Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate trees in Europe

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Abstract

Aim: Ongoing climate warming has been widely reported to delay the autumn phenology, which in turn impacts carbon, water, energy and nutrient balances at regional and global scales. However, the underlying mechanisms of autumn phenology responses to climate change have not been fully elucidated. The aim of this study was to determine whether brightening that was defined as the increase of surface solar radiation and warming during recent decades affect autumn phenology in opposite directions and explore the underlying mechanisms.

Location: Central Europe.

Time period: 1950-2016.

Major taxa studied: Four dominant European tree species in central Europe: *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur*.

Methods: We investigated the temporal trends of leaf senescence, preseason temperature and radiation by separating the period of 1950-2016 into two sub-periods (1950-1982 and 1983-2016) and determined the relationship between temperature, radiation and leaf senescence using partial correlation analysis.

Results: We found a significant warming and brightening trend after the 1980s in Central Europe, yet this led to only slight delays in leaf senescence which cannot be explained by the well-known positive correlation between leaf senescence and autumn warming. Interestingly, we found opposite effects between warming (partial correlation coefficient, $r = 0.37$) and brightening ($r = -0.23$) on leaf senescence. In addition, the temperature sensitivity of leaf senescence decreased with increasing radiation (-5.08 days·$°C^{-1}/10^8 J·m^{-2}$).

Main conclusions: The results suggested that brightening accelerated the leaf senescence dates, counteracting the warming-induced delays in leaf senescence, which may be attributed to photooxidative stress and/or sink limitation. This emphasizes the need to consider radiation to improve the performance of autumn phenology models.

Keywords: radiation, brightening, climate warming, leaf senescence, temperature sensitivity

1. Introduction

Global climate change causes substantial shifts in vegetation phenology, thereby affecting plant fitness as well as the functioning of terrestrial ecosystems and services they provide (Lieth, 1974; Cannell *et al.*, 1986; Menzel and Fabian, 1999; Peñuelas and Filella, 2001; Piao *et al.*, 2017; Geng *et al.*, 2020a). Previous studies have reported that global warming has advanced the onset of vegetation growth in spring (Fu *et al.*, 2015; Menzel *et al.*, 2020) and, to a lesser extent, delayed the timing of autumn leaf senescence (Ge *et al.*, 2015; Fu *et al.*, 2019a). Spring phenology has been fairly well investigated (Fu *et al.*, 2014b; Piao *et al.*, 2019; Menzel *et al.*, 2020), whereas the environmental drivers of autumn phenology are less understood (Gallinat *et al.*, 2015), likely because many factors, such as drought, nutrient availability, light conditions and temperature, interactively influence autumn phenology (Liu *et al.*, 2019; Buermann *et al.*, 2013; Vitasse *et al.*, 2021). Nevertheless, autumn phenology plays a fundamental role in the carbon cycle and the relationship between climate and the biosphere (Zhang *et al.*, 2020; Garonna *et al.*, 2014; Liu *et al.*, 2016; Piao *et al.*, 2008; Zhu *et al.*, 2012). Investigating autumn phenology is therefore integral to improving our understanding of the responses of terrestrial ecosystems to ongoing climate change.

Recent autumn phenology models predict that, in spite of the ongoing autumn warming trends, leaf senescence might slightly advance rather than delay over the rest of the century (Zani *et al.*, 2020). Gunderson *et al.* (2012) found a significant delaying effect of warming on autumn senescence of *Liquidambar styraciflua*, *Quercus rubra*, *Populus grandidentata*, and *Betula alleghaniensis* by conducting temperature-controlled experiment in Oak Ridge National Environmental Research Park, USA. Fu *et al.* (2018) investigated the spring and autumn phenology by using saplings of *Fagus sylvatica* in Belgium and found a significantly larger temperature response of autumn leaf senescence than of spring leaf-out. These seemingly inconsistent findings between natural and experimental conditions are likely due to the fact that autumn phenology is greatly affected by environmental cues besides temperature, such as photoperiod, solar radiation and early-season productivity which cannot be controlled in natural conditions (Chen *et al*., 2020; Estiarte and Peñuelas, 2015; Fu *et al*., 2014a; Way and Montgomery, 2015). For example, the senescence dates of European aspen vary very little between years, suggesting photoperiod as the primary driver of autumn leaf senescence (Fracheboud *et al*., 2009). In addition, previous research also demonstrated that the leaf senescence dates of oak and beech significantly advanced with elevation, but leaf senescence in ash and sycamore remained stable along elevational gradients which might be explained by photoperiod limitation (Vitasse *et al*., 2009). Overall, environmental cues are likely to interactively regulate leaf senescence (Fu *et al*., 2015; Hänninen, 2016; Maes *et al*., 2019; Liu *et al*., 2019; Zani *et al*., 2020), and exploring how different environmental cues interact is thus critical to better understand the timing of autumn phenology.

In recent years, reductions in atmospheric pollution and cloud cover have led to significant atmospheric brightening in several regions (Wild *et al*., 2007; Sanchez-Lorenzo *et al*., 2015), with the increased radiation likely affecting the physiological processes of plants (Gerald and Stanhill, 2007; Pfeifroth *et al*., 2018). For example, Nemani *et al*. (2003) found that forest net primary production in Amazon rain forests significantly increased over recent decades, which was largely driven by increased solar radiation. Similar results were also reported in Europe, Panama, Thailand and Malaysia (Trigo *et al*., 2002; Graham *et al*., 2003; Dong *et al*., 2012). Recently, increased vegetation growth during the growing season was reported to advance autumn phenology, which can likely be explained by the carbon sink limitation hypothesis (Zani *et al*., 2020). This suggests that solar radiation might affect autumn phenology processes through regulating plant productivity. A delay in leaf senescence dates under reduced light availability has recently also been shown in a manipulative experiment on four European trees (Vitasse *et al*., 2021). Yet, to our knowledge, the direct effects of atmospheric brightening on autumn phenology and the relationship between atmospheric brightening and the temperature sensitivity of leaf senescence (S_T, the change in days in leaf senescence per degree warming) under natural conditions have not yet been studied. Testing these effects will contribute to deciphering the physiological mechanisms of autumn leaf senescence of temperate trees in response to ongoing environmental changes.

Based on in situ phenological records during the period 1950-2016 in Central Europe, we here investigate the effects of temperature and radiation on autumn phenology by applying partial correlation analysis. We propose and test the hypothesis that atmospheric radiation controls autumn phenology through increasing leaf-level photooxidative stress. In addition, increased light availability might lead to elevated photosynthetic rates, which in turn should increase leaf-level carbon to nitrogen ratios, leading to an earlier initiation of leaf senescence (Paul and Foyer, 2001; Zani *et al.*, 2020). This hypothesis thus predicts that 1) increased atmospheric brightening and warming during recent decades affects autumn phenology in opposite directions, advancing and delaying the leaf senescence process, respectively, and 2) increasing solar radiation reduces the apparent temperature sensitivity of autumn phenology.

2. Material and methods

2.1 Datasets

Site-level daily mean air temperature and daily shortwave downward radiation of all phenological sites were derived from a gridded climate data set with a spatial resolution of 0.25° (E-OBS gridded dataset of the ECA, https://eca.knmi.nl//dailydata/index.php). The Mann-Kendall (MK) test was used to evaluate the monotonic temporal trend of the average autumn (from September to November) radiation across all sites (Kendall, 1948). UF and UB are statistical variables of the MK test. $UF > 0$ indicates an upward trend, $UF < 0$ indicates a downward trend. If UF and UB intersect between the critical straight lines, this indicates a significant trend shift (mutation) for the year corresponding to the intersection point (Kendall, 1948; Yue *et al*., 2002). According to the MK test, there was a turning point in autumn radiation in 1982, with, on average, significantly higher radiation in 1983-2016 compared to the 1950-1982 period (Fig. 1a, b). We then calculated the average temperature and radiation sums throughout the whole year and the growing season (from June to November) across all sites for the 1950-1982 and the 1983-2016 periods (Fig. S1.1). In addition, we analyzed the changes in seasonal radiation over the two periods and found that radiation increased across all seasons, but the amplitudes were different among seasons (Table. S1.1).

In situ leaf phenology records were obtained from the Pan European Phenology (PEP) network (http://www.pep725.eu/), which provides phenological observations of autumn leaf senescence dates across central Europe (Templ *et al*., 2018). The dates of leaf senescence were defined according to the BBCH (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie) code 94, which refers to the date when 50% of a trees' leaves show autumnal coloring. The date of autumn leaf senescence of each tree was represented by day of the year (DOY). Records were excluded from the analysis when autumn senescence occurred before DOY 181 (end of June) to avoid abnormal dates resulting from measurement error, extreme summer drought-induced leaf senescence, or diseases. Based on the turning point year of autumn radiation (1982), we only selected time series that had more than 15 years of leaf senescence records in both the period 1950-1982 and 1983-2016. In total, we selected 1,161 phenological sites and 169,771 phenological observations of four dominant deciduous tree species: *Aesculus hippocastanum* (horse chestnut), *Fagus sylvatica* (European beech), *Betula pendula* (European silver birch) and *Quercus robur* (Pedunculate oak), which were widely distributed trees and have autumnal phenology dates across central Europe available since 1950. The distribution of these sites is shown in Fig. S1.2.

2.2 Analysis of temporal changes in leaf senescence dates

For each species and time series (species × site combination), we calculated the average leaf senescence date (LSD) of the 1950-1982 and 1983-2016 periods as well as the difference in LSD between the two periods (△LSD). ANOVA was conducted to test for significant shifts in LSD between the two time periods.

2.3 Partial correlation analysis

The timing of leaf senescence is affected by the environmental conditions during the period before the phenological event, defined as the preseason (Fu *et al*., 2015; Geng *et al*., 2020b). In this study, we defined the preseason as the three months (90 days) prior to the mean date of leaf senescence for each time series. For each time series and year, we obtained the radiation sums and mean temperature during the preseason. We then conducted a partial correlation analysis to investigate the relationships between the timing of leaf senescence and one of the climate variables (radiation or temperature) while controlling another over the whole study period, as well as within the two sub-periods, for each time series. As leaf senescence is thought to be mainly induced by daily minimum temperature, but also affected by daily maximum temperature, we further tested the effect of either minimum (T_{min}) or maximum (T_{max}) temperature on leaf senescence using the above method. In addition, ANOVA was also used to determine the interactive effects of solar radiation and temperature on leaf senescence.

2.4 Temperature sensitivity of leaf senescence

To further explore the effect of radiation on the temperature sensitivity of leaf senescence, we investigated the correlation between the date of leaf senescence and temperature under different radiation conditions. We first divided the data into a gradient of six radiation subsets (R1-R6) for each species at each site according to the magnitude of radiation sums (RAD) following the method used in Fu *et al*. (2019b).

Then, for each radiation subset, we divided the data into six temperature subsets (T1-T6) according to the magnitude of mean temperature of the preseason (TEM), see details in Table S1.2. We thus ended up with 36 radiation-temperature combinations, for which we determined the mean leaf senescence dates, the mean temperature and radiation sums of the preseason. This allowed us to estimate the temperature sensitivity of leaf senescence (S_T), defined as the change in days in leaf senescence per degree warming, for each radiation subset using the linear regression analysis. In addition, we further divided the radiation and temperature into three or eight subgroups, to investigate whether the results of sensitivity of the leaf senescence would be influenced by the number of subgroups. The RAD and TEM were divided into three subgroups by using the Mean ± sd of RAD/TEM as breakpoints and into eight subgroups using the Mean ± 1/3×sd and the Mean ± 2/3×sd.

3. Results

3.1 Temporal changes in climate and leaf senescence dates

According to the MK test, the year 1982 was a turning point regarding autumn radiation over the period 1950-2016 (Fig. 1a, b). Separated by the year 1982, the preseason radiation significantly increased ($P < 0.001$) from an average of 10.3×10^8 $J\cdot m^{-2}$ during 1950-1982 to 10.9×10^8 $J\cdot m^{-2}$ during 1983-2016 (Fig. 1c). We obtained similar results when summing radiation over the whole growing season (from June to November), i.e., significantly brighter growing seasons were found for the 1983-2016 period compared to the 1950-1982 period (Fig. S1.1), which is consistent with previous study (Wild et al., 2005). Preseason temperatures were, on average, 0.7 °C warmer in 1983-2016 compared to 1950-1982 ($P < 0.001$, Fig. 1d), similar results were also detected for the whole year and growing season (Fig. S1.1).

Across the four studied species, the average LSD occurred slightly later (one days on average) during the period 1983-2016 (LSD = 282) than during the period 1950-1982

(LSD = 281) ($P < 0.001$, Fig. 2a). Within species, the average LSDs of *Betula pendula* (BP) and *Quercus robur* (QR) were significantly delayed but with very small amplitudes, i.e., from 1 to 3 days only, while the LSDs of *Aesculus hippocastanum* (AH) significantly advanced by 1 day (Fig. 2b). We also calculated the difference in LSD between the two sub-periods for each species at each site (△LSD, Fig. 3) and found similar results, i.e., across all species, △LSD did not significantly deviate from zero (△LSD = 0.9 ± 7.6 days). Within species, △LSD was delayed by 1.5 ± 7.9, 0.7 ± 7.5 and 2.5 ± 7.4 days, respectively, for *Betula pendula*, *Fagus sylvatica* and *Quercus robur*, for *Aesculus hippocastanum*, △LSD was advanced by 1.0 ± 7.2 days (Fig. 3). Overall, LSD did not significantly change over the period 1950-2016, with a delay of only 1 day in the period 1983-2016 compared to the period 1950-1982.

3.2 Correlations between leaf senescence dates and climatic factors

Both temperature and radiation affected the leaf senescence processes at the significance level of $P < 0.1$, and interestingly these effects were opposite. In line with previous studies, we found a positive partial correlation between temperature and LSD of $r = 0.37$ across all species, and $r = 0.27$, 0.32, 0.44 and 0.45 for *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur*, respectively, over the whole study period 1950-2016 (Fig. 4). Compared to the period 1950-1982, the partial correlation coefficient during the period 1983-2016 increased by 0.07 (from 0.32 to 0.39) across all species, with similar patterns observed within species. The distributions of partial correlation coefficients between leaf senescence and temperature or radiation are shown in Fig. 4a (all species) and Fig. S1.3 (each species separately).

Radiation was negatively correlated with LSD, suggesting that atmospheric brightening was likely associated with an earlier leaf senescence. The partial correlation between radiation and LSD was -0.23 across all species. Similar patterns were found within species, with partial correlation coefficients of -0.11, -0.20, -0.28

and -0.34 for *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur*, respectively, over the whole study period 1950-2016 (Fig. 4b). Interestingly, the partial correlation coefficients between LSD and radiation became more negative during the period 1983-2016 ($r = -0.27$) compared to the period 1950-1982 ($r = -0.17$). We further tested the interactively effects of temperature and radiation using ANOVA and found that significant interaction effects over the two separate periods ($P < 0.01$ for the period 1950-1982 and $P < 0.001$ for the period 1983-2016) and the whole period ($P < 0.001$). Similar results were also observed by considering the interactive effects of minimum/maximum temperature and radiation (Fig. S1.4), as well as using the radiation and temperature across the growing season (June-November, Fig. S1.5).

3.3 Temperature sensitivity of leaf senescence

Based on the temperature and radiation combination subsets (see details in Table S1.3), we found that the temperature sensitivity of LSD was significantly reduced under elevated radiation (Fig. 5). Based on the temperature and radiation combination subsets (Table S1.3), we found that warming significantly delayed the LSD dates by 21, 12, 7 and 3 days for R1 through R4 ($P < 0.05$, Fig. 5a) and the temperature sensitivity of LSD was significantly reduced with radiation increases (Fig. 5). Under strong radiation conditions, i.e., R5 and R6, the leaf senescence date was constant or even advanced by 9 days with warming. Overall, we found that the temperature sensitivity of leaf senescence was significantly reduced with increased radiation at an average rate of -5.08 days$\cdot$°C^{-1}/10^{8}J$\cdot$m^{-2} (Fig. 5b). Similar results were obtained by dividing the radiation and temperature into either three or eight subgroups (Fig. S1.6 and Fig. S1.7).

4. Discussion

4.1 The effects of warming and brightening on leaf senescence

Climate warming is expected to shift the autumn phenology of temperate and boreal plants, yet inconsistent results have been obtained so far (Chen *et al*., 2020; Liu *et al*., 2016; Piao *et al*., 2019). Here we show that the autumn leaf senescence dates of dominant European tree species slightly delayed during the warmer and brighter period 1983-2016 except for *Aesculus hippocastanum*, which is in line with previous findings (Fu *et al*., 2014a; Menzel *et al*., 2020; Meier *et al*., 2021). Accordingly, we found a predominantly positive correlation between preseason temperature and leaf senescence, likely explaining the slight delays in leaf senescence over recent years. Potential mechanisms proposed to explain the positive effect of temperature on leaf senescence dates involve enhanced activity of photosynthetic enzymes (Shi *et al*., 2014) and other physiological processes (Yang *et al*., 2015), slowing down the degradation of chlorophyll (Fracheboud *et al*., 2009) and postponing the onset of leaf senescence.

However, we found that the delays in leaf senescence dates were minor, only shifting by one day among the two sub-periods, which contradicted previous experimental studies, in which significant delays were found in response to autumn warming (8 days per °C warming, as reported in Fu *et al*., 2018). Our study suggests that the atmospheric brightening trend since the 1980s (Wild *et al*., 2005; Sanchez-Lorenzo *et al*., 2015) may have slowed down the expected delay due to warming. This opposing effect has been largely ignored in studies so far. As reported in previous studies, a change of 4-6 % in radiation may profoundly influence the temperature and hydrological cycle of terrestrial ecosystem (Ramanathan *et al*., 2001; Liepert *et al*., 2004). We found that, although preseason temperature plays an important role in the autumn phenology process, radiation affects leaf senescence in the opposite direction, advancing leaf senescence dates in Europe. This was consistent with a recent study conducted on samplings that showed that shade conditions largely delayed leaf senescence of three temperate tree species (Vitasse *et al*., 2021). Similar results were also obtained using large scale spatial datasets on 396 Northern Hemisphere woody species that including species that we used, and Renner and Zohner (2017) found that the time of leaf senescence in Eastern North America, which receive higher solar irradiation during autumn than Europe, was 11 ± 4 days earlier than in Europe in 2014 (Zohner and Renner, 2017; Renner and Zohner, 2019). In our study, we further demonstrated that the temperature sensitivity of leaf senescence was significantly reduced with brightening. Our results thus suggest that temperature and radiation counteract each other and interactively regulate the autumn leaf senescence processes.

4.2 A mechanistic explanation for the brightening effect on leaf senescence

To explain how climate warming and brightening can interact to affect leaf senescence, and why brightening should advance leaf senescence, we propose two mutually non-exclusive mechanisms: photoprotection and sink limitation. The photoprotection hypothesis predicts that once the light energy absorption of a leaf exceeds the capacity for light utilization, reactive oxygen species accumulate (Muller *et al*., 2001), increasing the risk of photo-oxidative damage (Juvany *et al*., 2013) and reducing the nutrient reabsorption capacity (Renner and Zohner, 2019). Pigments in autumnal leaves play critical roles in dissipating excess light energy (Ruban *et al*., 2002) and reactive oxygen species (Close and Beadle, 2003; Xu and Rothstein, 2018). Therefore, strong solar radiation may increase a plant's investment in anthocyanins and xanthophylls, and thus promote leaf coloring (Renner and Zohner, 2019).

The second potential mechanism is based on the sink-limitation hypothesis (Dox *et al*., 2020; Zani *et al*., 2020). Climate warming has led to increased tree productivity as a result of advances in growing season onset and enhanced photosynthesis during the growing season under elevated temperatures and increased light availability (Trigo *et al*., 2002; Nemani *et al*., 2003; Graham *et al*., 2003). The photosynthetically active radiation (PAR) increases under elevated solar radiation (Meek *et al*., 1984). This enhancement of photosynthesis may alter plant's source/sink balance, accelerating sink saturation and speeding up the senescence process (Zani *et al*., 2020). In other words, once the plant's carbon sink is saturated, leaf senescence will be induced, governed by interactions between photosynthate supply, phytohormones and nutrient supply (Fu *et al*., 2019a; Zani *et al*., 2020). Using experiments and long-term observations, Zani *et al*. (2020) demonstrated that increases in spring and summer productivity drive earlier autumn leaf senescence because of elevated light levels, temperature and carbon dioxide, supporting the critical role of sink limitation in governing autumn leaf senescence (Zani *et al*., 2020). In addition, previous studies found that autumn senescence tends to be positively associated with the onset of spring budburst (Fu et al., 2014a; Keenan and Richardson, 2015). Specifically, per day of earlier spring budburst, ~0.6 days earlier autumn leaf senescence was reported on average, additionally offsetting the delaying effects of warming (Keenan and Richardson, 2015). However, how spring phenology interacts with autumn temperature and brightening to affect the autumn leaf senescence process is still unclear and more experimental studies are needed.

Overall, the photoprotection and sink-limitation hypotheses provide plausible explanations for the negative effect of radiation on autumn senescence dates as well as for the declining temperature sensitivity of leaf senescence in response to brightening. Further experiments will be necessary to test the validity of these two hypotheses addressing the role of light conditions in regulating leaf senescence timing.

4.3 Future implications of the relationship between autumn phenology and atmospheric brightening

At regional scale, brightening largely depends on synoptic meteorological conditions as well as anthropogenic air pollution, such as the emissions of aerosols and aerosol precursors (Wild *et al*., 2007). Atmospheric brightening due to the reduction of anthropogenic aerosols may continue in the future (Haywood *et al*., 2011). Our findings suggest that the interactive effects of warming and brightening on the leaf senescence process will continue to cause reductions in autumn temperature sensitivity under the ongoing atmospheric brightening trends. However, the leaf senescence of understory trees may be delayed by the shade of overstory trees, and the growing season will be correspondingly extended (Gressler *et al.*, 2015; Vitasse *et al.*, 2021). So far, temperature and photoperiod have been widely used as the sole environmental variables coupled to autumn phenology models. However, autumn phenology models consistently fail to accurately simulate autumn phenology dates (Liu *et al.*, 2019), likely because of missing interactive effects with other important environmental factors, such as solar radiation. We therefore propose that solar radiation should be considered in phenology models to better simulate the autumn phenology processes. While the underlying physiological processes of leaf senescence are still largely unclear, the onset of physiological activity in spring (Fu *et al.* 2014a, Keenan and Richardson 2015, Zohner and Renner 2019), the mean daily maximum and minimum temperature (Chen *et al.*, 2020), and drought stress (Buermann *et al.*, 2013) have all been associated with leaf senescence. Therefore, comprehensive experiments focusing on the interactive effects among these environmental cues are needed to better understand the underlying autumn phenology processes and to improve predictions of the global carbon and water balance of terrestrial ecosystems under future climate change.

5. Conclusions

To our knowledge, this study is the first to reveal the antagonistic effect of warming and brightening on leaf senescence for the dominant tree species in central Europe. Brightening accelerates the leaf senescence process and reduces the temperature sensitivity of leaf senescence, counteracting the expected warming-induced delays in leaf senescence. The photoprotection and sink-limitation hypotheses provide plausible explanations for the negative effect of radiation on autumn senescence dates as well as for the declining temperature sensitivity of leaf senescence in response to brightening.

Our study emphasizes the need to consider radiation to improve the performance of phenology models.

Reference

Buermann, W., Bikash, P. R., Jung, M., Burn, D. H. and Reichstein, M. (2013). Earlier springs decrease peak summer productivity in North American boreal forests. *Environmental Research Letters*, *8*(2) : 024027.

Cannell, M. G. R., & Smith, R. I. (1986). Climatic warming, spring budburst and forest damage on trees. *Journal of Applied Ecology*, 177-191.

Chen, L., Hänninen, H., Rossi, S., Smith, N. G., Pau, S., Liu, Z., ... & Liu, J. 2020. Leaf senescence exhibits stronger climatic responses during warm than during cold autumns. *Nature Climate Change*, *10*(8): 777-780.

Close, D. C. & Beadle, C. L., 2003. The ecophysiology of foliar anthocyanin. *The Botanical Review*, *69*(2): 149-161.

Dong, S. X., Davies, S. J., Ashton, P. S., Bunyavejchewin, S., Supardi, M. N., Kassim, A. R., ... & Moorcroft, P. R. 2012. Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 3923-3931.

Dox, I., Gričar, J., Marchand, L. J., Leys, S., Zuccarini, P., Geron, C., ... & Campioli, M. (2020). Timeline of autumn phenology in temperate deciduous trees. *Tree physiology*, *40*(8), 1001-1013.

Estiarte, M., & Peñuelas, J. (2015). Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. *Global Change Biology*, *21*(3), 1005-1017.

Fracheboud, Y., Luquez, V., Bjorken, L., Sjodin, A., Tuominen, H., & Jansson, S. (2009). The control of autumn senescence in European aspen. *Plant Physiology*, *149*(4), 1982-1991.

Fu, Y. S., Campioli, M., Vitasse, Y., De Boeck, H. J., Van den Berge, J., AbdElgawad, H., ... & Janssens, I. A. (2014a). Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proceedings of the National Academy of Sciences*, *111*(20), 7355-7360.

Fu, Y. H., Piao, S., Op de Beeck, M., Cong, N., Zhao, H., Zhang, Y., ... & Janssens, I. A. (2014b). Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology and Biogeography*, *23*(11), 1255-1263.

Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., ... & Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, *526*(7571), 104-107.

Fu, Y. H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Liu, Y., ... & Campioli, M. (2018). Larger temperature response of autumn leaf senescence than spring leaf‐out phenology. *Global Change Biology*, *24*(5), 2159-2168.

Fu, Y. H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Geng, X., ... & Campioli, M. (2019a). Nutrient availability alters the correlation between spring leaf-out and autumn leaf senescence dates. *Tree Physiology*, *39*(8), 1277-1284.

Fu, Y. H., Zhang, X., Piao, S., Hao, F., Geng, X., Vitasse, Y., ... & Janssens, I. A. (2019b). Daylength helps temperate deciduous trees to leaf‐out at the optimal time. *Global*

Change Biology, *25*(7), 2410-2418.

Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, *30*(3), 169-176.

Garonna, I., De Jong, R., De Wit, A. J., Mücher, C. A., Schmid, B., & Schaepman, M. E. (2014). Strong contribution of autumn phenology to changes in satellite ‐ derived growing season length estimates across Europe (1982 – 2011). *Global Change Biology*, *20*(11), 3457-3470.

Ge, Q., Wang, H., Rutishauser, T., & Dai, J. (2015). Phenological response to climate change in China: a meta ‐ analysis. *Global Change Biology*, *21*(1), 265-274.

Geng, X., Fu, Y. H., Hao, F., Zhou, X., Zhang, X., Yin, G., ... & Peñuelas, J. (2020a). Climate warming increases spring phenological differences among temperate trees. *Global Change Biology*, *26*(10), 5979-5987.

Geng, X., Zhou, X., Yin, G., Hao, F., Zhang, X., Hao, Z., ... & Fu, Y. H. (2020b). Extended growing season reduced river runoff in Luanhe River basin. *Journal of Hydrology*, *582*, 124538.

Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., & Wright, S. J. (2003). Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences*, *100*(2), 572-576.

Stanhill, G. (2007). A perspective on global warming, dimming, and brightening. *Eos, Transactions American Geophysical Union*, *88*(5), 58-58.

Gressler, E., Jochner, S., Capdevielle-Vargas, R. M., Morellato, L. P. C., & Menzel, A. (2015). Vertical variation in autumn leaf phenology of *Fagus sylvatica* L. in southern Germany. *Agricultural and Forest Meteorology*, *201*, 176-186.

Gunderson, C. A., Edwards, N. T., Walker, A. V., O'Hara, K. H., Campion, C. M., & Hanson, P. J. (2012). Forest phenology and a warmer climate–growing season extension in relation to climatic provenance. *Global Change Biology*, *18*(6), 2008-2025.

Hänninen, H. (2016). Boreal and temperate trees in a changing climate. Biometeorology, Springer, Dordrecht, Netherlands.

Haywood, J. M., Bellouin, N., Jones, A., Boucher, O., Wild, M., & Shine, K. P. (2011). The roles of aerosol, water vapor and cloud in future global dimming/brightening. *Journal of Geophysical Research: Atmospheres*, *116*(D20).

Juvany, M., Müller, M., & Munné-Bosch, S. (2013). Photo-oxidative stress in emerging and senescing leaves: a mirror image?. *Journal of Experimental Botany*, *64*(11), 3087-3098.

Keenan, T. F., & Richardson, A. D. (2015). The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models. *Global Change Biology*, *21*(7), 2634-2641.

Kendall, M. G. (1948). Rank correlation methods.

Liepert, B. G., Feichter, J., Lohmann, U., & Roeckner, E. (2004). Can aerosols spin down the water cycle in a warmer and moister world?. *Geophysical Research Letters*, *31*(6).

Liu, G., Chen, X., Fu, Y., & Delpierre, N. (2019). Modelling leaf coloration dates over temperate China by considering effects of leafy season climate. *Ecological Modelling*, *394*, 34-43.

Liu, Q., Fu, Y. H., Zeng, Z., Huang, M., Li, X., & Piao, S. (2016). Temperature, precipitation, and insolation effects on autumn vegetation phenology in temperate China. *Global Change Biology*, *22*(2), 644-655.

Maes, S. L., Perring, M. P., Vanhellemont, M., Depauw, L., Van den Bulcke, J., Brūmelis, G., ... & Verheyen, K. (2019). Environmental drivers interactively affect individual tree growth across temperate European forests. *Global Change Biology*, *25*(1), 201-217.

Meek, D. W., Hatfield, J. L., Howell, T. A., Idso, S. B., & Reginato, R. J. (1984). A generalized relationship between photosynthetically active radiation and solar radiation[1]. *Agronomy Journal*, *76*(6), 939-945.

Meier, M., Vitasse, Y., Bugmann, H., & Bigler, C. (2021). Phenological shifts induced by climate change amplify drought for broad-leaved trees at low elevations in Switzerland. *Agricultural and Forest Meteorology*, *307*, 108485.

Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., & Estrella, N. (2020). Climate change fingerprints in recent European plant phenology. *Global Change Biology*, *26*(4), 2599-2612.

Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, *397*(6721), 659-659.

Müller, P., Li, X. P., & Niyogi, K. K. (2001). Non-photochemical quenching. A response to excess light energy. *Plant Physiology*, *125*(4), 1558-1566.

Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., ... & Running, S. W. (2003). Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, *300*(5625), 1560-1563.

Paul, M. J., & Foyer, C. H. (2001). Sink regulation of photosynthesis. *Journal of Experimental Botany*, *52*(360), 1383-1400.

Peñuelas, J., & Filella, I. (2001). Responses to a warming world. *Science*, *294*(5543), 793-795.

Pfeifroth, U., Bojanowski, J. S., Clerbaux, N., Manara, V., Sanchez-Lorenzo, A., Trentmann, J., ... & Hollmann, R. (2018). Satellite-based trends of solar radiation and cloud parameters in Europe. *Advances in Science and Research*, *15*, 31-37.

Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., ... & Vesala, T. (2008). Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, *451*(7174), 49-52.

Piao, S., Liu, Z., Wang, T., Peng, S., Ciais, P., Huang, M., ... & Tans, P. P. (2017). Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nature Climate Change*, *7*(5), 359-363.

Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., ... & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, *25*(6), 1922-1940.

Ramanathan, V. C. P. J., Crutzen, P. J., Kiehl, J. T., & Rosenfeld, D. (2001). Aerosols, climate, and the hydrological cycle. *Science*, *294*(5549), 2119-2124.

Renner, S. S., & Zohner, C. M. (2019). The occurrence of red and yellow autumn leaves explained by regional differences in insolation and temperature. *New Phytologist*, *224*(4), 1464-1471.

Ruban, A. V., Pascal, A., Lee, P. J., Robert, B., & Horton, P. (2002). Molecular configuration of xanthophyll cycle carotenoids in photosystem II antenna complexes. *Journal of Biological Chemistry*, *277*(45), 42937-42942.

Sanchez‐Lorenzo, A., Wild, M., Brunetti, M., Guijarro, J. A., Hakuba, M. Z., Calbó, J., ... & Bartok, B. (2015). Reassessment and update of long‐term trends in downward surface shortwave radiation over Europe (1939–2012). *Journal of Geophysical Research: Atmospheres*, *120*(18), 9555-9569.

Shi, C., Sun, G., Zhang, H., Xiao, B., Ze, B., Zhang, N., & Wu, N. (2014). Effects of warming on chlorophyll degradation and carbohydrate accumulation of alpine herbaceous species during plant senescence on the Tibetan Plateau. *PLoS One*, *9*(9), e107874.

Templ, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., ... & Zust, A. (2018). Pan European Phenological database (PEP725): a single point of access for European data. *International Journal of Biometeorology*, *62*(6), 1109-1113.

Trigo, R. M., Osborn, T. J., & Corte-Real, J. M. (2002). The North Atlantic Oscillation influence on Europe: climate impacts and associated physical mechanisms. *Climate Research*, *20*(1), 9-17.

Vitasse, Y., Baumgarten, F., Zohner, C. M., Kaewthongrach, R., Fu, Y. H., Walde, M., & Moser, B. (2021). Impact of microclimatic conditions and resource availability on spring and autumn phenology of temperate tree seedlings. *New Phytologist*.

Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R., & Delzon, S. (2009). Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia*, *161*(1), 187-198.

Way, D. A., & Montgomery, R. A. (2015). Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, cell & environment*, *38*(9), 1725-1736.

Wild, M., Ohmura, A., & Makowski, K. (2007). Impact of global dimming and brightening on global warming. *Geophysical Research Letters*, *34*(4).

Wild, M., Gilgen, H., Roesch, A., Ohmura, A., Long, C. N., Dutton, E. G., ... & Tsvetkov, A. (2005). From dimming to brightening: Decadal changes in solar radiation at Earth's surface. *Science*, *308*(5723), 847-850.

Xu, Z., & Rothstein, S. J. (2018). ROS-Induced anthocyanin production provides feedback protection by scavenging ROS and maintaining photosynthetic capacity in Arabidopsis. *Plant Signaling & Behavior*, *13*(3), 1364-77.

Yang, Y., Guan, H., Shen, M., Liang, W., & Jiang, L. (2015). Changes in autumn vegetation dormancy onset date and the climate controls across temperate ecosystems in China from 1982 to 2010. *Global Change Biology*, *21*(2), 652-665.

Yue, S., Pilon, P., & Cavadias, G. (2002). Power of the Mann–Kendall and Spearman's rho tests for detecting monotonic trends in hydrological series. *Journal of Hydrology*, *259*(1-4), 254-271.

Zani, D., Crowther, T. W., Mo, L., Renner, S. S., & Zohner, C. M. (2020). Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. *Science*, *370*(6520), 1066-1071.

Zhang, Y., Commane, R., Zhou, S., Williams, A. P., & Gentine, P. (2020). Light limitation regulates the response of autumn terrestrial carbon uptake to warming. *Nature Climate Change*, *10*(8), 739-743.

Zhu, W., Tian, H., Xu, X., Pan, Y., Chen, G., & Lin, W. (2012). Extension of the growing season due to delayed autumn over mid and high latitudes in North America during 1982–2006. *Global Ecology and Biogeography*, *21*(2), 260-271.

Zohner, C. M., & Renner, S. S. (2017). Innately shorter vegetation periods in North American species explain native–non-native phenological asymmetries. *Nature Ecology & Evolution*, *1*(11), 1655-1660.

Zohner, C. M., & Renner, S. S. (2019). Ongoing seasonally uneven climate warming leads to earlier autumn growth cessation in deciduous trees. *Oecologia*, *189*(2), 549-561.

Data Availability Statement: European phenology data are available at http://www.pep725.eu/; The climate data were derived from the E-OBS gridded dataset of the ECA, https://eca.knmi.nl//dailydata/index.php.

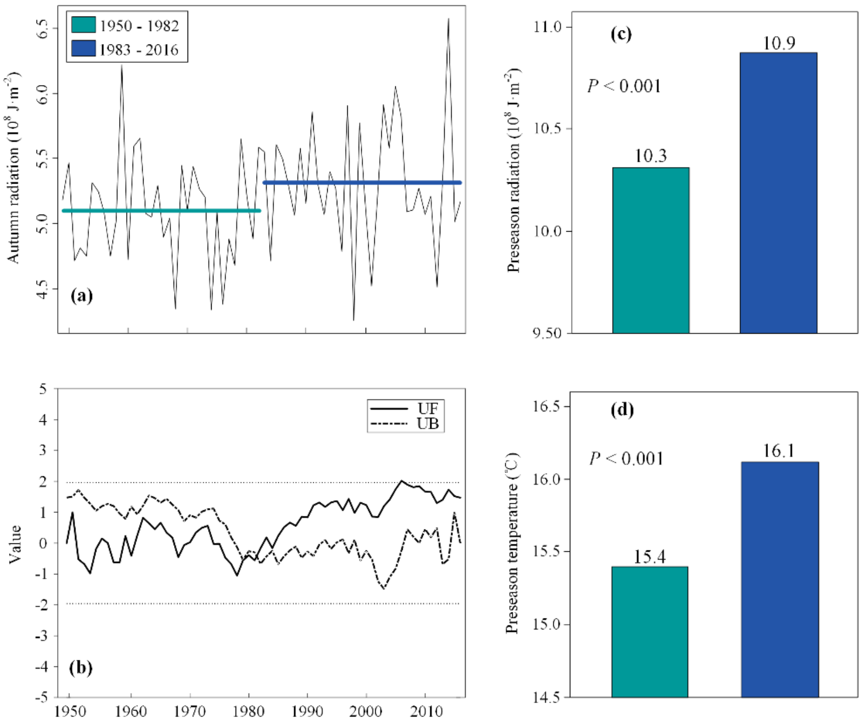


Fig. 1. Autumn radiation changes (a) and turning point test (MK test) (b) over the period 1950 - 2016. The two horizontal dotted lines in (b) are 95% confidence intervals, and the intersection of UF and UB inside these two lines indicates a significant mutation point. Panels c and d show the mean preseason radiation sums and mean preseason daily air temperatures during the period 1950-1982 (deep blue) and 1983-2016 (green). P is the significant level by using ANOVA.

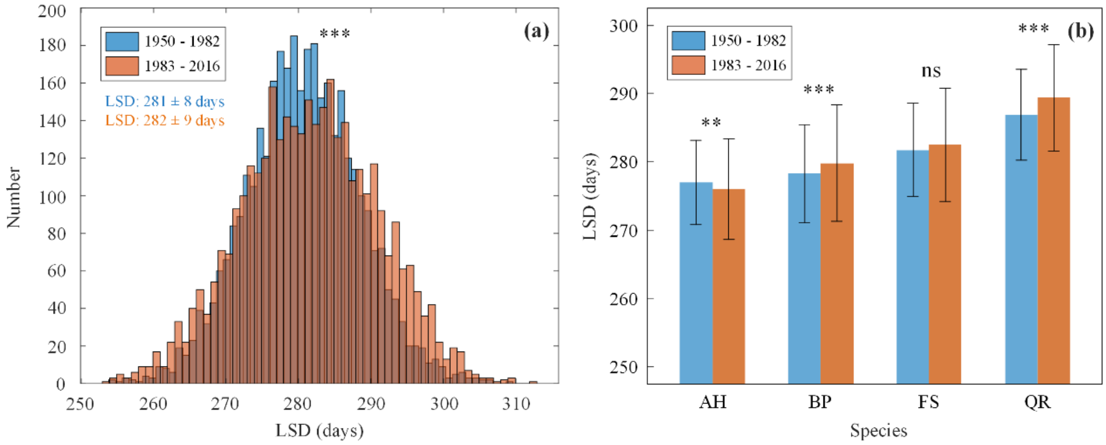


Fig. 2. Distribution of leaf senescence dates across all species and sites over the two periods, 1950-1982 (blue) and 1983-2016 (yellow) (a) and the mean leaf senescence date (mean ± sd) of each species for the two periods (b). AH, BP, FS and QR are species acronyms referring to *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur* respectively. “ns” indicates that no significant differences of the LSD exist between the two periods, ** and *** indicate $P < 0.01$ and $P < 0.001$, respectively.

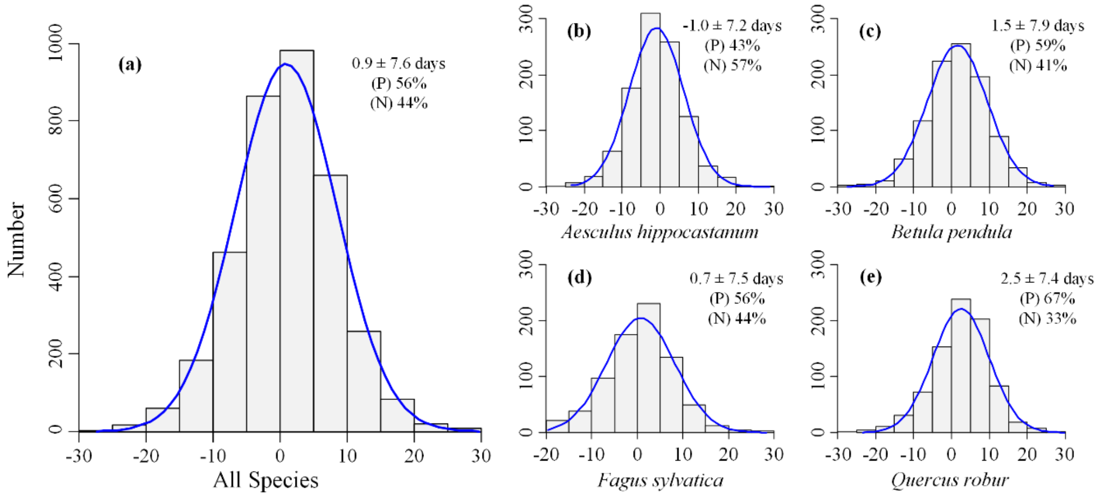
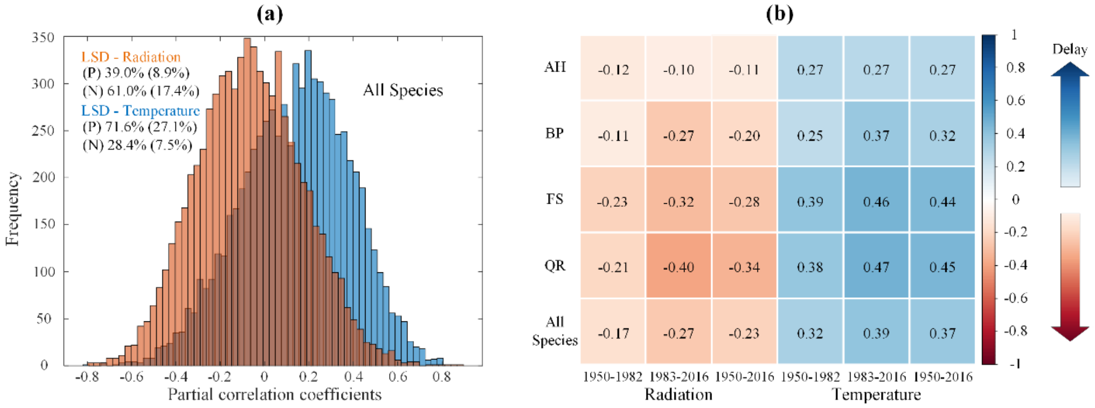
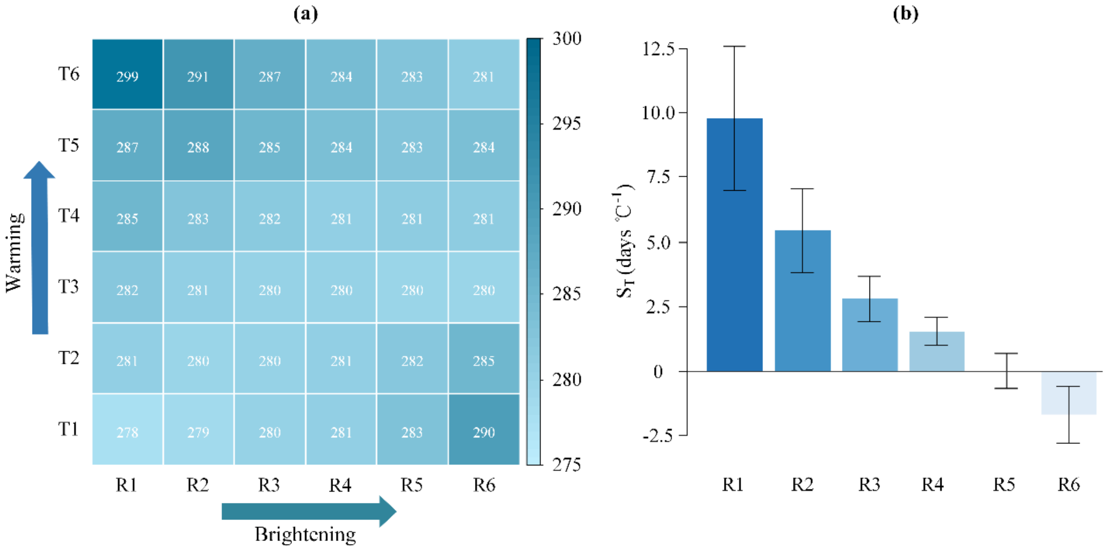


Fig. 3. The distribution of △LSD for all species (a), *Aesculus hippocastanum* (b), *Betula pendula* (c), *Fagus sylvatica* (d) and *Quercus robur* (e). △LSD is the difference of the mean site-level leaf senescence date (LSD) in 1983-2016 to the mean site-level LSD in 1950-1982. Percentages of positive (P) and negative (N) cases are provided in parentheses.



	Radiation 1950-1982	Radiation 1983-2016	Radiation 1950-2016	Temperature 1950-1982	Temperature 1983-2016	Temperature 1950-2016
AH	-0.12	-0.10	-0.11	0.27	0.27	0.27
BP	-0.11	-0.27	-0.20	0.25	0.37	0.32
FS	-0.23	-0.32	-0.28	0.39	0.46	0.44
QR	-0.21	-0.40	-0.34	0.38	0.47	0.45
All Species	-0.17	-0.27	-0.23	0.32	0.39	0.37

Fig. 4. (a) Distributions of partial correlation coefficients across all species. The orange and blue bars represent the partial correlation coefficients between leaf senescence and radiation or temperature, respectively. Percentages of positive (P) and negative (N) correlations and corresponding marginally significant correlations (*P* < 0.1, in parentheses) are also provided. (b) The partial correlation coefficients between leaf senescence dates and radiation or temperature, for *Aesculus hippocastanum* (AH), *Fagus sylvatica* (FS), *Betula pendula* (BP), *Quercus robur* (QR) and across all species (All). The color scale indicates the magnitude of the partial correlation coefficients, with positive values indicating senescence delays with increases in the climate variable and negative values indicating advances.



	R1	R2	R3	R4	R5	R6
T6	299	291	287	284	283	281
T5	287	288	285	284	283	284
T4	285	283	282	281	281	281
T3	282	281	280	280	280	280
T2	281	280	280	281	282	285
T1	278	279	280	281	283	290

Fig. 5. (a) The average dates of leaf senescence under six temperature (T1-T6) and six radiation (R1-R6) gradients. The number in the box refers to the average leaf senescence date under the 36 combinations of radiation and temperature. (b) The temperature sensitivity of leaf senescence under different radiation regimes (R1-R6).