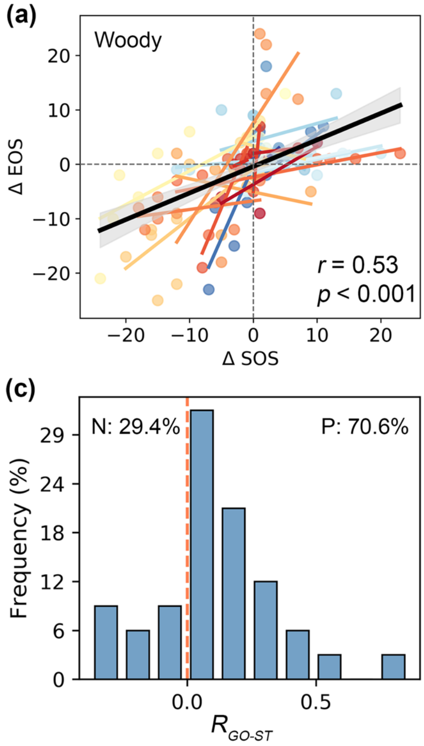

FIGURE 3 | Effects of developmental factors on senescence termination observed in experimental and pasture survey records. Relationship between shifts in senescence termination (ΔEOS) and growth onset (ΔSOS) observed in warming experiments for woody plants (a) and herbaceous plants (b). The black solid line shows the linear regression fit across all experiments and species. The different coloured lines represent connected points (for only two observations) or fitted linear regressions (for more than two observations). (c, d) Frequency of the partial correlations between senescence termination (ST) and growth onset (GO) and dry biomass by controlling the other factors. P and N indicate the percentages of positive and negative partial correlations, respectively.

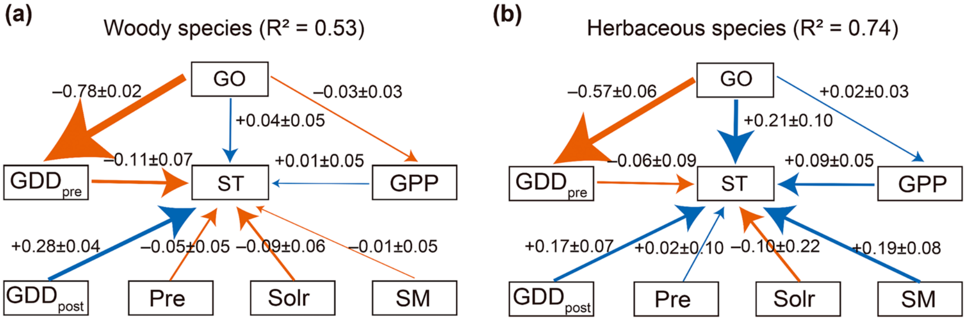

FIGURE 4 | Path analysis considering both environmental and developmental factors. Standard influence of growth onset (GO), growing degree days before summer solstice (GDD_{pre}), growing degree days after summer solstice (GDD_{post}), growing-season total gross primary production (GPP), precipitation (Pre), solar radiation (Solr) and soil moisture (SM) on senescence termination (ST) of (a) woody plants and (b) herbaceous plants inferred from structural equation models (SEM). Site location was included as a random effect. R^2 values represent the adjusted total explanatory power of all predictors. Blue and orange lines indicate the positive and negative effects of variables, respectively. The numbers next to lines and arrow/line widths depict the net effects (± standard errors) of each variable. Each value represents the average across all species.

key environmental cues using an extensive dataset of ground and experimental observations. Our findings revealed widespread trends toward advances in growth onset across Europe and China, while shifts in senescence termination were less pronounced (Figure 1a,b). Interestingly, we observed that hydrothermal conditions before senescence termination changed more significantly compared to those before growth onset between 1982 and 2014 (Figure 1d–g). The smaller shifts in senescence termination despite larger changes in environmental conditions thus suggest a complex interplay of multiple environmental and developmental factors throughout the growing season that co-determine leaf senescence onset and progress (Chen et al. 2020; Fu et al. 2018; Ren et al. 2022).

Our study demonstrates a widespread advancing effect of earlier growth onset on senescence termination, providing evidence for self-limitation of plant growth and development in both woody and herbaceous plants (Figures 2 and 3a–c). Previous studies have indicated such a link for a few tree species and regions (Fu et al. 2014; Keenan and Richardson 2015), whereas our research

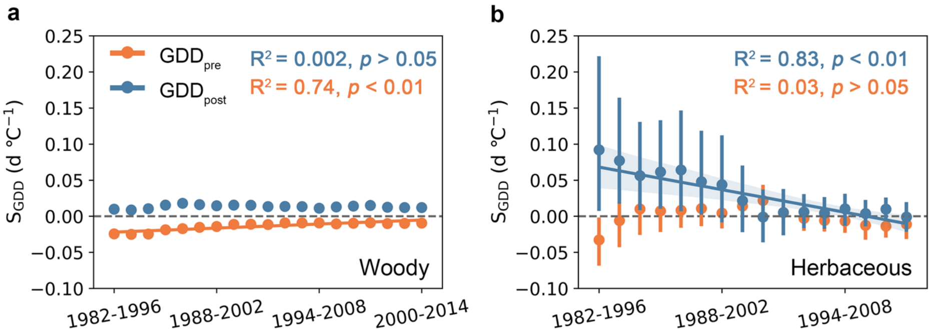

FIGURE 5 | The sensitivity of senescence termination to plant development rate. Sensitivity of senescence termination to growing degree days before (GDD$_{pre}$, orange) and after (GDD$_{post}$, blue) summer solstice for (a) woody plants and (b) herbaceous plants. The lines represent fitted linear regressions that passed the significance test.

substantially expanded this understanding. Moreover, our results show a lesser effect of total growing-season productivity or harvest biomass on senescence termination in most species and sites (Figures 2 and 3d), indicating limited influence of total annual photosynthesis on the late stages of senescence. This finding aligns with the perspective of Lu and Keenan (2022) but contrasts with the results reported by Zani et al. (2020). These differences may stem from several factors, including variations in datasets, model variables and the specific senescence stages under investigation. Overall, our study contributes additional evidence from both woody and herbaceous species in China to the ongoing discussion of carbon limitation. Intriguingly, accelerated early-season growth has been shown to accelerate the onset of leaf senescence (Figure 4), further implying a complex interplay of plant development and autumn senescence.

Our findings further indicate that growth onset affects senescence termination in woody plants primarily indirectly through enhancing the early-season development rate from growth onset to the summer solstice (Figure 4). Later-season development rate due to warming temperatures after the summer solstice had a strong delaying effect on senescence termination, in agreement with Zohner et al. (2023). Warmer conditions in late summer and autumn can help maintain high levels of Rubisco concentration and chlorophyll content to support plant photosynthetic activity and inhibit leaf degradation (Fracheboud et al. 2009; Stinziano and Way 2017). The net change in senescence termination dates of woody plants will be determined by the opposing effects of post-solstice warming and the enhanced pre-solstice development associated with warming and earlier growth onset (Liu et al. 2018; Luo et al. 2018; Dow et al. 2022). We also show that the sensitivity of senescence termination in woody plants to the rapid development rate caused by early-season warming has significantly declined in recent decades (Figure 5). This trend suggests that the effect of future temperature increases early in the season on senescence termination may gradually weaken, implying that projections based on past phenological trends may not be sufficient to accurately predict future changes in growing season length and plant productivity.

The responses of herbaceous plants to growth development and environmental factors appear more complex than those of woody plants. Growth onset was a more influential factor affecting senescence termination in herbaceous plants (Figure 2 and Figure 4), suggesting senescence termination may be directly affected by internal constraints related to leaf lifespan (Marqués et al. 2023), or oxidative stress-induced damage to the photosystems due to longer light exposure (Juvany et al. 2013; Ettinger et al. 2021; Vitasse et al. 2021). These factors may also play a decisive role in the variation of senescence termination in some woody species. Similar to woody plants, thermal conditions before and after the summer solstice exhibited opposite effects on senescence termination, and the delay in senescence termination over time largely resulted from higher temperatures after the summer solstice (Bigler and Vitasse 2021; Jiang et al. 2022). Yet, the sensitivity of senescence termination to late-season temperature has decreased over recent decades (Figure 5). Water supply also exerted a strong delaying impact on the senescence termination of herbaceous plants (Figure S7). The delays in senescence termination in herbaceous plants appear to be jointly driven by changes in growth onset, air temperature, solar radiation and water supply (Ren et al. 2022).

5 | Conclusions

In summary, our study highlights the differences between woody and herbaceous plants in leaf senescence regulatory mechanisms, which are manifested in both the response of senescence processes to developmental and environmental factors and the regulatory pathways from growth onset to senescence termination. Specifically, earlier growth onset mainly indirectly leads to earlier senescence termination by accelerating early-season development in woody plants, whereas in herbaceous plants it primarily directly contributes to earlier senescence termination. Our findings indicate that photosynthetic intensity during the growing season has no noteworthy effect on senescence termination in either plant type. Notably, although preseason warming accelerates plant development rates and thereby affects the senescence process, the sensitivity of the senescence process to these changes shows a declining trend, suggesting that the impact of future climate warming on plant senescence termination may gradually weaken. Furthermore, the differential responses of woody and herbaceous plants to environmental changes in autumn senescence may lead to alterations in ecosystem structure and function. These findings help to explain the lack of consistent patterns and the heterogeneity of senescence trends observed over recent decades across species and regions. Therefore, to improve future predictions of plant growth dynamics, it is essential to consider the combined effects of self-limitation and environmental changes on autumn plant senescence.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data acquired or used in this study are available from links in Table S1. The code scripts for the key analyses conducted in this study are available at: https://github.com/shupingji/autumn-senescence-termination.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.