Running title: Leaf senescence and climate warming

Shifts in leaf senescence across the Northern Hemisphere in response to seasonal warming

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Abstract

Shifts in plant phenology under ongoing warming affect global vegetation dynamics and carbon assimilation of the biomes. The response of leaf senescence to climate is crucial for predicting changes in the physiological processes of trees at ecosystem scale. We used long-term ground observations, phenological metrics derived from PhenoCam, and satellite imagery of the Northern Hemisphere to show that the timings of leaf senescence can advance or delay in case of warming occurring at the beginning (before June) or during (after June) the main growing season, respectively. Flux data demonstrated that net photosynthetic carbon assimilation converted from positive to negative at the end of June. These findings suggest that leaf senescence is driven by carbon assimilation and nutrient resorption at different growth stages of leaves. Our results provide new insights into understanding and modelling autumn phenology and carbon cycling under warming scenarios.

Key words: Climate change, phenology, carbon assimilation, nutrient resorption, phenocam, flux data

INTRODUCTION

Tree phenology mirrors the timing of budburst, leaf-out, flowering, leaf senescence and other related biological events (Richardson *et al.* 2013; Piao *et al.* 2019). Shifts in tree phenology alter the length of growing season (Cleland *et al.* 2007; Richardson *et al.* 2018) and influence the productivity of terrestrial forest ecosystems (Zhang *et al.* 2020). Phenological changes in trees provide a clear, visible signal of, and an important basis for modelling, how global warming influences terrestrial ecosystems (Chuine & Régnière 2017; Zhang *et al.* 2020). Advances in the dates of spring leaf-out in response to warming have been consistently observed over recent decades (Fu *et al.* 2015; Chen *et al.* 2018). Both advanced and delayed trends in leaf senescence have been reported under warming conditions (Menzel *et al.* 2006; Jeong *et al.* 2011; Gill *et al.* 2015). The ecological mechanisms underlying these contradictory warming responses remain unclear, making it difficult to predict how global warming will impact tree leaf senescence and forest ecosystem functioning in the future (Chen *et al.* 2020; Zhang *et al.* 2020).

The final stage through which tree leaves pass before death is accompanied by the degradation of various macromolecules (Woo *et al.* 2013). The main function of leaves at this late stage of the season is to remobilize nutrients from aging leaves into perennial trunks, twigs, and roots for overwintering and to support growth in the following spring (Vergutz *et al.* 2012). Trees have been shown to delay leaf senescence in order to remobilize more nutrients from old leaves (Estiarte & Penuelas 2015). The progress of leaf senescence therefore depends on whether nutrients have been resorbed to their maximum potential extent. However, the timing of leaf senescence is also determined by the maximum amount of assimilated carbon that can be stored (or sink limitation of photosynthesis) early in the growing season (Paul & Foyer 2001). If warming (or other

factors, e.g., elevated carbon dioxide and light levels) speeds up the rate of photosynthesis and subsequently the rate at which this maximum storage capacity is reached, then leaf senescence will be advanced (Fu *et al.* 2014).

Using 500,000 phenological records for 15 temperate trees at 5,000 sites, phenological metrics derived from PhenoCam and satellite imagery, and carbon flux measurements from 72 sites in the Northern Hemisphere (Fig. S1), we carried out detailed analyses of the responses of leaf senescence to warming during the growing season and aim to disentangle the mechanisms underlying the observed contrasts in the responses of leaf senescence to warming and provide an ecological basis for predicting the trajectory of leaf senescence under future warming.

METHODS SUMMARY

Phenology and climate data

Leaf senescence data were obtained from three large phenological datasets in the Northern Hemisphere: PEP725 phenological database, PhenoCam network and MODIS phenology product. The FLUXNET2015 dataset was used to examine the temporal variations in photosynthetic carbon assimilation in growing season. Gridded daily temperatures, precipitation, radiation, and humidity data with a spatial resolution of 0.25° in Europe were collected from the database E-OBS. Gridded CLM/ERAi soil moisture (0-10cm) data between were downloaded from KNMI Climate Explorer. Global monthly mean temperature data with 0.5° spatial resolution were downloaded from the Climate Research Unit (CRU TS Version 4.04).

Statistical analysis

Using the PEP725 data, we calculated the daily, weekly, and monthly temperature sensitivity (S_T, change in days per degree Celsius) of leaf senescence during the

growing season between May and September for each species at each site. From the calculated daily, weekly and monthly S_T of leaf senescence, we found that responses of leaf senescence to warming changed from negative in May and June to positive between July and September. We therefore divided the entire season into two periods: early season (May-June) and late season (July-September), and further calculated the mean S_T during the two periods to obtain the S_T during the early ($S_{T\text{-}Early}$) and late ($S_{T\text{-}Late}$) season, respectively. The sum of $S_{T\text{-}Early}$ and $S_{T\text{-}Late}$ of leaf senescence was used to represent the overall warming responses of leaf senescence during the whole season while leaves were present. We also calculated the monthly S_T of leaf senescence between May and September during 2000-2018 based on the dates of leaf senescence extracted from the PhenoCam network and MODIS phenology product.

Using the PEP725 network, we examined the effects of growing degree days (GDD) on the leaf senescence dates (change in days GDD^{-1}) in years under low and high nighttime temperature conditions during the early and late growing season. We calculated and compared the S_T of leaf senescence during the early, late, and entire season during the coldest period 1953-1972 and the warmest period 1992-2011 over the past 60 years. Using partial correlation analysis, we excluded the covariate effects of soil moisture, precipitation, radiation, humidity and further examined the relationship between monthly mean temperature from May to September and leaf senescence dates. Furthermore, we quantified and compared the relative influences of temperature, soil moisture, precipitation, radiation, humidity on leaf senescence date in the growing season using boosted regression trees (BRTs).

Using the FLUXNET2015 dataset, we examined the temporal changes in the photosynthesis carbon assimilation during the growing season based on the Net Ecosystem Exchange (NEE); we calculated and compared the differences in the nighttime respiration during the early season (May and June) and the number of frost days (T_{min} <0℃) in late autumn (October and November) during years with low and high nighttime temperature.

Full methods and any associated references are available in the Supplementary Methods.

RESULTS

Using records of leaf senescence for 15 temperature tree species at 5,000 sites from the PEP725 network, we found the mean S_T of leaf senescence was negative in May and June, while it gradually converted to positive between July and September (Fig. 1a, residual degrees of freedom df=1.02×10^5). Based on the daily and weekly S_T of leaf senescence, we also observed a significant increase in S_T throughout the entire season (Fig. S2a, df=159, P<0.001; Fig. S2b, df=20, P<0.001). According to the linear mixed models, the overall S_T of leaf senescence during the early and late season across all species and sites were approximately -1.14 and +1.33 days ℃$^{-1}$, while S_T of leaf senescence of the total season was +0.12 days ℃$^{-1}$ (Table S2). After excluding the effects of other climate variables, using partial correlation analysis we also observed a negative response of leaf senescence to temperature during the early season, but a positive response during the late season (Fig. S3, df=4.02×10^4, P<0.05). According to the calculated relative influence, temperature had the strongest effect on leaf senescence, followed by soil moisture and radiation (Fig. S4).

Using the PhenoCam network, we again observed a transition in the S_T of leaf senescence in North America from May to September (Fig. 1b, *df*=558, *P*<0.001). Based on phenology metrics extracted from MODIS, we consistently observed a transition in the S_T of leaf senescence from May to September across all biomes except deserts and xeric shrublands in the Northern Hemisphere (Fig. 1c, *df*=1.30×10^5, *P*<0.001). In May and June, the effects of temperature on leaf senescence were negative across temperate and boreal biomes (Fig. 1c, *df*=1.30×10^5, *P*<0.001). We also observed negative effects of temperatures in May and June on leaf senescence in tundra, alpine, Mediterranean regions, deserts and xeric shrublands (Fig. 1c, *df*=1.30×10^5, *P*<0.001). The effects of temperature gradually became positive in August or September in these biomes (Fig. 1c, *df*=1.30×10^5, *P*<0.001). The spatial distribution of the monthly S_T from May to September in the Northern Hemisphere was shown in Fig. S5.

Using the FLUXNET2015 data, we detected an obvious changing point at the end of June (DOY 180) for the net daily carbon assimilation (Fig. 2, n=1.46×10^3, *P*<0.05). Generally, net carbon assimilation was positive during the early season (before June) but was negative during the late season (after June) (Fig. 2a, *P*<0.001). This suggested that carbon assimilation mainly occurs before June. The difference in the net carbon assimilation between early season (before June) and late season (after June) in forest was the largest, followed by grassland and savanna (Fig. 2b, *df*=1.46×10^3, *P*<0.05).

Results showed that the timing of leaf senescence was also advanced by greater GDDs during the early season (May-June), but delayed by greater GDDs during the late season (July-September) (Fig. S6ab, *df*=1.39×10^4, *P*<0.001). We found that during the early season, the negative effect of GDDs on leaf senescence was stronger during

years with low nighttime temperatures (Fig. S6a, n=1.39×10^4, P<0.001). Furthermore, during the late season the positive effect of GDDs on leaf senescence was weaker during years with low nighttime temperature (Fig. S6b, df=1.39 × 10^4, P<0.001). When nighttime temperature was higher, nighttime ecosystem respiration was significantly greater during the early season (Fig. S6c, df=840, P<0.05), while the number of frost days was significantly lower during the late season (Fig. S6d, df=844, P<0.001).

To assess the effects of climate warming on leaf senescence, we used the PEP725 dataset to calculate and compare the S_T of leaf senescence between the coldest and the warmest 20-year periods: 1953-1972 and 1992-2011. We found that both the $S_{T\text{-}Early}$ and $S_{T\text{-}Late}$ of leaf senescence were significantly higher during 1992-2011 than those during 1953-1972 (Fig. 3, df=1.63×10^4, P<0.05). However, $S_{T\text{-}Late}$ of leaf senescence during 1992-2011 increased more compared to $S_{T\text{-}Early}$ of leaf senescence (Fig. 3, n=1.63 ×10^4, P<0.05). The S_T of leaf senescence during the whole growing season, i.e., the sum of $S_{T\text{-}Early}$ and $S_{T\text{-}Late}$ of leaf senescence, also showed a significant increase (Fig. 3, df=1.63×10^4, P<0.05).

DISCUSSION

Earlier leaf senescence reduces photosynthetic carbon assimilation and nutrient resorption efficiency (i.e., the proportion of nutrients resorbed from old leaves) (Estiarte & Penuelas 2015). However, trees experiencing late leaf senescence are more at risk from frost (Schwartz 2003), which may reduce nutrient resorption (Estiarte & Penuelas 2015). The optimal timing of leaf senescence is therefore likely to be a trade-off between photosynthetic carbon assimilation and autumnal nutrient resorption at different stages in the seasonal functioning of leaves (Fracheboud *et al.* 2009) (Fig. S7). When trees reach their maximum carbon storage capacity, they will initialize nutrient

resorption and senescence. Accordingly, more efficient accumulation of carbohydrates with warmer temperatures in the early season will result in a relatively shorter period being required to reach the maximum carbon storage capacity (Peng *et al.* 2013). Thus, early season warming advances leaf senescence. Using the flux data, we further found net carbon assimilation converted from positive to negative at the end of June (DOY 180). This provides direct physiological evidence that photosynthetic carbon assimilation mainly occurred during the early season (before June). However, warmer temperatures later in the season may reduce the risk of late autumn frost (Vitasse *et al.* 2014), enhancing the activities of photosynthetic enzymes (Shi *et al.* 2014) and reducing the rate of chlorophyll degradation (Fracheboud *et al.* 2009; Estiarte & Penuelas 2015). This may prolong nutrient remobilization from leaves, reduce degradation rate of organelle dismantling, increase leaf longevity and eventually delay the final stage of leaf senescence (Kikuzawa 1995). Therefore, leaf senescence was advanced by warming during the early season, but was delayed by the warming during the late season in temperate regions. However, leaf senescence was advanced by warming throughout both early and late seasons in deserts and xeric shrublands. This may result from drought stress caused by warmer autumns in arid regions increasing evaporative demand (Chen *et al.* 2017) and thus initiating leaf senescence early (Estiarte & Penuelas 2015; Chen *et al.* 2020), supported by the positive correlations between soil moisture and leaf senescence in May and July.

The parameter growing degree-days (GDD) only takes into account the heat accumulated above the minimum threshold of temperature that must be exceeded for tree growth (Miller *et al.* 2001) and therefore provides a more accurate physiological assessment of leaf senescence in response to warming (Chen *et al.* 2020). Our observation that leaf senescence was advanced by GDD-based warming during the

early growing season, but was delayed by GDD-based warming during the late resorption season, are consistent with the contrasting warming responses of leaf senescence reported previously (Menzel *et al.* 2006; Jeong *et al.* 2011; Gill *et al.* 2015). These results similarly support trade-off of leaf senescence between carbon assimilation and nutrient resorption. We further examined this trade-off by comparing the warming responses of leaf senescence when the nighttime temperature changed, because of the asymmetric effects of nighttime temperature on carbon assimilation during the early growing season and frost avoidance during the late resorption season (Peng *et al.* 2013; Chen *et al.* 2020). As a result, trees will reach their maximum carbon capacity quickly when nighttime temperatures are lower according to such a trade-off assumption. By contrast, trees can be expected to accomplish nutrient resorption rapidly during the late season in order to reduce the risk of frost when nighttime temperatures are lower (Silvestro *et al.* 2019). Consistent with this, we found that the signals of the effects of warming on leaf senescence were stronger or weaker when the nighttime temperature was lower during the early or late season respectively. Our findings indicate that not only the carbon sink limitation in the early season but also nutrient resorption in the late season should be considered when modelling autumn phenology of temperate trees under future warming scenarios. More important, our statistical analyses of leaf senescence during the warmest 20-year periods across both seasons suggest that global warming may delay leaf senescence in the future.

In addition to temperature, photoperiod may influence tree phenology (Körner & Basler 2010). The previous work has evidenced that autumnal phenological events are commonly more sensitive to photoperiod compared with spring events (Way & Montgomery 2015). However, such a conservative response to warming may be due to the counterbalancing effects of warming on leaf senescence at different seasons.

Additionally, despite the photoperiodic control of leaf senescence (Way & Montgomery 2015), we found that temperature alone had strong predictive power even when photoperiod was not considered, indicating the dominant role of temperature in leaf senescence.

Overall, our findings based on three large and complementary datasets illustrate that the onset of leaf senescence is advanced under early season warming, but delayed when warming occurs in the late stages of the growing season. Although further controlled warming experiments in different seasons should be conducted to test the contrasting seasonal climatic responses of leaf senescence, our study provides new insights into how to accurately predict whether leaf senescence will be delayed or advanced in response to climate warming (Menzel *et al.* 2006). If future warming spans both early and late seasons in temperate regions, as found previously (Menzel *et al.* 2006; Gill *et al.* 2015), leaf senescence could be delayed, rather than advanced.

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DATA ACCESSIBILITY

The ground observation phenological data are available at www.pep725.eu. The phenological metrics derived from digital camera imagery are available at

https://lpdaac.usgs.gov/. The phenology data extracted from satellite images can be downloaded from https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1674. The climate data used in this study are available at http://ensembles-eu.metoffice.com and https://crudata.uea.ac.uk /cru/data/hrg/ cru_ts_4.04/cruts.2004151855.v4.04/.

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FIGURE CAPTIONS

Fig. 1 Temperature sensitivities (S_T, change in days ℃$^{-1}$) of leaf senescence during the growing season between May and September. The calculated S_T was based on **(a)** records of leaf senescence for 15 temperate tree species at 5,000 sites in Europe, and phenological metrics extracted from **(b)** the PhenoCam network and **(c)** the MODIS phenology product (MCD12Q2 version 6) for different biomes. 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 biomes are Tundra (TUN), Boreal Forests/Taiga (BFT), Temperate Broadleaf & Mixed Forests (TBM), Temperate Conifer Forests (TCF), Temperate Grasslands, Savannas & Shrublands (TGS), Montane Grasslands & Shrublands (MGS), Mediterranean Forests, Woodlands & Scrub (MFW), and Deserts & Xeric Shrublands (DXS). The asterisks indicate a significant difference in the S_T during the early (May-June) and the late (July-September) season (P<0.05).

Fig. 2 Change in the net daily photosynthetic carbon assimilation (g $Cm^{-2}d^{-1}$). The estimation of the net carbon assimilation was calculated by multiplying the Net Ecosystem Exchange (NEE) by −1. The length of each box in **(b)** 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 net photosynthetic carbon assimilation during the early season (before June) and late season (after June). Different color lines and boxes represent different vegetation types. The dashed vertical line indicates the change point of net photosynthetic carbon assimilation (DOY 180).

Fig. 3 Temperature sensitivities (S_T, change in days °C^{-1}) of leaf senescence in 15 temperate tree species during 1953-1972 and 1992-2011. Calculations of the S_T values

were based on the temperature in early (May and June), late (July-September) and entire (May-September) growing seasons. 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 between 1953-1972 and 1992-2011 ($P<0.05$).

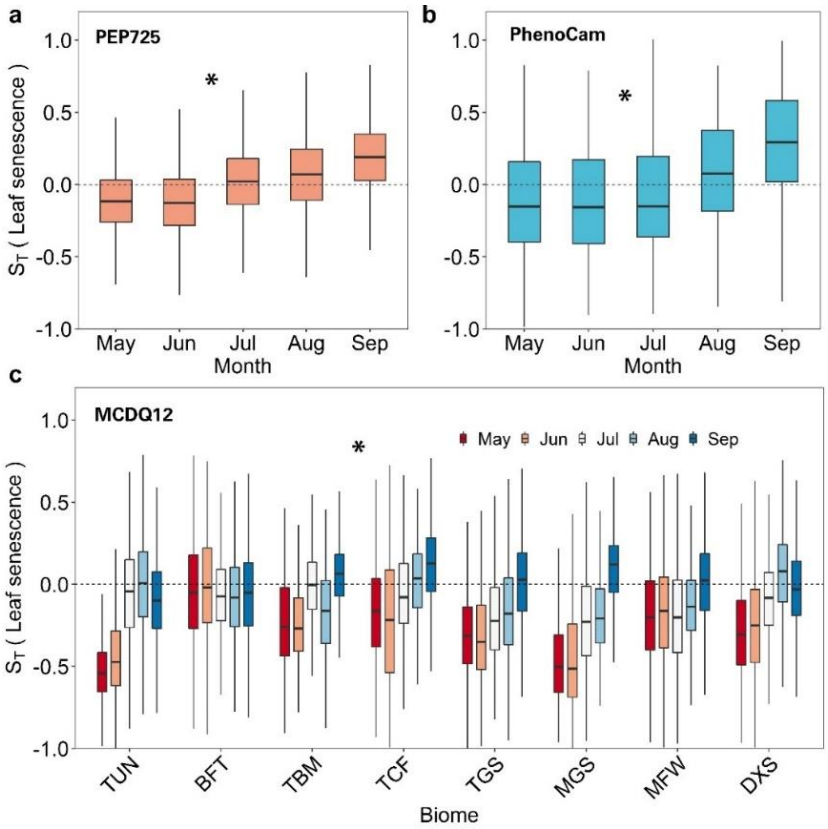
a
PEP725
b
PhenoCam
c
MCDQ12
S_T (Leaf senescence)
1.0
0.5
0.0
-0.5
-1.0
May
Jun
Jul
Aug
Sep
Month
*
TUN
BFT
TBM
TCF
TGS
MGS
MFW
DXS
Biome

Fig. 1

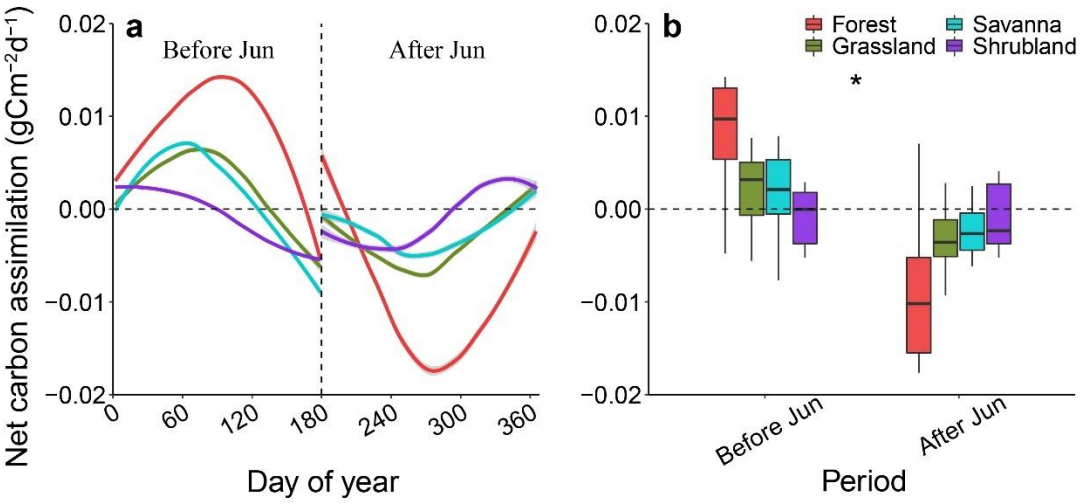
a
Before Jun
After Jun
Net carbon assimilation (gCm^{-2}d^{-1})
0.02
0.01
0.00
−0.01
−0.02
0
60
120
180
240
300
360
Day of year
b
Forest
Savanna
Grassland
Shrubland
*
Before Jun
After Jun
Period

Fig. 2

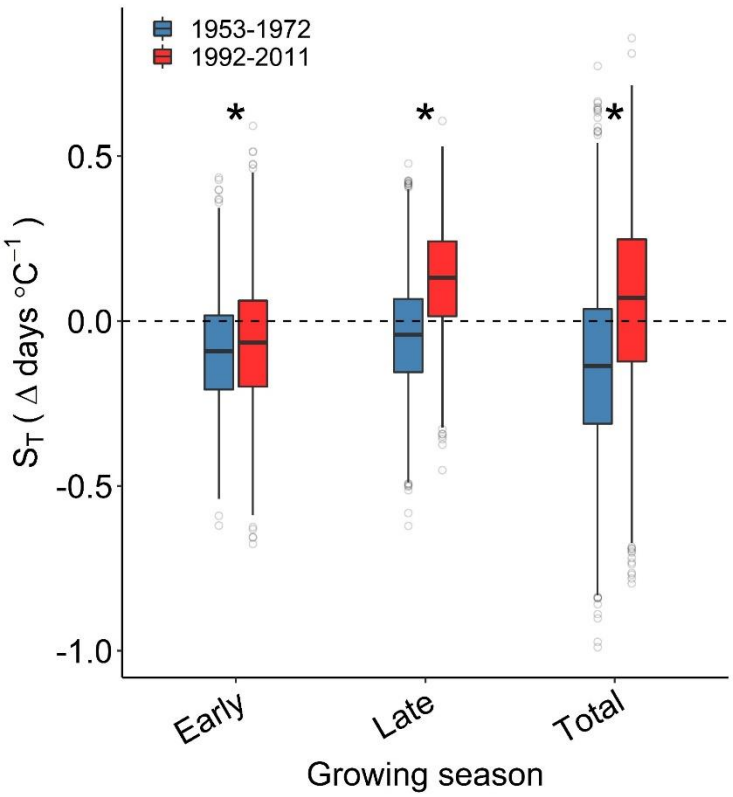
1953-1972
1992-2011
*
*
*
0.5
0.0
-0.5
-1.0
S_T (Δ days °C^{-1})
Early
Late
Total
Growing season

Fig. 3